# A monograph of the genus *Passerina* L. (Thymelaeaceae)

by

**CHRISTINA LINDITH BREDENKAMP**

Submitted in partial fulfilment of the requirements for the degree

**PHILOSOPHIAE DOCTOR**

in the Faculty of Natural and Agricultural Sciences
(Department of Botany)
**UNIVERSITY OF PRETORIA**
**PRETORIA**

Promoter: Prof. Dr. A.E. van Wyk

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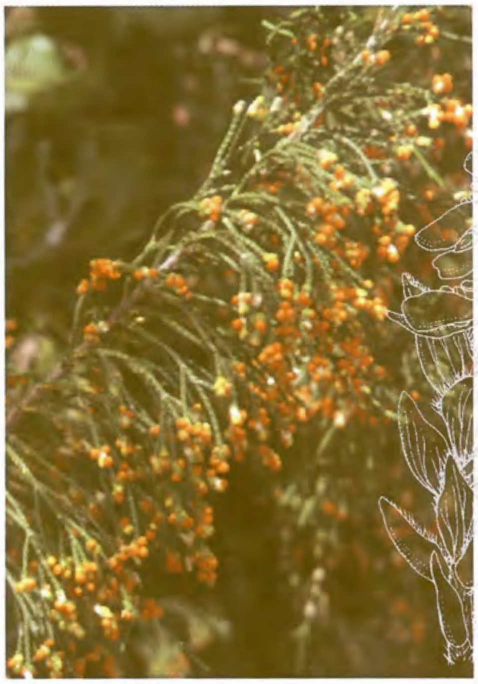
Passerina burchellii


Passerina quadrifaria


Passerina falcifolia


Passerina rigida


Passerina paleacea


Passerina drakensbergensis


Passerina corymbosa


Passerina truncata subsp. truncata


Passerina rigida

# ABSTRACT

## A monograph of the genus *Passerina* L. (Thymelaeaceae)

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A monograph of *Passerina* L., a mainly southern African genus, is presented. The genus comprises 20 species and four subspecies. A few species occur along the Great Escarpment, two with outliers in East Africa, but most are concentrated in the Cape Floristic Region. Palynological, macromorphological and anatomical evidence was used in the delimitation of the genus and its infrageneric taxa. A cladistic study supports *Passerina* as a monophyletic genus. Taxonomic and phylogenetic significance of the character set and the most important generic characters were evaluated. A genus treatment and key to species are given. Each species treatment includes a taxonomic description, diagnosis and notes on etymology, economic value and distribution. Illustrations of representative species are provided and distribution maps are included for each species. A list of excluded species names highlights the previous cosmopolitan taxonomic interpretation of *Passerina*, as many names are now in synonymy under other genera of the Thymelaeaceae.

KEYWORDS: anatomy — cladistics— flower — morphology — monograph — palynology — *Passerina* — phylogeny — phytogeography — southern Africa — taxonomy — Thymelaeaceae.

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# CHAPTER 1

# INTRODUCTION

## 1.1 Thymelaeaceae

Domke (1934) proposed a widely adopted subfamilial classification for the Thymelaeaceae and divided the family into four subfamilies, namely Gonystyloideae, Aquilarioideae, Gilgiodaphnoideae and Thymelaeoideae. The genus *Passerina*, subject of this monograph, is classified under the Thymelaeoideae. Based on palynological evidence Archangelsky (1971: Figure 10) added the new subfamilies Octolepidoideae, Microsemmatoideae and Synadrodaphnoideae and raised the Gonystyloideae to the family Gonystylaceae (also recognized by Takhtajan 1997, amongst others). New evidence on the structure of the pollen wall in *Passerina* resulted in the elevation of the subtribe Passerininae Endl. to the monogeneric tribe Passerineae (Endl.) Bredenk. & A.E.van Wyk (Chapter 4.1). Evidence obtained from floral morphology, anatomy, embryology and palynology indicates that the Thymelaeaceae has a strong malvalean relationship, an affinity also supported by molecular data (APG 1998; Magallón *et al.* 1999). The possible phylogenetic relationships of the Thymelaeaceae are discussed in Chapter 4.5 of the present study.

The Thymelaeaceae is currently considered a family of ± 58 genera and ± 720 species. (Mabberley 1989, Brummitt 1992, Takhtajan 1997). It is subcosmopolitan and the distribution of the genera is listed by Mabberley (1989), as follows:
Africa

Temperate southern Africa, *Dais* L., *Englerodaphne* Gilg, *Gnidia* L., *Lachnaea* L., *Passerina* L., *Peddiea* Harv., *Struthiola* L., *Synaptolepis* Oliv.
Tropical Africa, *Craterosiphon* Engl. & Gilg, *Dicranolepis* Planch., *Octolepis* Oliv., *Synandrodaphne* Gilg.

Asia

*Aetoxylon* Airy Shaw, *Amyxa* Tiegh., *Drapetes* Lam., *Eriosolena* Blume, *Pentathymelaea* Lecomte, *Rhamnoneuron* Gilg, *Restella* Pobed., *Wikstroemia* Endl.

Australia

*Arnhemia* Airy Shaw, *Drapetes* Lam., *Pimelea* Banks & Sol., *Oreodendron* C.T.White.

Europe

*Daphne* L., *Diarthron* Turcz.

Japan

*Daphnimorpha* Nakai, *Edgeworthia* Meisn.

Madagascar

*Stephanodaphne* Baill.

Malesia

*Aquilaria* Lam., *Enkleia* Griff., *Gonystylus* Teijsm. & Binn., *Linostoma* Wall. ex Endl., *Phaleria* Jack.

Mediterranean region

*Thymelaea* Mill.

New Caledonia

*Deltaria* Steenis, *Lethedon* Spreng., *Solmsia* Baill.

Northern and southern America

*Daphnopsis* Mart. & Zucc., *Dirca* L., *Funifera* Leandro ex C.A.Mey., *Goodallia* Benth., *Lagetta* Juss., *Lasiadenia* Benth., *Linodendron* Griseb., *Lophostoma* Meisn., *Ovidia* Meisn., *Schoenobiblus* Mart.

Sri Lanka

*Gyrinops* Gaertn.

Perhaps the economically most important character in the family is its tough fibrous bark. The bark of *Wikstroemia*, *Daphne*, *Edgeworthia*, *Thymelaea* and *Daphnopsis* is used for rope, and in the manufacturing of bank notes and strong paper. Flexible shoots of *Dirca* are used for baskets. Bark of *Pimelea* was used as a source of twine by early settlers in Australia.

Many genera are also known for their medicinal value. The wood of *Wikstroemia* is a source of incense and that of *W. ovata* C.A.Mey. is a strong purge. In China the bark of *Daphne* is used as an apparently safe and efficient abortifacient; it contains the glycoside daphnin and an acrid resin (mezerein) giving plants a bitter taste. The decaying heartwood of *Aquilaria malaccensis* Lam. is saturated with a resin which is the basis of incense and when distilled it is used in perfume and medicine.

The genera *Pimelea*, *Edgeworthia* and *Daphne* are cultivated for horticultural purposes. The scent of *Daphne* flowers is carnation-like and attractive to Lepidoptera; some members are moth-pollinated. *Gonystylus bancanus* (Miq.) Kurz. is a peat swamp-forest tree, with knee-roots. Its lightweight commercial timber is used for dowelling and is much exported from Indomalesia.

In southern Africa, the bark of various genera is used for tying down thatch, for plaiting into whip thongs and for twine. *Dais cotinifolia* L. is an ornamental tree with attractive flowers, occurring mostly along the eastern regions of the country.

## 1.2 *Passerina*

*Passerina* comprises 20 species and four subspecies. The genus is centered in the Cape Floristic Region, where ten species and four subspecies are endemic and four species are near-endemic. Three species are endemic to the Northern, Western and Eastern Cape Provinces, as well as KwaZulu-Natal, although they are variously distributed in these provinces. *P. drakensbergensis* is endemic to the Bergville District in KwaZulu-Natal. *P. montivaga* is found from Mossel Bay and Oudtshoorn to the Eastern Cape and along the escarpment northwards to Zimbabwe and *P. montana* is distributed from the eastern mountains and Great Escarpment of southern Africa to Zimbabwe and Malawi. The latter two species are near-endemic to the Great Escarpment of southern Africa.

The name *Passerina* is derived from the Latin *passer* (= a sparrow) as the seeds resemble a sparrow's beak. The vernacular name 'sparrow-wort' was suggested by Miller (1768) for all *Passerina* species and Wendland (1798) used the name *fadenförmige Vogelkopf*. According to Smith (1966) *gonna* is a collective vernacular name once used by the Khoekhoe for various members of Thymelaeaceae in southern Africa, e.g. several species of *Passerina* and *Struthiola*.

Many members of *Passerina* grow on sand dunes and in sandy areas, with parts of the woody stem subterraneous, forming runners and developing an extended root system. Most of these plants are pioneers and resprouters, increasing their chances of survival in disturbed areas. These plants are excellent sand binders and are suitable for reclaiming problematic sandy areas, especially after the clearing of invader species. They could also be propagated along coastal areas exposed to sea winds.

*Passerina filiformis* is quite ornamental at maturity and these plants have been cultivated in Britain and Europe since the time of Linnaeus. *P. falcifolia* grows into small ornamental trees and could be used more widely in horticulture. Although *Passerina* species do not have showy flowers, *P. obtusifolia* is used in the wild flower industry in the Robertson area.

Ash from *Passerina obtusifolia* was traditionally used by the people of Genadendal in the Western Cape in the home industry of soap-making. Although certain species have been recorded in cancer research, these plants are not currently known for their medicinal value. The bark is exceedingly tough and is used for tying down thatch. According to Watt & Breyer-Brandwijk (1962) it is also plaited into whip thongs and used as twine. Members of the genus are not browsed by stock as the plants are apparently unpalatable (Story 1952).

### 1.3 Problem statement

The following account attempts to address many problems historically encountered during the revision of this taxonomically difficult genus, see Table 7.1 (Chapter 7). In his *Species plantarum*, Linnaeus (1753) described *P. filiformis*, *P. hirsuta*, *P. ciliata* and *P. uniflora*, of which *P. filiformis* is the only species that is currently recognized in *Passerina*. Wikström (1818) recognised 41 species of *Passerina* and the subspecies *P. filiformis* subsp. *divaricata*; of these only four species are presently recognized in *Passerina*. In the interim the subspecies was raised to species level and is presently known as *P. falcifolia*. Thunberg (1825) recognized nine species of which only one is currently maintained. His concept of *P. glomerata*, *P. ericoides* and *Lachnaea conglomerata* were completely incorrect and caused confusion right up to the present study. During this period, various species were described by other botanists, not mentioned in Table 7.1 (Chapter 7). Meisner (1840; 1857: 563–565) redefined the genus by clarifying 92 'species exclusae' which were mostly synonymous with other cosmopolitan genera in the Thymelaeaceae and he retained only four species and six subspecies. The account of Wright (1915) on *Passerina* was mostly based on the generic concept of Meisner (1857), but Wright's species concept was poorly defined. He recognized ten species, of which three were new, as well as three subspecies. He recognized *P. ericoides* and *Chymococca empetroides*, both now in synonymy of *P. ericoides*. Although Thoday (1924) provided a much improved classification of the group, the circumscription and identification of several species remained problematic, especially in the herbarium.

The following principal problems were identified:

- the genus concept of *Passerina*;
- justification of Meisner's decisions on the 92 names, regarded as 'species exclusae' by Meisner (1840; 1857: 563–565) and placed in synonymy with other cosmopolitan genera in the Thymelaeaceae;
- the need for methods to reliably identify herbarium material of *Passerina*, to improve on the classification and nomenclature of Thoday and to identify possible new species and subspecies;
- the need for additional diagnostic characters for the identification of infrageneric taxa in *Passerina*, as these were previously identified mainly on morphological characters.

## 1.4 Objectives

All the existing taxonomic treatments were based solely on the study of herbarium material. Large numbers of herbarium specimens are now available for study and, supplemented by extensive fieldwork, the present systematic revision of *Passerina* was undertaken. A multidisciplinary approach was followed with potential taxonomic evidence derived from various sources. The objectives of the study are to:

- study the pollen morphology to evaluate its taxonomic significance;
- study the morphology and anatomy of the leaves, inforescences and flowers to ascertain characters of taxonomic significance;
- study the phytogeography of the group;
- undertake an infrageneric phylogenetic analysis;
- produce a monographic treatment of the genus.

## 1.5 Hypotheses

Hypotheses tested include:

- *Passerina* is a monophyletic genus that probably evolved as a result of environmental pressure of the climate in the predominantly winter-rainfall area of the Western Cape;
- the most important climatic features driving phylogenetic change would be windy conditions in spring and drought in summer;
- phylogenetic change would yield characters that are taxonomically significant at both the genus and species levels;
- *Passerina* probably adapted to specific environmental conditions, as it is the only southern African member of the Thymelaeaceae with an anemophilous habit;
- pollen morphology may be taxonomically useful;
- the unique secondary reticulum in the pollen wall of *Passerina* evolved in conjunction with the anemophilous habit;
- leaf structure may be taxonomically useful;
- leaf epidermal features probably evolved because of summer drought;
- anatomical features of the various leaf structural types (Chapter 4.4) probably evolved because of increasing dry conditions, with expanding speciation further away from the centre of diversity of the genus in the Western Cape;
- floral structure may be taxonomically useful.
- fleshy berries evolved from dry fruits, probably as a result of the selective pressure of bird dispersal and maritime conditions (*Passerina* is the only southern African genus in the Thymelaeaceae with fleshy berries);

- the classifications proposed by previous students of the genus;
- *Passerina* is probably not closely related to other genera in the Thymelaeaceae and, based on the above-mentioned characters, it can be regarded as phylogenetically advanced.

## 1.6 Layout of this thesis

Following the introduction (Chapter 1), a historical review of *Passerina* is provided (Chapter 2), followed by materials and methods used (Chapter 3). The taxonomic significance of characters is discussed in Chapter 4, where the identity of the mucilaginous epidermal cell walls and the comparative analyses of the palynology, morphology and anatomy are described. The phytogeography of the genus is dealt with in Chapter 5 and its phylogeny in Chapter 6. The taxonomic treatment of *Passerina* (Chapter 7) discusses the nomenclature, detailed description of the genus, the 20 species and four subspecies as well as the etymology, uses, distribution and ecological aspects of the taxa. Chapter 8 is a general discussion and the conclusions are presented in Chapter 9.

# CHAPTER 2

# HISTORICAL REVIEW

## 2.1 Thymelaeaceae

### 2.1.1 *Interfamilial classification*

As the sexual system of classification of Linnaeus (1754) was of great utility in identification, it was widely adopted until superseded by the natural system of De Jussieu (1789). The latter author differentiated, described and named 100 'natural orders' corresponding to most major families and grouped the related families into classes. Thus the Thymeleae were grouped together with the Eleagni, Proteae, Lauri, Polygoneaea and Atriplices into 'class 6'. Bentham & Hooker (1880) placed the Thymelaeaceae in the Monochlamydeae, Daphnales. According to the system of A. Engler the Thymelaeaceae was placed in the Archichlamydeae, Myrtiflorae, Thymelaeineae (Gilg 1894a; Engler 1903; De Dalla Torre & Harms 1900–1907; Brummitt 1992). The interfamilial taxonomic relationships of the Thymelaeaceae from 1930–1999 are discussed in Chapter 4.5 of the present study.

### 2.1.2 *Infrafamilial classification*

Applying the sexual system of classification, Linnaeus (1754) placed the genus *Passerina* under Class VIII, Octandria, 1. Monogynia. This system was followed until De Jussieu (1789) instated the family Thymelaeaceae, with the following genera and author citations: *Dirca* L., *Lagetta* Juss., *Daphne* L., *Passerina* L., *Stellera* L., *Struthiola* L. *Lachnaea* L., *Dais* L., *Gnidia* L., *Nectandra* Berg. and *Quisqualis* L. Wikström (1818) accepted the Thymelaeaceae, but based the infrafamilial classification on the number of stamens, following Linnaeus. The most important contributions towards the infrafamilial classification of the Thymelaeaceae, based on morphological characters, were made by Endlicher (1847), Meisner (1857), Bentham & Hooker (1880) and Gilg (1894a). Using anatomical characters, further contributions were made by Van Tieghem (1893), Gilg (1894b) and Leandri (1930).

The most comprehensive work on the circumscription of the Thymelaeaceae and infrafamilial taxa is reflected in the publication by Domke (1934). He divided the family into four subfamilies, namely Gonystyloideae, Aquilarioideae, Gilgiodaphnoideae and Thymelaeoideae. The last-mentioned subfamily included the southern African genera *Synaptolepis*, *Peddiea*, *Dais*, *Gnidia* (including *Lasiosiphon*), *Struthiola*, *Lachnaea* (=*Cryptadenia*) and *Passerina*. Domke's (1934) classification was followed by that of Archangelsky (1971: Figure 10) who proposed the new subfamilies Octolepidoideae, Microsemmatoideae and Synadrodaphnoideae and raised the Gonystyloideae to the family Gonystylaceae (also recognized by Takhtajan 1997, amongst others). Concerning the classification of *Passerina*, the subtribe Passerininae Endl. was raised to the tribe Passerineae (Endl.) Bredenk. & A.E.van Wyk (Chapter 4.1) based on palynological evidence. Subsequently support for the recognition of the Passerineae was obtained from comparative leaf and floral morphology, as well as from leaf anatomy (Chapters 4.4 and 4.5).

## 2.2 *Passerina*

### 2.2.1 *Intergeneric classification*

In his comprehensive work on the circumscription of the Thymelaeaceae and infrafamilial taxa, Domke (1934) gave a complete historical review of the intergeneric classification of *Passerina*. He included the Southern African genera *Dais*, *Gnidia* (= *Lasiosiphon*), *Struthiola*, *Lachnaea* (=*Cryptadenia*) and *Passerina* in the tribe Gnidieae, subtribe Gnidiinae of the subfamily Thymelaeoideae. The present study (Chapter 4.1) places *Passerina* in the monogeneric tribe Passerineae on the basis of mainly pollen characters. Currently *Passerina* is considered advanced at the intergeneric level, as many of the advanced character states present in other genera of the Thymelaeoideae are all found together in this genus. The most prominent characters distinguishing *Passerina* are the exserted, extrorse anthers and the unique anemophilous habit (Chapters 4.1 and 4.5).

### *2.2.2 Infrageneric classification*

In his *Species plantarum*, Linnaeus (1753) described *P. filiformis*, *P. hirsuta*, *P. ciliata* and *P. uniflora*. Publications mentioned in the applicable protologue and in synonymy to the various species that predate the nomenclatural starting point for the Spermatophyta [International Code of Botanical Nomenclature, Article 13.1 (Greuter *et al.* 2000)] are Linnaeus's *Hortus Cliffortianus* (1737), Van Royen (1740), Plukenet

(1700: 180), Breyne (1678) and Burman (1739). The generic name *Passerina* appearing in *Species plantarum* (Linnaeus 1753) is associated with the subsequent description given in Linnaeus's *Genera plantarum* (1754) (Greuter *et al.* 2000, Article 13.4).

Wikström (1818) published a comprehensive account on *Passerina*. Further work on the genus was done by Thunberg (1825a), emending some of Wikström's species and describing several new ones. Meisner (1840; 1857: 563–565) redefined the genus by clarifying 92 'species exclusae' which were mostly synonymous with other cosmopolitan genera in the Thymelaeaceae. The distribution of the remaining species clearly indicated that *Passerina* was a smaller genus, largely confined to southern Africa. At the beginning of the 20th century, Wright (1915) revised the Thymelaeaceae for the *Flora capensis* and Thoday (1924) published a revision of *Passerina*. Table 7.1 (Chapter 7) is a summary of taxa recognized in the most comprehensive works on *Passerina* from Linnaeus (1753) to the present study.

In his treatment of *Passerina*, Meisner (1840) divided the genus into section I. *Pentamerae* and section II. *Tetramerae*. *P. polycephala* E.Mey., *P. anthylloides* L.f. and *P. calocephala* Meisn., with pentamerous flowers (section I), were eventually all placed in the genus *Gnidia* (Meisner 1857; Gilg 1894a). Meisner (1857) did not divide *Passerina* into infrageneric taxa, a pattern followed by all subsequent treatments and no further mention was made of the relevant sections. In the present genus treatment the sectional classification is not maintained.

# CHAPTER 3

# MATERIALS AND METHODS

Material from the following herbaria was studied (acronyms according to Holmgren *et al.* 1990): BM, BOL, BREM, C, GRA, K, LINN, M, MEL, MO, NBG, P, PR, PRC, PRE, PRU, S, SBT, TCD, UPS, W, WU. A database of all specimens was compiled on the Microsoft Access Relational Database Management System for Windows, Version 2.0.

Live and preserved (dried and liquid) material of all the species and subspecies in *Passerina* was studied. As far as possible, material was collected from at least five different localities for every taxon. Leaves, bracts and flowers were morphologically examined with the aid of a stereo-microscope. Illustrations were made from herbarium material by means of a drawing tube. Measurements were taken using a dissection microscope and a calibrated eyepiece. Because the laminas of most leaves and floral bracts are cymbiform or rolled, the depth was measured, with dimensions indicated as length × depth.

## 3.1 LM

The light microscope (LM) was used for palynology, general leaf anatomy, epidermal studies and floral anatomy (Chapters 4.1–4.5). Leaf and floral 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)]. The material was washed in water, dehydrated and embedded in glycol methacrylate (GMA) following the methods of Feder & O'Brien (1968). Embedded material was serially sectioned. 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).

### 3.2 SEM

The scanning electron microscope (SEM) was used in palynology and epidermal studies (Chapters 4.1 and 4.3).

### 3.3 TEM

The transmission electron microscope (TEM) was used for palynology and in the study of the structure of mucilaginous epidermal cell walls in *Passerina* (Chapters 4.1 and 4.2).

### 3.4 Phylogeny

The program HENNIG 86 version 1.5 (Farris 1988) and the accompanying manual (Lipscomb 1994) were used to analyse the data. The distribution of characters on the selected tree was examined using the tree editor 'DOS EQUIS'. For the determination of bootstrap values, data were also analysed using the software package PAUP 4.0 for Macintosh (Swofford 1991).

### 3.5 Terminology and author citations

Terminology used in the descriptions of pollen morphology, leaf epidermal structure, leaf anatomy, and inflorescences and flowers is mentioned under the respective sections of Chapter 4. General descriptive terminology follows Stearn (1973) and Radford *et al.* (1974). Works consulted on the application of cladistic methodology and terminology are given in Chapter 6. Author citations follow Brummitt & Powell (1992).

### 3.6 Taxonomic concepts

The delimitation of species and subspecies in *Passerina* is based on both macromorphological leaf, bract, inflorescence and floral characters as well as leaf anatomical and geographical characters. Each taxon is based on a unique combination of characters.

### 3.7 Conservation status

With the exception of *Passerina esterhuyseniae* (from the northern Cederberg Mountains) known from herbarium material only, all other species and subspecies of *Passerina* were studied in the wild. Assessments were done using the guidelines of the IUCN Species Survival Commission (2000).

# CHAPTER 4

# TAXONOMIC SIGNIFICANCE OF CHARACTERS

## 4.1 Palynology

BREDENKAMP, C.L. & VAN WYK, A.E. 1996. Palynology of the genus *Passerina* (Thymelaeaceae): relationships form and function. *Grana* 35: 335–346.

CONTENTS

Grana 35: 335–346, 1996

# Palynology of the genus *Passerina* (Thymelaeaceae): relationships form and function

CHRISTINA L. BREDENKAMP and ABRAHAM E. VAN WYK

Bredenkamp, C. L. & Van WYK, A. E. 1996. Palynology of the genus *Passerina* (Thymelaeaceae): relationships form and function. – Grana 35: 335–346. ISSN 0017-3134.

Pollen of the genus *Passerina* L. differs markedly from that of other southern African members of the Thymelaeaceae. Grains of most members of the Thymelaeaceae are characterised by a typical croton pattern, comprising rings of more or less trihedral sexine units mounted on an underlying reticulum of circular muri. In *Passerina*, however, 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 not homologous with the basal reticulum of typical crotonoid grains in the family. The croton pattern has often been used as indication of a possible relationship between the Euphorbiaceae and Thymelaeaceae. Pollen of *Passerina* is adapted to anemophily. Grain sculpturing clearly demonstrates secondary derivation of a reticulate pattern from the typical croton pattern, through reduction, aggregation and fusion. Pollen of *Passerina* represents a climax of a continuum of variation in the exine of pollen in the Thymelaeaceae. As *Passerina* is considered phylogenetically advanced in the subfamily Thymelaeoideae, the subtribe Passerininae is raised to tribal rank, namely tribe Passerineae.

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Established by Linnaeus (1737, 1753), the genus *Passerina* comprises about 17 species, all restricted to southern Africa (Thoday 1924, Bond & Goldblatt 1984). The palynological study of *Passerina* was undertaken as part of a monographic study of the genus. This study revealed that the pollen of the genus differs markedly from that of the other southern African genera of the Thymelaeaceae and indicated many similarities between the Thymelaeaceae and Euphorbiaceae (Nowicke 1994, Erdtman 1952, 1969).

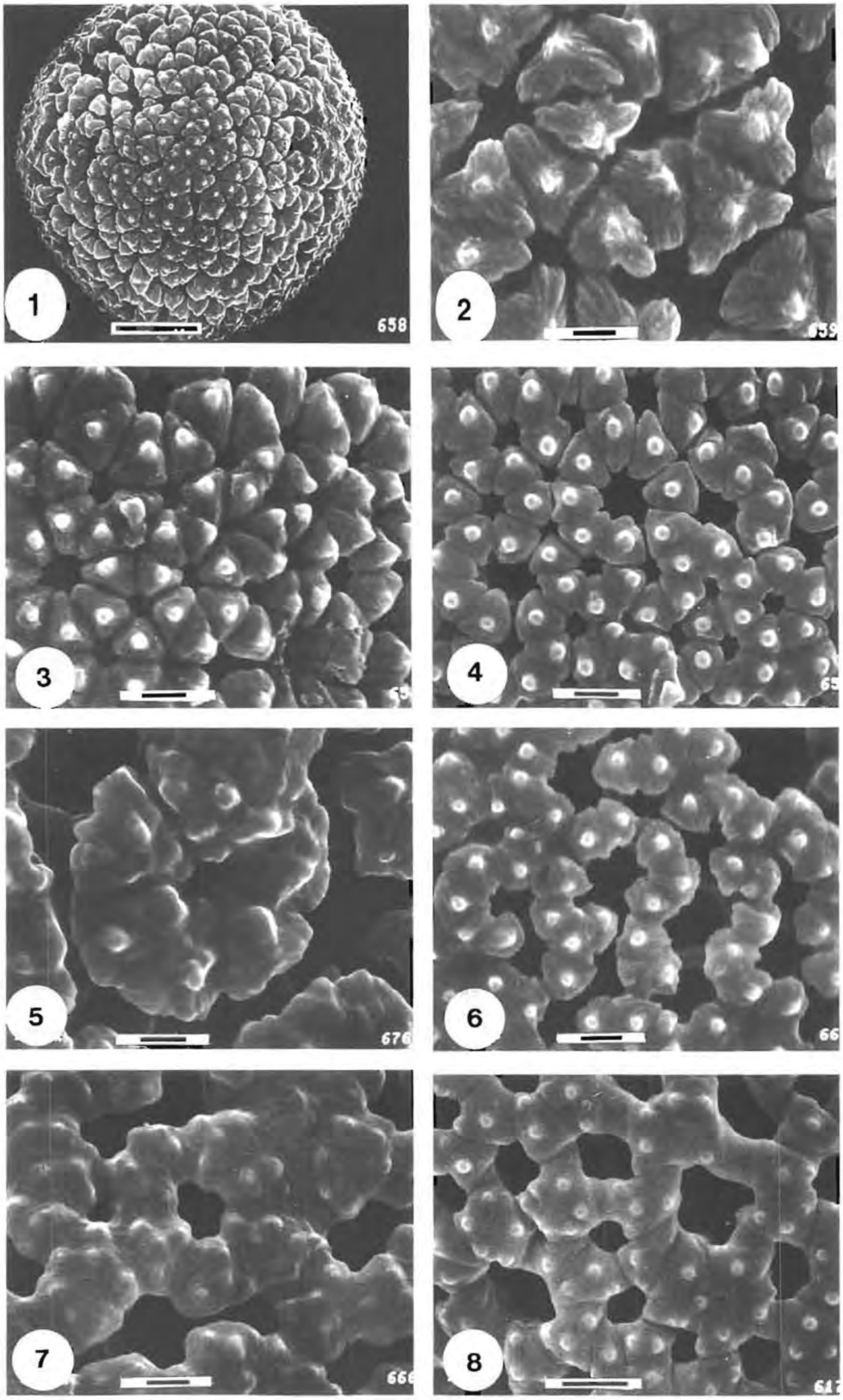
Archangelsky (1966, 1971), using light microscopy (LM), recognised ten pollen groups in the Thymelaeaceae, of which two are represented by southern African Thymelaeaceae. The present LM, SEM and TEM study revealed new information, including a clear distinction between the pollen of *Gnidia* L. and *Passerina* L., which were both regarded as cryptostellate by Archangelsky (1966). Descriptions of the pollen of *Aetoxylon* (Airy Shaw) Airy Shaw, *Amyxa* Tiegh. and *Gonystylis* Teijsm. & Binn. by Nowicke et al. (1985) indicated that the phylogenetic relationships of the Thymelaeaceae were controversial issues.

Pollen of Thymelaeaceae is remarkably uniform: spheroid in shape (Mohl 1835) and polyforate (Blaise 1959), panporate (Archangelsky 1966) or pantoporate (Punt et al. 1994), with a crotonoid tectum or a derivative thereof (Nowicke et al. 1985). The term "crotonoid pattern" was proposed by Erdtman (1952, 1966) who describes the sexine as follows: "regularly arranged excrescences (triangular or ±circular in cross section) supported (always?) by a baculate or baculoidate, or spongy layer" and arranged regularly in circles around foveoloid areas delimited by muroid ridges." Punt (1961) describes the *Croton* type of pollen for the Euphorbiaceae as having no apertures, but Nowicke (1994), using electron microscopy, disputes this and reports the presence of 3-colpate and pantoporate pollen in the Crotonoideae, thus concluding a close structural relationship between the pollen of the Crotonoideae and the Thymelaeaceae. Thanikaimoni et al. (1984) describe the omniaperturate pollen of *Croton matourensis* Aubl. and conclude that the "crotonoid pattern appears lax due to the well developed muri which delimit the lumina." Further, the ornamentation of the sculptural units is linked to the pollination mechanism. Nowicke et al. (1985) describe the subunits of *Croton* as triangular in surface view and forming a continuous array, but in the Thymelaeaceae these units appear to be attached to a basal ringlike network of muri (also described in literature as horizontal rods). An almost perfect continuum of variation in the distinction of the subunit has also been found for the Thymelaeaceae by Nowicke et al. (1985).

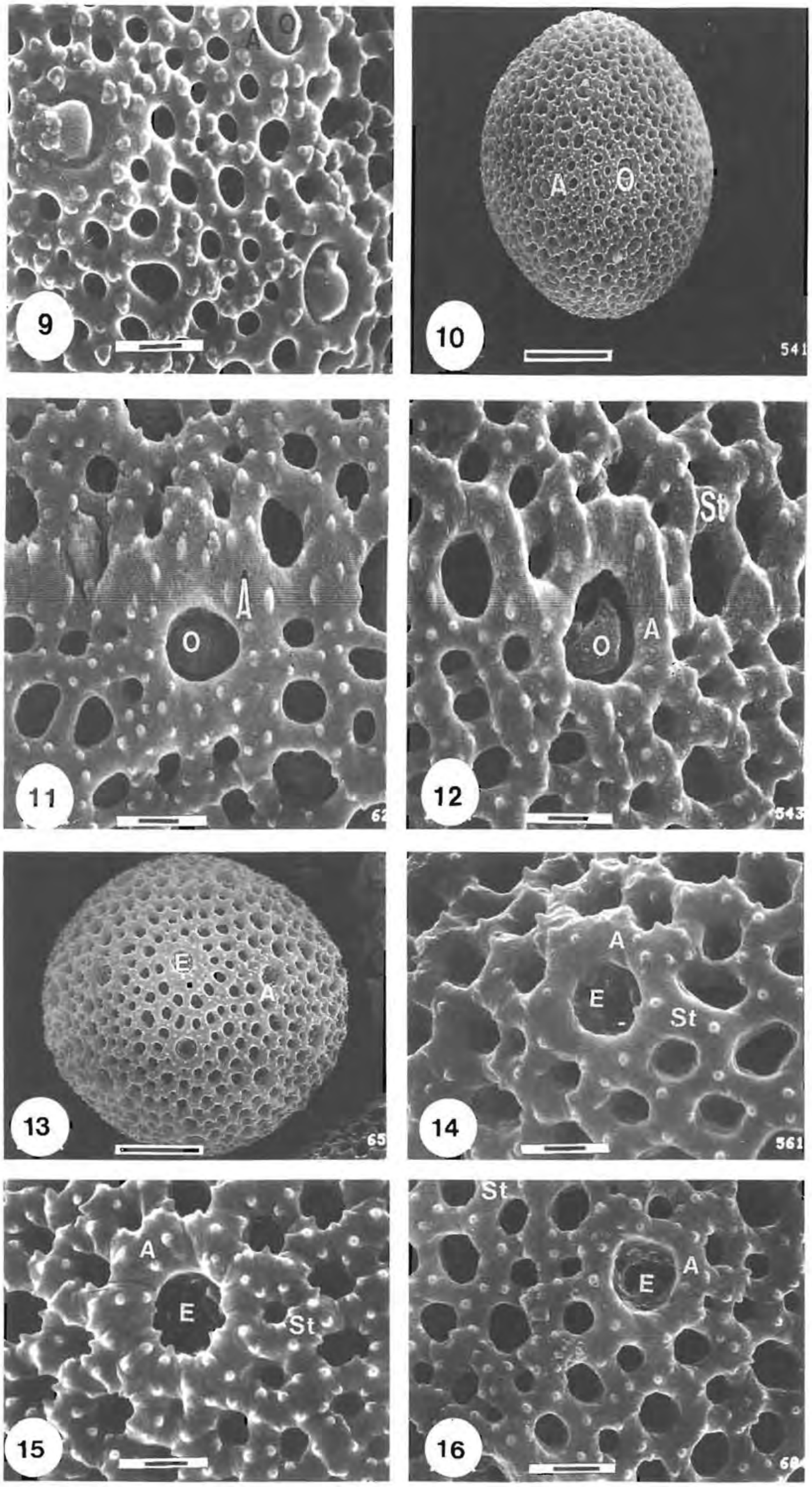
The present paper describes the pollen of *Passerina* and illustrates this continuum for southern African genera of the Thymelaeaceae. General trends in the evolution of palynological features in Thymelaeaceae and Gonystylaceae are proposed.

## MATERIALS AND METHODS

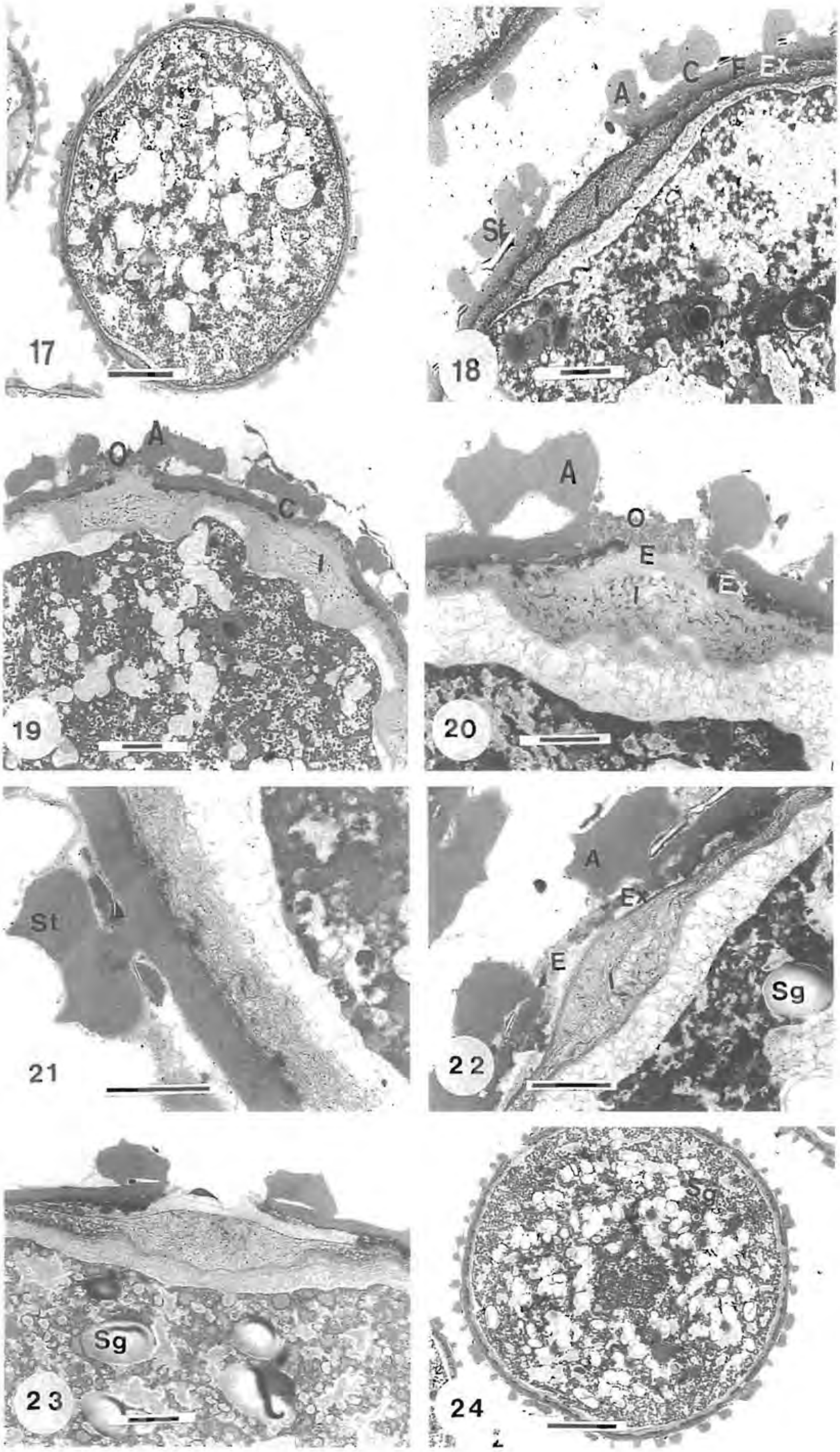
During field work, aspects of pollination biology such as floral morphology, flower colour, presence or absence of nectar and scent, were recorded for the genus *Passerina*. Pollen of the 16 currently recognised species of *Passerina* in southern Africa (Arnold & De Wet 1993) as well as pollen of the genera *Cryptadenia* Meisn., *Dais* L., *Englerodaphne* Gilg, *Gnidia* L., *Lachnaea* L., *Peddiea* Harv., *Struthiola* L. and *Synaptolepis* Oliv. was studied by LM and electron



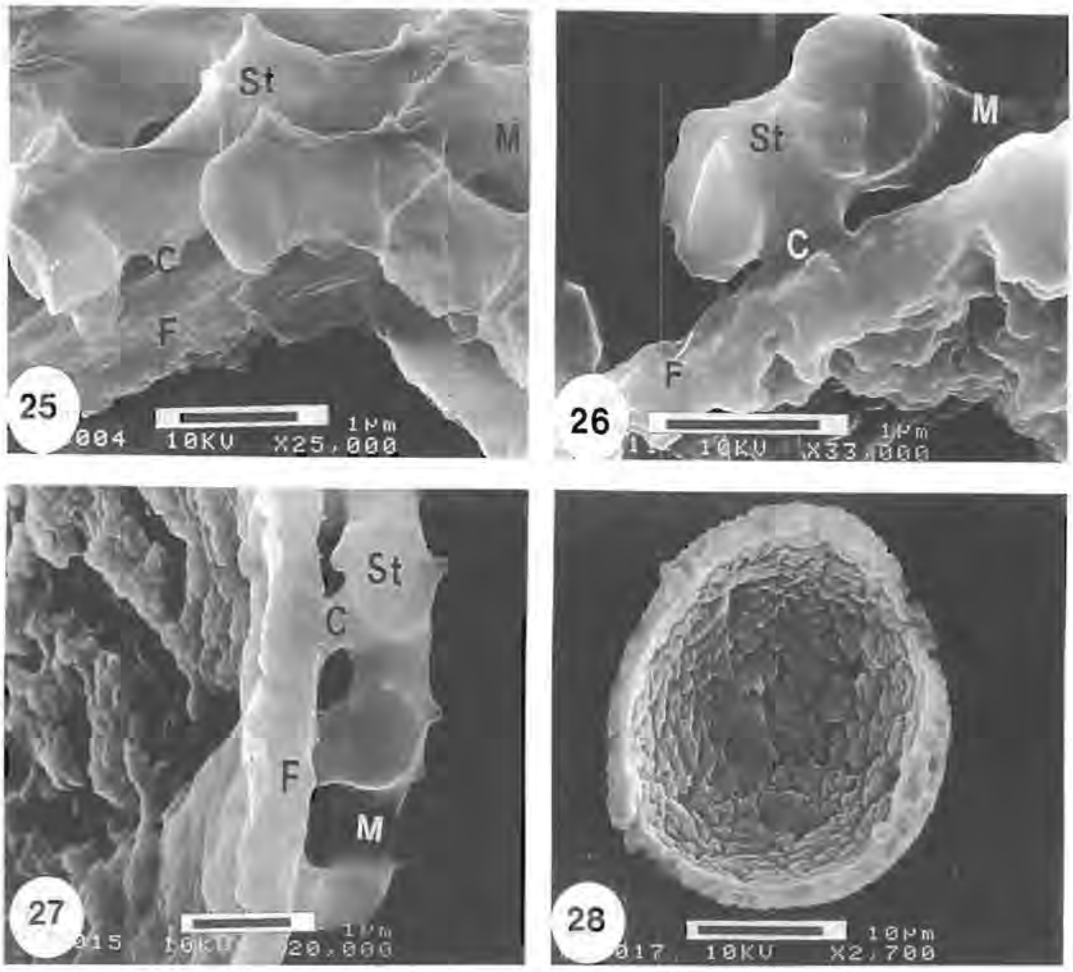
(For description see page 339).



(For description see page 339).



(For description see page 339).



*Figs. 25–28.* SEM micrographs of fractured pollen grains of *Passerina filiformis* (Killick 238), showing detail of the wall structure. (33–35) Transverse view of fractured wall, illustrating the secondary reticulum. (36) Fractured pollen grain showing surface of internal wall. C = columella, F = footlayer, M = murus and St = secondary reticulum. The black scale bar is 1 µm in Figs. 33–35 and 10 µm in Fig. 36.

microscopy. Anthers with pollen grains were removed from open flowers of herbarium specimens housed in the National Herbarium (PRE). For TEM, fresh flowers were collected, 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. Species names and voucher specimens are supplied under "Specimens investigated".

## SEM

Four methods were followed:

(1) Unacetolized pollen samples were air-dried on SEM stubs, sputter-coated with gold and viewed with an ISI-SX-25 SEM.

(2) Polliniferous samples were sonicated in 50% acetone for four minutes and then collected on 12 µm nuclepore filters locked in a multiple funnel manifold (Bredenkamp & Hamilton-Attwell 1988). Pollen was put through a graded ethanol series and the filters containing the pollen were air dried on SEM stubs, sputter-coated and viewed.

(3) Polliniferous samples were acetolyzed (Erdtman 1960) and thoroughly washed, first with distilled water and then ethanol. For LM, pollen was mounted in glycerine jelly and permanently sealed with entellan (Art. 7961, E. Merck, Darmstadt) (Frip 1983). Measurements of pollen grains were made with a Kontron image analyser and are based on at least 10 grains per sample. For SEM, the pollen-ethanol mixture was air-dried on SEM stubs, sputter-coated with gold and viewed.

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*Figs. 1–8. SEM micrographs of pollen grains of some southern African members of the Thymelaeaceae. (1) Lachnaea eriocephala* (Richardson 15). 2–8 Portions of pollen wall showing detail of exine. (2) *Lachnaea eriocephala* (Richardson 15). (3) *Struthiola ciliata* (Bredenkamp 997). (4) *Gnidia capitata* (Van Rooyen 2178). (5) *Dais cotinifolia* (Germishuizen 5762). (6) *Englerodaphne pilosa* (Geldenhuys 1282); note presence of basal reticulum. (7) *Synaptolepis kirkii* (Ward 8473). (8) *Passerina paleacea* (Pillans 783). All specimens prepared by acetolysis technique (Erdtman 1960). The black scale bar is 10 µm in Fig. 1 and 1 µm in Figs. 2–8.

Figs. 9–16. SEM micrographs of selected species of Passerina showing whole grains as well as portions of pollen wall with detail of exine. (9) Unacetolyzed pollen of *P. ericoides* (Taylor 4042). (10) *P. obtusifolia* (Oliver 3679). (11) *P. paludosa* (Thoday 100). (12) *P. obtusifolia* (Oliver 3679). (13–14) *P. comosa* (Andreae 1288). (15) *P. galpinii* (Burgers 2259). (16) *P. vulgaris* (R.A. Dyer 180). A = annulus, E = endoaperture, O = operculum, and St = secondary reticulum. With exception of Fig. 13, which was prepared by the acetolysis technique, Figs. 10–16 were prepared by means of ultrasonic technique of Bredenkamp & Hamilton-Attwell (1986). The black scale bar is 1 µm in all figures, except for Figs. 10 and 13, where it is 10 µm.

Figs. 17–24. TEM micrographs of selected species of *Passerina* showing ultrathin sections of pollen grains. (17) cross section of whole grain and (18) enlargement showing detail of porus of *P. ericoides* (Bredenkamp 962). (19–21) *P. galpinii* (Bredenkamp 932), (19) part of cross section of whole grain, (20–21) enlargements showing detail of porus and structure of pollen wall. (22) *P. vulgaris* (Bredenkamp 924) showing detail of porus and intine. (23) *P. pendula* (Bredenkamp 908) and (24) *P. vulgaris* (Bredenkamp 924) showing starch granules. A = annulus, C = columella, E = endoaperture, Ex = endexine, F = footlayer, I = intine, O = operculum, St = secondary reticulum and Sg = starch grain. The black scale bar is 1 µm in all figures, except for Figs. 17 and 24, where it is 5 µm.

(4) Acetolyzed grains were crushed at liquid nitrogen temperatures, thawed and dusted onto double sided carbon adhesive tape. Coated with chromium and viewed with a Jeol 6 000 F field emission SEM.

## TEM

TEM was used for the study of the wall structure in selected species. Anthers with pollen grains were removed from open flowers fixed in a 0.1 M phosphate-buffered solution at pH 7.4, containing 2.5% formaldehyde, 0.1% glutaraldehyde and 0.5% caffeine. Pollen was rinsed in 0.075 M phosphate buffer, pH 7.4–7.5, postfixed for one hour in 0.25% aqueous $OsO_4$, washed in three changes of water and dehydrated in a graded acetone series. Quetol 651 resin (Van der Merwe & Coetzee 1992) was used for embedding. Ultrathin sections were contrasted in 4% aqueous uranyl acetate for 10 minutes and rinsed in water three times. The sections were then contrasted with lead citrate (Reynolds 1963) and rinsed in water. A Phillips 301 TEM was used for examination of the sections. Descriptive terminology follows Erdtman (1969) and Punt et al. (1994).

## RESULTS

### General description of pollen grains of selected members of southern African Thymelaeaceae

*Lachnaea eriocepahala L.* (Figs. 1–2)
Pollen grains monads, spheroid and pantoporate, mean diameter 49 µm (Table I). Wall tectate and supra-ornate, sexine thicker than nexine, attached to nexine by means of columellae which unite into tectum above. Tectum reticulate (basal reticulum) with supra-tectal triangular projections which are trihedral to shallowly trihedral with basal sides straight or emarginate, surfaces of lateral sides striate, with one single central spinule (see also Beyers 1992).

*Cryptadenia uniflora* Meisn.
Pollen grains monads, spheroid and pantoporate, mean diameter 53 µm (Table I). Wall tectate and supra-ornate, sexine thicker than nexine, sexine attached to nexine by means of columellae which unite into tectum above. Tectum reticulate with supra-tectal triangular projections which are trihedral, with basal sides straight, surface of lateral sides striate (see also Beyers 1992: 101).

*Struthiola ciliata* (L.) Lam. (Fig. 3)
Pollen grains monads, spheroid and pantoporate, mean diameter 38 µm (Table I). Wall tectate and supra-ornate, sexine thicker than nexine, sexine attached to nexine by means of columellae which unite into tectum above. Tectum reticulate with supra-tectal triangular projections which are trihedral, with basal sides straight, surface of lateral sides striate, with one single central spinule and units closely packed.

*Gnidia capitata* L. f. (Fig. 4)
Pollen grains monads, spheroid and pantoporate, mean diameter 33 µm (Table I). Wall tectate and supra-ornate, sexine thicker than nexine, sexine attached to nexine by means of columellae which unite into tectum above. Tectum reticulate with supra-tectal triangular projections which are trihedral, with basal sides straight and one single central spinule; some subunits tightly packed, possibly fused, others separated revealing horizontal rods (muri of basal reticulum).

*Dais cotinifolia* L. (Fig. 5)
Pollen grains monads, spheroid and pantoporate, mean diameter 66 µm (Table I). Wall tectate and supra-ornate, sexine thicker than nexine, sexine attached to nexine by means of columellae which unite into tectum above. Tectum reticulate with supra-tectal triangular projections which are trihedral; subunits with emarginate margins and fused into groups with exposure of muri of basal reticulum; spinules central and at bases of subunits.

*Englerodaphne pilosa* Burtt Davy (Fig. 6)
Pollen grains monads, spheroid and pantoporate, mean diameter 36 µm (Table I). Wall tectate and supra-ornate; sexine thicker than nexine, attached to nexine by means of columellae which unite into tectum above. Tectum reticulate with supra-tectal triangular projections which are trihedral, with one single central spinule, most subunits fused, forming half-circles or various patterns, muri of basal reticulum exposed.

*Synaptolepis kirkii* Oliv. (Fig. 7)
Pollen grains monads, spheroid and pantoporate, mean diameter 53 µm (Table I). Wall tectate and supra-ornate, sexine thicker than nexine, sexine attached to nexine by means of columellae which unite into tectum above. Tectum reticulate with supra-tectal triangular projections which are trihedral, spinules in groups of 4–6, most subunits almost completely fused, muri of basal reticulum exposed.

Table I. *Pollen diameter in eight genera of the family Thymelaeaceae (measurements in* µm*).*

| Taxon | Count (n) | Sum Σ | Mean $\bar{x}$ | Standard deviation σ |
|---|---|---|---|---|
| *Cryptadenia uniflora* | 39 | 2,060 | 53 | 7 |
| *Dais cotinifolia* | 37 | 2,450 | 66 | 3 |
| *Englerodaphne pilosa* | 50 | 1,800 | 36 | 3 |
| *Gnidia capitata* | 80 | 2,620 | 33 | 2 |
| *Lachnaea eriocephala* | 11 | 540 | 49 | 4 |
| *Peddiea africana* | 48 | 2,270 | 47 | 3 |
| *Struthiola ciliata* | 68 | 2,600 | 38 | 3 |
| *Synaptolepis kirkii* | 16 | 840 | 53 | 10 |

### Description of pollen grains in the genus *Passerina* (Figs. 8–28)

Pollen grains monads, spheroid and pantoporate. Mean diameter of grains 32–44 µm (Table II). Pores composite (Thanikaimoni 1986: 120), endoapertures (ora) round or elongate, with uneven margins (Figs. 13–16). Pores 18–44, slightly protruding and larger than lumina of reticulation, distinguished by annuli (Figs. 10–11, 19–20 and 22)
04, 19–20 and 22). Opercula present in pores of unacetolyzed pollen grains (Figs. 9–12 and 19–20). "Supratectal" subunits, (as in typical croton pattern of most Thymelaeaceae), fused completely (Figs. 8, 19–21 and 25–28) to form a continuous secondary reticulum, often exhibiting faint indentations demarcating subunits (Fig. 15). Basal reticulum (rods) as in typical croton pattern no longer discernable (replaced by secondary reticulum derived from fused sexine subunits), and apparently lost through reduction, or fusion with the new reticulum. Spinules present on muri, average number of

Table II. *Pollen diameter in* Passerina *(measurements in* µm*)*.

| Taxon | Count (n) | Sum $\Sigma$ | Mean $\bar{\chi}$ | Standard deviation $\sigma$ |
|---|---|---|---|---|
| *P. burchellii* | 54 | 2,260 | 42 | 3 |
| *P. comosa* | 54 | 2,120 | 39 | 3 |
| *P. drakensbergensis* | 83 | 3,030 | 37 | 3 |
| *P. ericoides* | 53 | 2,020 | 38 | 10 |
| *P. falcifolia* | 53 | 2,340 | 44 | 4 |
| *P. filiformis* | 42 | 1,570 | 37 | 4 |
| *P. galpinii* | 56 | 231 | 42 | 3 |
| *P. glomerata* | 44 | 1,760 | 40 | 3 |
| *P. montana* | 57 | 2,050 | 36 | 3 |
| *P. obtusifolia* | 61 | 2,410 | 39 | 3 |
| *P. paleacea* | 57 | 1,870 | 33 | 3 |
| *P. paludosa* | 59 | 2,260 | 38 | 2 |
| *P. pendula* | 60 | 2,280 | 38 | 4 |
| *P. rigida* | 51 | 1,930 | 38 | 2 |
| *P. rubra* | 53 | 1,700 | 32 | 2 |
| *P. vulgaris* | 76 | 2,810 | 37 | 3 |

spinules surrounding a pore 9–28. Intine thickened at apertures, stratified, consisting of outer continuous polysaccharide layer and enzymatic inclusion (Thanikaimoni 1986) (Fig. 22). Horizontal network (muri) supported by columellae implanted on well developed footlayer (Figs. 18–22 and 25–28). Footlayer more strongly developed than endexine which displays granular electron-dense particles. Cytoplasm with many electron-dense particles, also containing large numbers of starch grains.

## DISCUSSION

### Form and function

In southern Africa *Passerina* is the only genus of the Thymelaeaceae that is wind-pollinated. The plants are ericoid shrublets, shrubs or small trees. They are resprouters, usually growing in sandy soil and even on primary sand dunes along the coast, always exposed to wind. These plants are often pioneers along roadsides or in disturbed places. Leaves are decussate, concave or closely involute, lined with woolly hairs, adapted to dry windy summers. Inflorescences and flowers are also adapted to dry, warm and windy summers as the relatively small flowers are arranged in terminal spikes or heads, subtended by bracts usually broader than the leaves. The calyx is 4-lobed, tube flask-shaped or subcylindric and lobes are spreading. Petals are absent and the flowers are without nectar and odour (Thoday 1924).

*Adaptations of the flower to anemophily.* – *Passerina* is largely endemic to the Fynbos Biome of the Cape and northern extensions of this biome on the eastern mountains of southern Africa. This biome is characterised by steep coastal mountains giving rise to "berg" winds. Extreme wind conditions appear all along the coastal plains. In the Eastern Cape Kopke (1988) reports persistent north-westerly winds as a feature of summer and winter, and high level winds from the north in summer. In view these wind patterns, the specialised wind pollination of *Passerina* seems very appropriate.

Flowering time is short, mostly between September and October, usually after the rainy season when wind velocities are high. Pollination takes place in the morning when flower colour is yellowish, orangy or pale pink. Calyx lobes are open and eight stamens exceed the calyx lobes in length, exposing anthers which are conspicuously yellow and bulging with pollen. Anthers are extrorse (unique for the Thymelaeaceae in southern Africa) and open explosively. All pollen is shed at once and towards the afternoon the anthers are empty, calyx lobes bend at right angles to the tube, and flower colour becomes a deeper red. The stigma is mop-like (penicillate) and dry.

Wind-pollinated plants are not obligately anemophilous, many may be facultatively entomophilous (Crane 1986). Non-sticky pollen grains could also be transported by insects with sticky or hirsute bodies, relating to amphiphily (Thanikaimoni 1986). The insect visual spectrum ranges from 300 to 700 nm and red tones would be invisible to bees, explaining why bees usually visit flowers which are yellow to blue (Richards 1986). Although the pollination of *Passerina* is mainly anemophilous, the yellow flowers are perceived by insects when the pollen is shed and they serve as secondary pollen vectors. However, birds are attracted to orange or red. This could explain the change in flower colour in *Passerina* from yellow, when the pollen is shed, to red later in the day. The persistent red calyx envelops the developing fruit and the dispersal of fruit by birds is a greater possibility.

*Adaptations of pollen to anemophily.* – Muller (1979) speculates that the functional significance of the crotonoid pattern is difficult to interpret. It can be considered a system of excrescences which upon volume reduction achieves efficient closure around porelike structures. Its apparently independent evolution in unrelated angiosperms suggests at least some adaptive advantage. A closed smooth surface appears to be a secondary modification in many cases, especially in wind-pollinated species. This trend was apparent in *Passerina* which portrayed a much smoother secondary reticulum.

*Grain size and transport.* – Effective wind transport obligates that the total structure of the pollen grain is influenced by aerodynamic considerations. Wind-dispersed pollen should be rather small, light, smooth and not sticky (lacking pollenkit) (Punt 1986). The diameter of the pollen of *Passerina* fell within the range of 32–44 µm. Muller (1979) and Crane (1986) agree that wind-dispersed grains fall within a spectrum of 20–30(–60) µm. For a typical wind-dispersed pollen grain (diameter 30 µm) in still air at 20 °C, the Reynolds number is around 0.1 at a terminal settling velocity of 5 cm $s^{-1}$ (Crane 1986).

*Wall structure.* – The pollen wall of *Passerina* has a reticulum secondarily derived from the complete fusion of what was originally supratectal elements (still present in those extant Thymelaeaceae with crotonoid pollen). It clearly represents an evolutionary stage towards the development of a smoother exine sculpture. Smooth pollen can be advantageous in wind pollination as it serves to decrease pollen clumping and secondarily it allows reduction in effective radius without an overall thinning of the exine (Wodehouse

1935). The loss of ornamentation in anemophilous plants can be due to the energetic cost of sporopollenin Bolick (1990). One may speculate that, given enough time, grains of *Passerina* may loose their reticulate sculpture and become psilate. The present reticulate state may reflect a historical constraint introduced by the basal reticulum from which the current reduction has been derived.

Muller (1979) speculates that changes in pollen occur in response to selective pressure, any exine structure can be regarded as a compromise between the protective, harmomegathic and reservoir functions. The protective function of the pollen wall in *Passerina* was evident in the radial and tangential differentiation of exine layers which absorb the bending stresses during hydration and dehydration (Thanikaimoni 1986). The conspicuous homogeneous foot-layer (sole) also serves as a closed sealing layer.

Harmomegathic mechanisms involve the reaction of the complete pollen wall to the turgor pressure of the cytoplasm (Blackmore & Barnes 1986). Pantoporate grains of *Passerina* are well adapted to contraction upon dehydration and stretching during rehydration. The columellae in the pollen wall increase the possibility of bending and it has a well developed non-sporopollenous intine and aperture membranes (Figs. 18–20) which would be more capable of stretching and contracting than the exine. Intine is constrained by the exine, except at the apertures where it is distinctly thickened.

Reservoir function can be connected with characteristic cavities which hold tapetum-derived materials which play a significant role in producing an adhesive surface or as recognition substances. Thanikaimoni (1986) reports that pollen grains of anemophilous species have scanty electron-lucent heterogeneous pollenkit locked in the exine cavities and are less or not adhesive.

*Apertures.* – The pantoporate condition found in *Passerina* has obvious selective advantages. Protection of the cytoplasm and ease of germination are two factors with contradictory requirements. The pantoporate condition favours the reduction of large apertures for the protective function and compensates by optimising germination by increased number of apertures (Punt 1986). Increase in aperture number would obviously reduce the mechanical efficiency of the wall but this is taken care of by the compensative increase in exine thickness at the non-apertural region (Thanikaimoni 1986). The operculum is acquired to protect the water content of the pollen grain. Punt (1986) argues that smaller apertures inhibit desiccation. The xeromorphic adaptation of multi-aperturate operculate pollen grains with thick exine has a selective advantage in that it combines the mechanism against desiccation and that for quick germination to ensure rapid fertilisation (Thanikaimoni 1986). Multiple apertures also play an important role in the process of rehydration of the pollen grains as this process depends on the establishment of continuous water films between the apertural intine and the dry stigma surface. More apertures that are in contact with the stigma would obviously be activated and germination of pollen tubes would be more effective.

*Dehydration.* – TEM sections of the pollen grains of *Passerina* indicated that the grains varied considerably in their degree of hydration at the time of dispersal (Figs. 18–19). Starch granules were evident in grains of all members of the genus (Figs. 22–24). According to Heslop-Harrison (1979) the developing pollen lies immersed in the locular fluid during the first period of partial dehydration in the anther. Water will be withdrawn along water potential gradients occasioned by deficits developed elsewhere in the anther. The accumulation of starch at this time will presumably steepen the gradient by sequestering osmoticum and raising the water potential, thus enhancing the dehydration of the pollen grain. Baker & Baker (1979) claim a relationship between the presence of starch and wind pollination, this could possibly be due to the reduction in the mass of the pollen grain after dehydration. Further dehydration occurs in the air and desiccation attributable to the environment is most extreme in wind-dispersed pollen, demanding xeromorphic adaptations. Contrary to what one would expect, starch was also present in grains of all other southern African genera of Thymelaeaceae.

*Settling on stigma.* – In *Passerina* the stigma was mop-like (penicillate). According to Crane (1986) it is unlikely that plumose stigmas function as true sieves in angiosperms; it is more likely that inertial impaction is the means by which pollen becomes impacted on the stigma, but the possibility of electrostatic attraction should not be underestimated. However, this stigma type is normally associated with wind pollination.

*Rehydration.* – The source of water entering the pollen is the stigma. Stigmas without a free-flowing secretion pool are termed "dry" (Heslop-Harrison 1979). Our observation showed that the stigma in *Passerina* possibly represented the "dry" type. Heslop-Harrison (1979) states that dry stigmas offer rather difficult conditions for pollen hydration, and adjustment to these must require specialization of the exine and the apertural mechanisms. The evolution of porate exines seems to be such a specialization as porate exines are associated with dry stigmas. Apertures closest to the stigma form the first routes for the ingress of water. Enzymatic softening of the intine begins earlier at these sites.

*Compatibility, pollen tube mechanism.* – In *Passerina* the apertural intine was clearly stratified (Fig. 22). The enzymatic inclusion is sealed above and below by a continuous polysaccharide layer until hydration. The outer layer is then loosened and ultimately becomes disrupted with release of the underlying enzymes. The inner layer then becomes the precursor of the pollen tube. It conveys with it the poral intine with its enzyme load which degrades the cuticle of the stigmatic papilla (Thanikaimoni 1986). The functions of the enzymatic load of the apertural intine are still to be explained, but they play a role in: (a) softening of the intine at the germination site, as essential prelude to emergence of the tube tip, and (b) early interactions with the stigma, most probably during penetration of the cuticle and perhaps in the early nutrition of the pollen tube (Heslop-Harrison 1979).

Table III. *Summary of key pollen morphological characters in southern African Thymelaeaceae.*

| CHARACTER | TAXON | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | *Lachnaea eriocephala* | *Cryptadenia uniflora* | *Struthiola ciliata* | *Gnidia capitata* | *Dais cotinifolia* | *Englerodaphne pilosa* | *Synaptolepis kirkii* | *Passerina* |
| Mean diameter µm | 49 | 53 | 38 | 33 | 66 | 36 | 53 | 32–44 |
| Sexine triangular projections | | | | | | | | |
| Shape | Trihedral | | | | | | Indeterminate due to fusion | |
| Basal sides | Straight or emarginate | | Straight | | Emarginate | Indeterminate due to fusion | | |
| Lateral sides | Striate | | | Smooth | Striate | | Smooth | |
| Spinule | Single and central | | | | Central and at base | Single and central | Groups of 4–6 | Variable numbers |
| Arrangement | Separate | | Separate, closely packed | Possibly fused, tightly packed | Fused into groups | Fused, forming patterns | Almost completely fused | Completely fused forming a secondary reticulum |
| Horizontal rods (basal reticulum) | Present | | | | | | | Absent |

### Taxonomic implications

In the present study a continuum of variation in the distinction of the triangular subunit of the croton pattern (Nowicke et al. 1985) for the southern African genera of Thymelaeaceae was illustrated (Figs. 1–8). In *Lachnaea eriocephala* (Figs. 1–2) the trihedral subunits had emarginate basal sides and the surfaces of the lateral sides were striate, with one single central spinule. In *Struthiola ciliata* and *Gnidia capitata* (Figs. 3–4) the subunits had straight basal sides, but in *Gnidia capitata* some subunits were tightly packed, possibly fused, while others were separated revealing mural rings. In *Dais cotinifolia* (Fig. 5) the subunits had emarginate margins, spinules were present at the bases of the subunits and fusion of the subunits into groups, with exposure of the mural rings, was clearly visible. In *Englerodaphne* (Fig. 6) most of the subunits were fused forming half-circles or an array of patterns, while fusion was almost complete in *Synaptolepis* (Fig. 7). The pollen of *Passerina paleacea* (Fig. 8) could be regarded as the climax of this continuum of variation, as all the subunits had fused completely to form a continuous secondary reticulum. The pollen wall of some members of *Passerina* still exhibited faint indentations demarcating the subunits (Figs. 8, 15), while the pollen wall was devoid of striation in many others.

### Taxonomic position of the Thymelaeaceae

The Thymelaeaceae comprises about 500 species in 50 genera (Airy Shaw 1973, Cronquist 1981). A survey of the literature of the Thymelaeaceae reveals the confusion that exists with regard to the identity of the family and its taxonomical and phylogenetic relationships. Domke (1934) envisages a genetic relationship between the Thymelaeaceae, Malvaceae and Euphorbiaceae. Heinig (1951) discusses the relationships of the Thymelaeaceae with the Myrtales, Saxifragaceae, Lythraceae, Gonystylaceae and Malvales and comes to the conclusion that a polyphyletic origin of the Thymelaeaceae could be sought in both the Flacourtiaceae and Tiliaceae. Cronquist (1968) considers the Thymelaeaceae as completely at home in the Myrtales on account of the more primitive genera having an obviously compound pistil and he is convinced that the ancestry of the Myrtales lies in the Rosales. Takhtajan (1969) considers the Thymelaeales to have a common origin with the Euphorbiales and Malvales, all arising from a Flacourtiaceae-type ancestor. According to Archangelsky (1971) both the Euphorbiales and the Thymelaeales belong to the subclass Dilleniidae and originated from ancestral lines of the Dilleniales→Violales→Malvales. Hutchinson (1973) considers the phylogeny of the family as Magnoliales→Dilleniales→Bixales→Gonystylaceae→Thymelaeaceae.

Dahlgren (1975*a*, 1975*b*) places the Thymelaeales between the Euphorbiales and the Myrtales. In his treatment of the angiosperms (Dahlgren, 1980), the dicotyledons are divided into 24 superorders. Within the superorder Malviflorae a close affinity between the Malvales and Euphorbiales, as well as their affinity to the Urticales and the Thymelaeales, is recognised. In the classification diagram the relative positions approximated to the mutual similarity of attributes do not reflect phylogenetical affinity between the Malviflorae and Myrtiflorae. The inclusion of the Thymelaeaceae in the Myrtales is overviewed by Dahlgren & Thorne (1984). Most members of the family possess Myrtalean characters of which some of the most important are intraxylary phloem, tough fibres permeating the phloem, 4-merous, perigynous flowers and an obturator descending from the base of the stylar canal to the ovules. On the other hand, the embryological and chemical evidence strongly argues against Myrtalean affinities. The very distinctive pollen of the Thymelaeaceae (which is also illustrated by this paper) is totally removed from that of any Myrtales and similar to that of most Euphorbiaceae. Mere sharing of the crotonoid pattern between taxa should never be interpreted as certain evidence of close evolutionary relationship. Note, however, that despite its very distinct appearance, the croton pattern has undoubtedly evolved convergently in many unrelated angiosperms (e.g. *Aragoa*-pollen (Scrophulariaceae), Nilsson & Hong1993) and is also present from an early stage in the fossil record (Muller 1979). Gertrud Dahlgren's (1989) diagram, illustrating a modified classification of the dicotyledons, sensu Dahlgren (1980), still maintains the close affinity between the Malvales, Euphorbiales, Urticales and Thymelaeales, included in the superorder Malvanae. In the latest revision of the classification of the Class Angiospermae, Thorne (1992) accepts the superorder Malvanae, but includes the Thymelaeaceae in the order Euphorbiales.

In spite of the views of Dahlgren & Thorne (1984), Cronquist (1988) argues that it is unnecessary to place the Thymelaeaceae in any other order than the Myrtales. He suggests the recognition of an order Thymelaeales, providing for this one family, but is of the opinion that this order would still stand alongside the Myrtales.

### Relationships of taxa within the Thymelaeaceae

Archangelsky (1966) reviewed the pollen of 52 genera of the Thymelaeaceae and two of the Gonystylaceae. The reticulate pollen of *Octolepis* Oliv. is considered as the most primitive and crotonoid ("stellate" sensu Archangelsky) sculpturing is one of the complex variables of reticulate sculpturing. Typical crotonoid pollen are found in the genera *Dirca* L., *Ovidia* Meisn. and *Dicranolepis* Planch., while in the genera *Pimelia* Banks *et* Soland., *Gnidia* L., *Passerina* L., *Lethedon* Spreng., *Solmsia* Baill., *Daphnimorpha* Nakai, and Gonystylaceae the sculpture characteristic of the exine deviates from crotonoid to cryptocrotonoid ("cryptostellate"). Although Domke (1934) places the genera *Gonystylus* Teijsm. & Binn. and *Amyxa* Tiegh. in a subfamily Gonystyloideae of the Thymelaeaceae, the unique exine of the pollen of Gonystylaceae is so different that Archangelsky (1971) and Nowicke et al. (1985) distinguish the Gonystylaceae as a separate family. Archangelsky (1971) considers the Passerininae as a subtype, distinct from the pollen subgroups Dicranolepideae, Phalerieae, Daphneae, Thymelaeinae and Gnidiinae, with the pollen of *Thymelaea* as the common ancestral type.

Although the pollen of the genus *Passerina* is considered as "cryptostellate" (Archangelsky 1966, 1971), our study shows that the exine differs totally from that of the unique Gonystylaceae as well as the Thymelaeinae and Gnidiinae. The present study shows the continuum of variation from the separate triangular subunits on a basal reticulum (interconnecting tectal rods) of the croton pattern (Nowicke et al.1985) to the plain reticulum in *Passerina*. The reticulum in *Passerina* can be regarded as secondary, and derived through fusion of the supratectal trihedral subunits of an ancestral type depicting the typical croton pattern, accompanied by a loss of the basal reticulum.

### Phylogeny

Most southern African genera of the Thymelaeaceae possess pollen with the crotonoid pattern which is known to have emerged early in the fossil record (Muller 1979). In the context of land plants, wind dispersal is widespread and probably a primitive condition. Wind pollination, however, is considered secondary and the initial shift to anemopily is thought to have occurred in the dry to seasonally dry tropics during the mid-Cretaceous (Crane 1986). Thanikaimoni (1986) discusses the phylogenetic value of apertural forms and concludes that the periporate pollen of *Buxus* L. can be derived from a tricolpate type by reduction of apertural area. The columellate wall in *Passerina* consists of an outer tectum and an infrastructure of cylindrical columns resting on a basal layer. This wall type is highly organised and occurs primarily in the angiosperms. Although the columellate pattern occurs in grains attributed to the earliest angiosperms, it is also present in a number of pre-Cretaceous pollen types, one from as early as the upper Carboniferous (Taylor & Zavada 1986). These authors suggest that plants with alveolar pollen walls might be more probable candidates as angiosperm ancestors than those with the homogeneous, unorganised pollen walls. In relation to the other southern African genera of the Thymelaeaceae, the pantoporate pollen grain of *Passerina* with its uniquely derived secondary reticulum can be regarded as phylogenetically advanced.

## CONCLUSION

We agree with the ordinal placement of the Thymelaeaceae proposed by Dahlgren (1980). Concerning the classification within the Thymelaeaceae, the system of Domke (1934) has become outdated as Archangelsky (1971: Fig. 10) instated the new subfamilies Octolepidoideae, Microsemmatoideae and Synandrodaphnoideae as well as the family Gonystylaceae. Melchior (1964) has already stated that the tribe Gnidieae should be Thymelaeeae. However, if it is taken into consideration that the genus *Passerina* is anemophilous, lacks petals and petaloid scales, possesses a perigynous flower, extrorse anthers and pantoporate pollen with a secondary reticulum derived through fusion of sexine elements (and loss of typical crotonoid basal mural rings), it seems obvious that *Passerina* is phylogenetically more advanced than other genera in the subfamily Thymelaeoideae. Pollen of *Passerina* also represents the end result of an evolutionary specialization towards anemophily. Although it is recognised that the croton pattern (e.g. most Thymelaeaceae) is derived from the reticulate pattern (*Octolepis*), one must guard against equating all reticulate sculpturing as primitive, as indicated by the secondary reticulate pattern of *Passerina*.

As Archangelsky (1971), on the basis of pollen morphology, suggested *Thymelaea* as the common ancestor of the Aquilariidae and the subfamily Thymelaeoideae, it seems appropriate not to form a new subfamily, but to raise the taxonomical position of the subtribe Passerininae (under the tribe Gnidieae) to the tribe Passerineae.

### Tribus Passerineae (Domke) Bredenkamp & Van Wyk, stat. nov.

Subtribus Passerininae Domke in Untersuchungen über die systematische und geographische Gliederung der Thymalaeaceen: 108, 1934.

At the species level in *Passerina*, however, it is clear that although there are differences in the number of pores, the width of the annuli and the number of spinules, there does not seem to be clear discontinuity between species. An artificial classification at this level was therefore abandoned.

## ACKNOWLEDGEMENTS

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## SPECIMENS INVESTIGATED

Details of specimens examined. Fresh material collected for the TEM study of the wall structure is marked with an asterisk (*). All specimens are housed at PRE.

*Cryptadenia uniflora* Meisn. Western Cape; Letty 194
*Dais cotinifolia* L. Mpumalanga; Germishuizen 5762
*Englerodaphne pilosa* Burtt Davy. Western Cape; Geldenhuys 1282
*Gnidia capitata* L.f. Gauteng; Van Rooyen 2178
*Lachnaea eriocephala* L. Western Cape; Richardson 15
*Passerina burchellii* Thoday. Western Cape; Bolus 684
*P. comosa* C.H.Wr. Western Cape; Andreae 1288
*P. drakensbergensis* Hilliard & B.L.Burtt. KwaZulu-Natal; Edwards 974
*P. ericoides* L. Western Cape; Taylor 4042
**P. ericoides*. Western Cape; Bredenkamp 962
*P. falcifolia* C.H.Wr. Western Cape; Tysson 1449
*P. filiformis* L. KwaZulu-Natal; Killick 238
*P. galpinii* C.H.Wr. Western Cape; Burgers 2259
**P. galpinii*. Western Cape; Bredenkamp 932
*P. glomerata* Thunb. Western Cape; Taylor 6145
**P. glomerata*. Western Cape; Bredenkamp 973
*P. montana* Thoday. Mpumalanga; Giess 13136
*P. obtusifolia*. Thoday. Western Cape; Oliver 3679
**P. obtusifolia*. Western Cape; Bredenkamp 904
*P. paleacea* Wikstr. Western Cape; Pillans 783
**P. paleacea*. Western Cape; Bredenkamp 961.
*P. paludosa* Thoday. Western Cape; Thoday 100
*P. pendula* Eckl. & Zeyh. Eastern Cape; Fourcade 3043
**P. pendula*. Eastern Cape; Bredenkamp 908
*P. rigida* Wikstr. KwaZulu—Natal; Ward 7211
*P. rubra* Thoday. Eastern Cape; Acocks 22365
*P. rubra*. Western Cape; Bredenkamp 905
*P. vulgaris* Thoday. Western Cape; R.A. Dyer 180
*P. vulgaris. Eastern Cape; Bredenkamp 924
*Peddiea africana* Harv. Western Cape; Haasbroek 1908
*Struthiola ciliata* (L.) Lam. Western Cape; Bredenkamp 997
*Synaptolepis kirkii* Oliv. KwaZulu-Natal; Ward 8473

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## 4.2 Mucilaginous epidermal cell walls

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# Structure of mucilaginous epidermal cell walls in *Passerina* (Thymelaeaceae)

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Leaves of *Passerina* are inversely ericoid. Adaxial epidermal cells are relatively small; abaxial ones are large and tanniniferous. Mucilaginous epidermal cells are usually present in many Thymelaeaceae, including *Passerina*, mainly in the abaxial epidermis. They are unequally divided by a periclinal wall-like septum into two separate compartments: (1) the outer, adjacent to the cuticle, containing mostly tanniniferous substances and (2) the inner, containing mucilage. This type of epidermis has often been incorrectly described as uni-, bi- or multiseriate. Transmission electron microscopy revealed mucilage, characterized by microfibrils, embedded between the innermost wall-like septum and outermost layers of the inner periclinal cell wall. As accumulation of mucilage increases, the innermost (adjacent to the cell contents) layer of the original periclinal cell wall is pressed against the cytoplasm, thus forming a clearly demarcated cellulose periclinal wall which divides the epidermis cell into two compartments, the inner with mucilage and the outer comprising the cell lumen. Existing controversy is critically discussed. Our observations confirm the authenticity of mucilagination in epidermal cell walls.

ADDITIONAL KEY WORDS:—cellulose – gelatinization – hydration – inner periclinal wall – slime – TEM.

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## INTRODUCTION

*Passerina* L. comprises about 17 species, all confined to southern Africa (Thoday, 1924; Bond & Goldblatt, 1984). Members are perennial woody shrublets with ericoid leaves and reduced flowers, adapted to wind pollination. Most of the species are restricted to the Cape Floristic Region. The present paper emanates from a leaf-anatomical survey of the genus, undertaken as part of a monographic study of the group.

An outstanding feature of the leaf epidermis in many members of Thymelaeaceae is the presence of epidermal cells with so-called 'gelatinized' or mucilaginous inner periclinal cell walls. This type of epidermal cell has also been recorded in various other plant families (Solereder, 1908), and is particularly prevalent in taxa from regions with a Mediterranean climate. Following the gelatinization of the inner tangential cell wall, these epidermal cells appear distinctly two-celled, with an inner 'cell' filled with mucilage, and an outer one with a large vacuole, often containing tanniniferous substances. However, the structural interpretation of these cells in the plant-anatomical literature contains many inaccuracies. Hence, although the epidermal structure has been described in many ericoid-leaved members of the Cape and other Mediterranean floras, erroneous structural interpretations are common. For example, Christodoulakis, Tsimbani & Fasseas (1990) interpret the mucilaginous epidermis of *Sarcopoterium spinosum* (L.) Spach (Rosaceae) as "being composed of a flat mucilage-containing outer lumen with very thick outer wall and cuticle, a tannin-containing, mucilage-secreting cell in the middle, with thin walls around it, and a very large innermost lumen with mucilage." According to Gregory & Baas (1989) the tertiary wall has been described as a division wall, but its deposition is not preceded by a true cell and nuclear division. This concept of a multiseriate epidermis, encountered in many papers, is rejected by Gregory & Baas (1989) on the basis that ontogenetic studies are not available.

In spite of reports on the mucilaginous epidermis in leaves of various orders, families and genera by Solereder (1908), Haberlandt (1914), Frey-Wyssling & Mühlethaler (1965), Napp-Zinn (1973) and Frey-Wyssling (1976), Gregory & Baas (1989) doubt the classical interpretation that the inner mucilaginous portion of these cells originates from previously deposited cell wall material which is transformed into mucilage. They maintain that mucilage is deposited by the cytoplasm between the cell wall proper and the plasmalemma. Although this has been described in some taxa, e.g. in epidermal idioblasts of *Hibiscus schizopetalus* (Mast.) Hook.f. (Bakker & Gerritsen, 1992), the interpretation of the mucilaginous epidermis in *Passerina* needed clarification by means of an ontogenetic study. The present paper, based on results from light microscopy (LM) and transmission electron microscopy (TEM), describes the structure of mucilaginous epidermal cells in *Passerina* during maturation.

It also records the common occurrence of mucilaginous epidermal cells in various genera, families and orders and speculates on the ecological value of this adaptation to the Cape Mediterranean climate.

## MATERIAL AND METHODS

Fresh leaf material of 16 species of *Passerina* (Appendix) was collected, 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 (a modified Karnovsky fixative, Karnovsky, 1965). Whenever possible, material from at least five different localities was studied for each species.

### *LM*

LM was used for the study of the general leaf anatomy. The tenth leaf from the growing point of a twig was used for sectioning. 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 in cross section. 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).

### *TEM*

TEM was used for the clarification of the structure of mucilaginous epidermal cell walls observed in the study of the general leaf anatomy. The second, fifth and tenth leaf, from the growing point of *Passerina falcifolia*, *P. paleacea* and *P. ericoides* were used in the TEM study of the wall structure. Leaf segments of ± 1 mm$^2$ were fixed in a 0.1 M phosphate-buffered solution at pH 7.4, containing 2.5% formaldehyde, 0.1% glutaraldehyde and 0.5% caffeine (a modified Karnovsky fixative, Karnovsky, 1965). The material was rinsed in 0.075 M phosphate buffer, pH 7.4–7.5, post-fixed for one hour in 0.25% aqueous $OsO_4$, washed in three changes of water and dehydrated in a graded acetone series. Quetol 651 resin (Van der Merwe & Coetzee, 1992) was used for embedding. Ultrathin sections were contrasted in 4% aqueous uranyl acetate for 10 minutes and rinsed in water three times. The sections were then contrasted with lead citrate (Reynolds, 1963) and rinsed in water. A Phillips 301 TEM was used for examination.

## RESULTS

### *Generalized description of leaf epidermis*

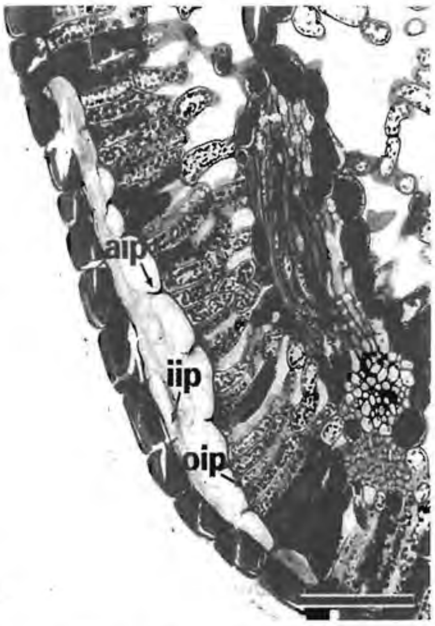
Observations are based on light microscopy of cross sections. LEAVES ericoid, adaxial surface concave, forming a groove which is more or less appressed to the stem; abaxial surface convex. ADAXIAL EPIDERMIS (Fig. 1) uniserial, with a thin cuticle. Epidermal cells relatively small, periclinal diameter (10–)15–25(–35) µm, anticlinal diameter 10–17(–20) µm; cell walls thin; vacuoles large, containing tanniniferous substances. Unicellular hairs and stomata present. MARGIN CELLS larger than adaxial epidermal cells, containing ample amounts of tannin; mucilage scanty. ABAXIAL EPIDERMIS uniserial with cuticle well developed, (10–)20–30(–60) µm thick, smooth or papillate. Trichomes absent, except for unicellular hairs in *P. comosa*. Stomata absent. Epidermal cells more or less oblong in outline; outer periclinal walls straight or convex, inner periclinal walls straight, convex or bulging towards the mesophyll; periclinal diameter of cells (20–)35–45(–60) µm, anticlinal diameter (20–)50–75(–105) µm. MUCILAGINATED CELL WALLS increase progressively from leaf margin to midrib, affecting mainly inner periclinal but also anticlinal cell walls. Mucilage with a layered appearance (also accounting for the misconcept of a multiseriate epidermis, Figs 4–6), occupying about two-thirds of the epidermal cell and separated from the cytoplasm by the innermost cellulose layer of the inner periclinal cell wall (Figs 1–6). CYTOPLASM compressed by mucilage, remaining as a thin layer appressed to the large, usually tanniniferous vacuole. ANTICLINAL LAYER of inner periclinal cell wall often plicate but gradually straightening and often diminishing as mucilage increases in cell walls, eventually breaking under pressure of accumulating mucilage to form a mucilage-filled cavity between the remains of the epidermal cells and large areas of mesophyll (Figs 1–3).

### *Ontogeny of mucilaginous epidermal cells*

Formation of mucilage in epidermal cell walls is initiated in the second leaf below the growing point. Initially the inner periclinal cell wall thickens and becomes conspicuously striated (Fig. 7). Mucilage accumulates in the centre of the inner periclinal cell wall, resulting in the innermost (iip) and outermost cellulose layers (oip) of the cell wall being pushed apart. Microfibrils are visible in the mucilage and are orientated in the same direction as cellulose fibres of the inner periclinal cell wall (Figs 8 & 9). Both the inner periclinal and adjacent parts of the anticlinal walls are affected by this increasing mass of mucilage. The inner periclinal cell wall appears to be elastic and stretches to accommodate the increasing volume of

Figures 1–6. Light micrographs (LMs) of leaves of *Passerina* species in cross section, illustrating mucilagination of inner periclinal cell walls of epidermal cells. ab = abaxial epidermis, ad = adaxial epidermis, aw = anticlinal cell wall, c = cuticle, cy = cytoplasm, e = epidermal cell, ip = inner periclinal cell wall, aip = anticlinal layer of inner periclinal cell wall, iip = innermost layer of inner periclinal cell wall, oip = outer layer of inner periclinal cell wall, m = mucilage, mf = microfibrils, op = outer periclinal cell wall, p = palisade parenchyma, v = vacuole. Scale bar = 100 µm except in Fig. 4 where = 10 µm. Fig. 1. *P. falcifolia* (Bredenkamp 917), showing adaxial and abaxial epidermis with mucilage accumulating abaxially. Fig. 2. *P. falcifolia* (Bredenkamp 915), area of mucilage accumulation enlarged, mucilage separated from cytoplasm by innermost cellulose layers of inner periclinal cell walls (iip), rupture of anticlinal layers of inner periclinal cell walls (aip) and outer layers of inner periclinal cell walls (oip) forming a boundary between mucilage and palisade parenchyma. Fig. 3. *P. ericoides* (Bredenkamp 962), showing rupture of anticlinal layers of inner periclinal cell walls (aip) in epidermal cells and amorphous mucilage in mucilage cavity. Fig. 4. *P. ericoides* (Bredenkamp 956), illustrating layered appearance of mucilage. Fig. 5. *P. paleacea* (Bredenkamp 961), mucilage (m), occupying about two-thirds of epidermal cell. Fig. 6. *P. paleacea* (Bredenkamp 960), mucilaginous epidermal cells enlarged, illustrating striated appearance of mucilage.

1



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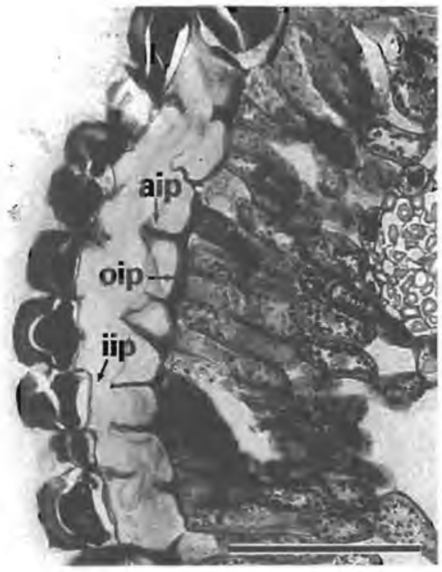

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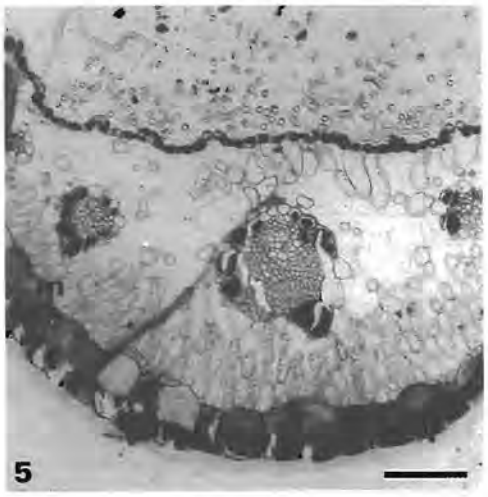

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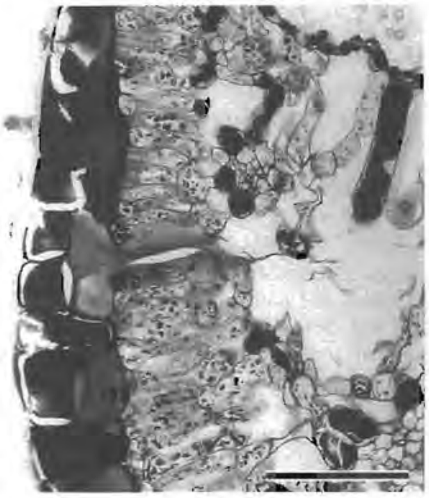

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mucilage (Fig. 10, aip). The original anticlinal wall is pushed outwards and becomes pronouncedly plicate (Fig. 10, aw). However, anticlinal cell walls may also become mucilaginous, as illustrated by the orientation of the microfibrils of the mucilage accumulated between the anticlinal cell wall and the cytoplasm (Fig. 10, mf). Mucilaginated cell walls expand until the innermost cellulose layer of the inner periclinal wall presses almost against the vacuole, separated only by a very thin layer of cytoplasm (Fig. 10, cy).

Both early and intermediate stages of mucilagination are present in the fifth leaf below the growing tip (Figs 11 & 12). At this stage delineation of mucilage seemingly originating from the inner periclinal wall (aip) and that originating from the anticlinal wall (aw) (Fig. 12) is clearly demonstrated by orientation of microfibrils. The appressed cytoplasm and tannin-filled vacuole are wedged in between layers of mucilage (Fig. 12).

Mucilaginated cell walls stabilize towards the tenth leaf below the growing tip (Figs 13–16). Finally, the epidermal cell is characterized by a tannin-filled vacuole occupying most of the outer compartment of the cell and cytoplasm pressed against the vacuole by the surrounding mucilage (Fig. 13). The innermost cellulose layer of the inner periclinal cell wall 'is swollen' due to the increase of mucilage and becomes very conspicuous, superficially creating the impression of a second, mucilage-filled lumen (Figs 13–15). Mucilage, with microfibrils orientated in the same direction as cellulose of the inner periclinal wall, now occupies a large proportion of the inner portion of the cell. Finally, the anticlinal layers of the inner periclinal cell walls may rupture as a result of the pressure of the accumulating mucilage, and a larger intercellular mucilage-filled cavity is formed. At this stage the mucilage is completely hydrated and the identity of the microfibrils is lost (Fig. 16).

## DISCUSSION

### *Climate and the distribution of* Passerina

*Passerina* is confined largely to the Cape Floristic Region, its distribution extending easterly and northerly along the eastern mountains, coastline and escarpment of southern Africa. The climate is for the most part Mediterranean or semi-Mediterranean. In the west it rains in winter, except at high altitudes where moisture from fog and cloud condensation is provided by south-easterly winds in summer.

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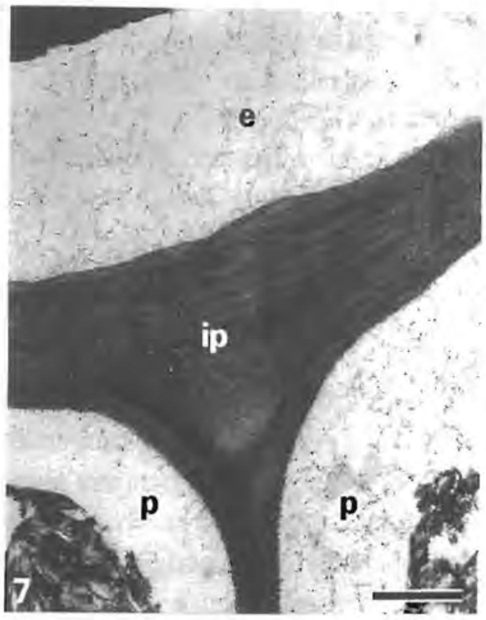
Figures 7–12. Transmission electron micrographs (TEMs) of abaxial epidermal cells in leaves of *P. falcifolia* (Bredenkamp 917) in cross section, showing initiated and progressed mucilagination of inner periclinal and anticlinal epidermal cell walls. Figs 7–10. Representing second leaf and Figs 11 & 12, fifth leaf below growing tip. Scale bar = 1 μm except Fig. 8 where = 5 μm. Fig. 7. Striated inner periclinal cell wall during initiation of mucilagination. Fig. 8. Mucilage accumulated between the innermost and outermost cellulose layers of the inner periclinal cell wall (iip and oip respectively). Fig. 9. Higher magnification of accumulated mucilage in inner periclinal cell wall in Figure 8. Fig. 10. 'Elastic' anticlinal layer of inner periclinal cell wall (aip) and plicate anticlinal cell wall (aw). Fig. 11. Delineation of mucilage originating from inner periclinal wall and that originating from anticlinal wall. Fig. 12. Higher magnification of mucilage in Figure 11, showing orientation of microfibrils correlating with origin from inner periclinal and anticlinal walls.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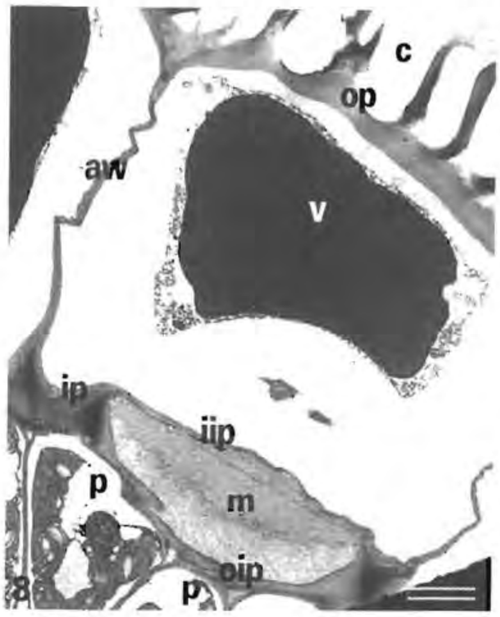
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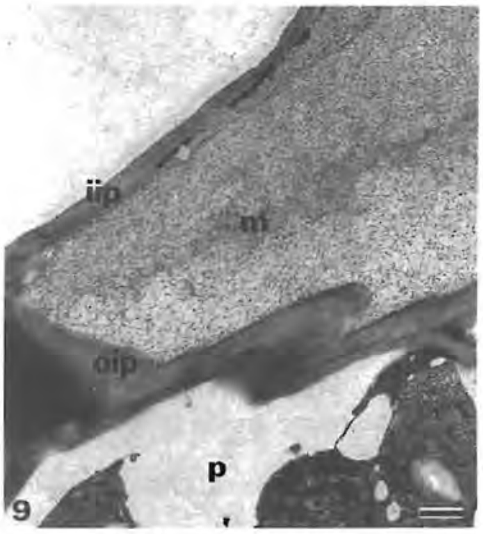
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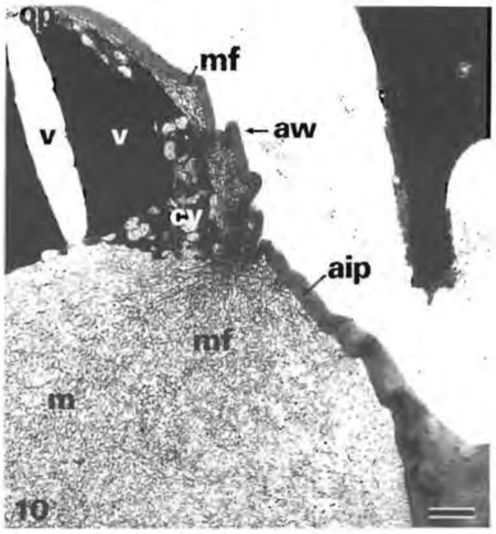
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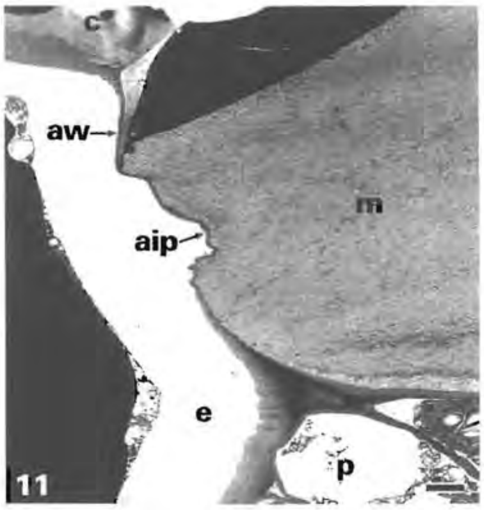
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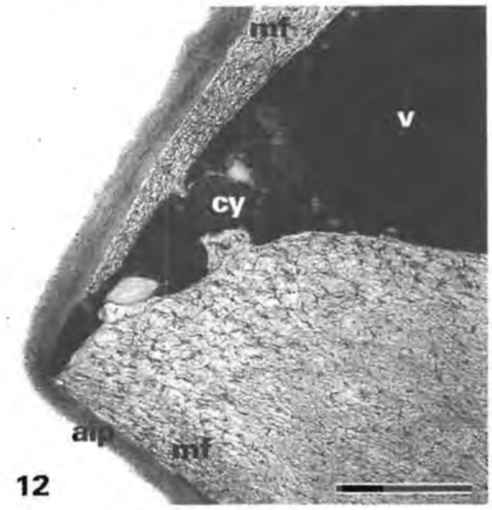
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Along the south coast, winter rainfall is complemented by some summer rain which increases eastwards. The western Karoo and Namaqualand are characterized by winter precipitation and summer drought (Campbell, 1985; Cowling *et al.*, 1995). KwaZulu-Natal and the eastern mountains of southern Africa are predominantly summer-rainfall areas.

### *General morphology of* Passerina

The plants are perennial shrublets, shrubs or small trees. They are resprouters, usually growing in sandy soil on plains, mountains and even on primary sand dunes along the coast, always exposed to wind. Some species are often pioneers along roadsides or in disturbed places. Leaves are decussate, concave or closely involute, ericoid and lined with woolly hairs, the latter apparently an adaptation to the dry windy summers of the Mediterranean or semi-Mediterranean climate.

### *Mucilaginous cell walls in epidermal cells*

#### *Historical review*

Solereder (1908) documented the 'gelatinization' of the epidermis of the leaf in various orders, families and genera of dicotyledons, including the Thymelaeaceae. Based on the origin of mucilage, he distinguished between two types of mucilaginous epidermal cells, namely those with mucilage derived from the gelatinization of portions of the cell wall, and special mucilage-secreting cells. Haberlandt (1914) described the 'mucilaginous inner walls' commonly present in certain Sapindaceae and Rutaceae, and Napp-Zinn (1973) used the term 'Verschleimung (Gelifikation)' to describe this transformation of the cell wall in reporting on the presence of the phenomenon in many taxa.

More recently Baas & Gregory (1985) and Gregory & Baas (1989) concluded that, in most cases, mucilage production in cells results from the Golgi apparatus producing numerous vesicles filled with polysaccharides which are deposited between the plasmalemma and the cell wall by reverse pinocytosis. These authors refuted the following interpretations: assimilating function of the cell wall; mucilagination or gelification; previously deposited wall material transformed into mucilage; deposition of cellulose layers on top of unilateral slime deposits in epidermal cells; a tertiary division wall not preceded by true nuclear and cell division; multiseriate

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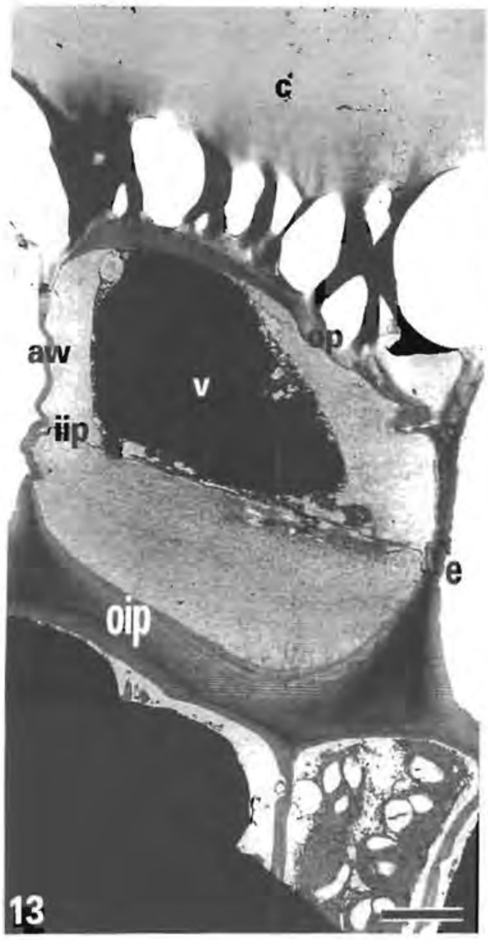
Figures 13–16. TEMs of abaxial epidermal cells in leaves of *P. falcifolia* (Bredenkamp 917) in cross section, showing progressed mucilagination of inner periclinal and anticlinal cell walls. Representing tenth leaf below growing tip. Scale bar = 1 µm except in Figures 13 and 16 where = 5 µm. Figs 13–15. Innermost cellulose layer of the inner periclinal cell wall (iip) clearly demarcated. Fig. 14. Larger magnification of right side of epidermal cell in Fig. 13, showing innermost layer of inner periclinal cell wall (iip) separated from outer layer of inner periclinal cell wall (oip) by mucilage containing microfibrils (mf). Fig. 15. Larger magnification of left side of epidermal cell in Figure 13, showing innermost layer of inner periclinal cell wall (iip), separating mucilage originating from inner periclinal wall and that originating from anticlinal wall (aw). Fig. 16. Ultimate rupture of anticlinal layer of inner periclinal cell wall (aip), initiating formation of mucilaginous cavity.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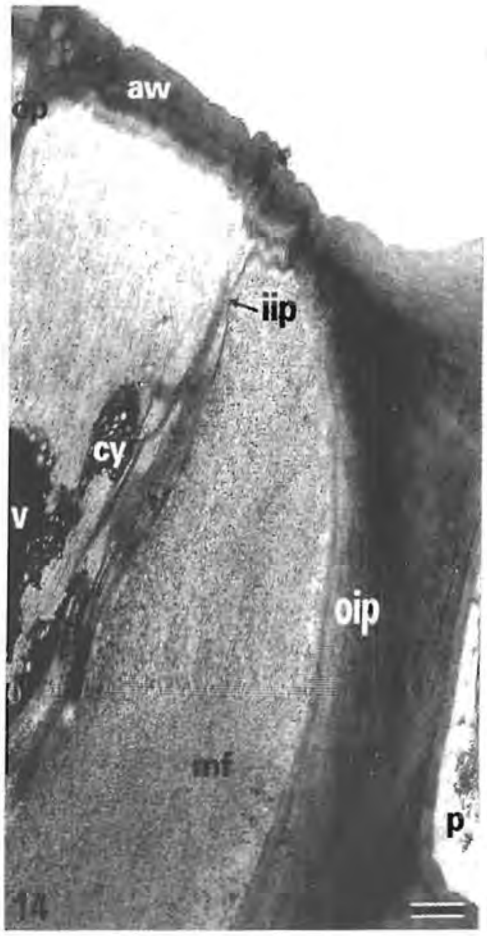
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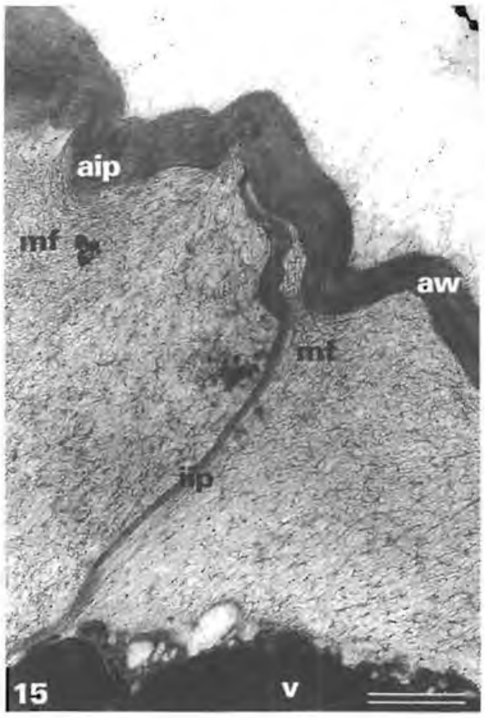
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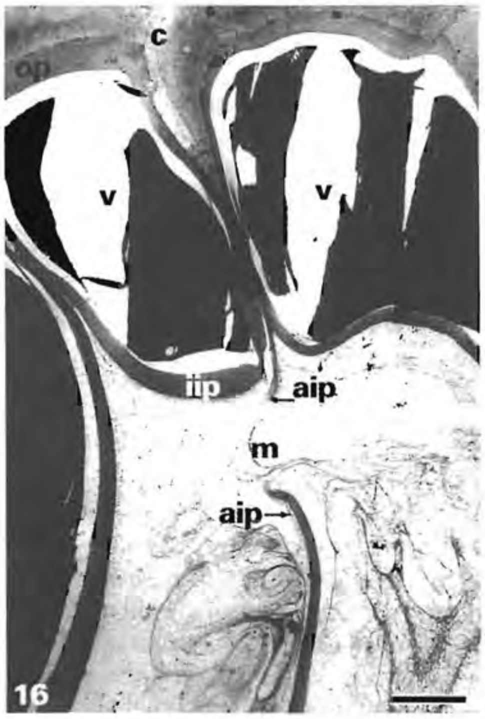
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mucilaginous epidermis. Trachtenberg & Fahn (1981) supported the secretory function of the Golgi apparatus in mucilage production, although Fahn (1988) added that mucilage may accumulate either inside the cell wall or in the space between it and the retreating protoplast.

Bakker & Gerritsen (1992) discussed the structure of mucilage cells in the shoot apex and mesophyll as well as the leaf epidermis (single cells or idioblasts) of *Hibiscus schizopetalus*. However, mucilage secretion in these cells should not be confused with mucilagination of epidermal cell walls as indicated for *Passerina* in the present study. Their study reported the involvement of the Golgi apparatus, the rough endoplasmic reticulum as well as the presence of plastids with starch granules in the deposition of mucilage between the plasmalemma and the cell wall. No 'tertiary wall' is formed.

Although many authors agree on the Golgi apparatus as the source of mucilage, Kristen, Liebezeit & Biedermann (1982) found a direct release of polysaccharides and proteins by the tubular components of the endoplasmic reticulum in *Isoetes lacustris* L. Likewise, Trachtenberg (1984) studying mucilage secretion in *Aloe arborescens* Mill., found polysaccharides and structural changes mainly in the plastids of young leaves. In mature leaves secretory evidence appears to be centred in the plasma membrane.

In addition to the above mentioned controversy on the origin of mucilage, many authors have misinterpreted mucilaginous epidermal cells. Yakovleva (1988), reporting on the ultrastructure of slime cells of the leaf epidermis in 35 dicotyledonous plant species, described three types of slime cells based on the location of the slime in relation to the cell wall. In the first type the slime remains within the cell lumen, separated from the cytoplasm by the cell wall. The second type is characterized by the release of slime outside the cell wall, and the third type by the presence of two layers of slime. Yakovleva's erroneous interpretation of the 'first type' (*sic*) is frequent in the literature. What Yakovleva (1988) interpreted as a slime-filled lumen is in reality the central gelatinized part of the inner periclinal cell wall. According to our view, all three types of slime cells fit perfectly into the concept of mucilaginous epidermal cell walls. The interpretation by Christodoulakis *et al.* (1990) on the mucilaginous epidermal cells of *Sarcopoterium spinosum* (Rosaceae), closely agrees with that of Yakovleva (1988). Similar erroneous interpretations have been made by Carlquist (1990) who interpreted the mucilaginous epidermal cell walls in leaves of *Geissoloma* Lindl. ex Kunth as a multiseriate epidermis. Lersten & Curtis (1992) also interpreted epidermal cells with mucilaginous inner periclinal cell walls in certain species of *Polygonum* L. as a biseriate epidermis. In their paper on anatomical adaptations in the leaves of selected fynbos species, Van der Merwe, Van der Walt & Marais (1994) also incorrectly described epidermises with mucilaginous cell walls as multiseriate.

### *Process of mucilagination of epidermal cell walls in* Passerina

Mucilaginous epidermal cells in *Passerina* are the result of cell wall transformation, thus agreeing with the classic interpretation of cell wall 'gelatinization'. Early stages of mucilagination of the periclinal as well as anticlinal cell walls are reflected by conspicuous striations of the affected walls (Fig. 7). The cell walls become progressively more mucilaginous as hydration of the matrix progresses (Frey-Wyssling, 1976). Microfibrils in this cellulose mucilage are orientated in the same direction as the original cellulose wall. As mucilagination continues, faintly marked layer boundaries become discernible. The undulated anticlinal cell wall, as well as the anticlinal layers of the inner periclinal cell wall, stretches to accommodate the increasing volume of

TABLE 1. Comparison of the process of mucilagination in the cell walls of *Passerina* with mucilage formation in mucilaginous cells and idioblasts

| Mucilagination of cell walls | Mucilage formation in cells and idioblasts |
|---|---|
| 1. Mostly in epidermal cells of leaves and seed coats. In *Passerina*, most epidermal cells of the abaxial leaf epidermis are affected. | 1. In the cortex and mesophyll of stems and leaves, more rarely in the epidermis. |
| 2. Periclinal and anticlinal epidermal cell walls mucilaginous. Inner periclinal wall most active and forming most of the mucilage. | 2. Cell walls do not become mucilaginous. |
| 3. Polyuronans of cell wall matrix hydrate and swell to a soluble colloidal mucilage. | 3. Mucilage secreted mainly by Golgi apparatus and endoplasmic reticulum, accumulating between cell membrane and cell wall |
| 4. Cellulose mucilage (Frey-Wyssling, 1976) interspersed by ultrastructural microfibrils. | 4. Pectin mucilage (Frey-Wyssling, 1976) without ultrastructural microfibrils. |
| 5. Innermost layer of inner periclinal cell wall (erroneous 'tertiary wall') separates mucilage from cytoplasm; appressed to vacuole. | 5. No cell wall or part of cell wall (erroneous 'tertiary wall') present. Mucilage accumulates between plasmalemma and original cell wall. |

mucilage. The cytoplasm remains clearly delineated from the mucilage by the innermost layer of the inner periclinal cell wall and is appressed to the vacuole containing tanniniferous substances. With further hydration, the layered boundaries of the mucilage become less obvious, the microfibrils disappear and an amorphous jelly remains. At this stage the anticlinal layers of the inner periclinal cell walls between adjacent epidermal cells often disintegrate, causing a cavity bordered by the innermost layers of the inner periclinal cell walls and the original inner periclinal cell walls of a group of epidermal cells (Figs 1–3). This cavity, filled with an amorphous mucilage, forms a lining for the adjacent palisade parenchyma cells.

Mucilagination as described for *Passerina* is a genetically induced attribute of the cell wall and should not be confused with the process of mucilage formation in mucilage idioblasts, mucilage cells and cells bordering mucilage cavities. In these latter cases the mucilage is secreted mainly by the Golgi apparatus and the endoplasmic reticulum and accumulates between the cell membrane and the cell wall. The importance of mucilage formation by the Golgi apparatus should not be underestimated as there are many diverse and important mucilage producing cells present in plants. The two processes are compared in Table 1.

### *Chemical composition of epidermal cell walls*

For the interpretation of cell wall architecture we mainly follow Brett & Waldron (1996). The earliest formed layer of the cell wall is the middle lamella, the next layer deposited by daughter cells is the primary cell wall, which continues to be deposited while the cell is growing in surface area. When cell differentiation takes place, a further secondary wall is laid down. All the wall layers consist of two phases: a microfibrillar phase and a matrix phase. Components of the matrix phase include pectins as well as hemicelluloses. The microfibrillar phase is distinguishable from the matrix phase by its high degree of crystalinity and its relatively homogeneous chemical composition. It is composed of extremely long thin microfibrils consisting of cellulose molecules aligned parallel to the long axis of the microfibril.

Matrix polysaccharides are formed in the endoplasmic reticulum and Golgi apparatus (Ray, Eisinger & Robinson, 1976; Brett & Waldron, 1996), while cellulose is formed by enzymes in the plasmamembrane (Brett & Waldron, 1996). Wall hemicelluloses are characterized mostly by polyuronans. These substances have a considerable hydration capacity. In contact with water they swell to a soluble colloidal gel with a very high water content and are consequently responsible for the formation of mucilage in cell walls (Frey-Wyssling, 1976).

Classical histologists distinguish between cellulose- and pectin-slimes (Frey-Wyssling, 1976). On a chemical basis this classification seems questionable, but ultrastructurally cellulose-slimes appear to be reinforced by fibrils which are absent in pectin-slimes. Ultrastructural fibres are conspicuous in the mucilaginous cell walls of *Passerina* (Figs 8–15), thus agreeing with the concept of a 'cellulose slime'.

According to Frey-Wyssling (1976) cellulose-slimes comprise cell walls with a matrix swollen to such an extent that their ultrastructural cellulose fibrils become separated from each other. The fibrils can slide along one another, with loss of the original elasticity of the cell wall. In spite of fundamental change in mechanical properties, a gel (mucilage) reinforced by fibrils is still present. This is a rehydration process only, no mucilage is added from the cytoplasm. Frey-Wyssling (1976) reasoned that although cellulase is available in higher plants, it is not used for recycling the glucose components of cellulose. The process of senescence should therefore not be confused with mucilagination.

### *Possible functions of mucilage*

During this century many authors have speculated on the functions of mucilage in plants. Solereder (1908) suggested that gelatinization of the epidermis of the leaf serves for the storage of water. For Haberlandt (1914) the greatly thickened mucilaginous inner walls of epidermal cells probably represent a water storing device, a function which in the typical epidermis would be assigned to the cell sap of the vacuole. In a review of speculation on functions of mucilage cells in vegetative organs, Gregory & Baas (1989) concluded that no ecological preference can be deduced because of a lack of data on habitat and life form, and they emphasized the need for experimental data.

Mucilaginous epidermal cell walls are particularly common in plants from regions with a Mediterranean climate (Van der Merwe *et al.*, 1994). In the seasonally dimorphic subshrub *Sarcopoterium spinosum*, Christodoulakis *et al.* (1990) describe a 'large mucilage lumen' in each of the affected epidermal cells. Although we disagree with their interpretation of the mucilaginous epidermis, the analogy of the epidermal structure between *S. spinosum* and *Passerina* is striking, especially as both are adapted to Mediterranean conditions. They speculate that the 'mucilage lumen' has a similar role to that of the hydatenchyma of plants from arid or salty areas. Water is absorbed during the relatively humid season of spring and conserved for the vital activities of the leaves during the long arid summer. Mucilage may also act as a light density filter protecting the palisade tissue from excessive radiation.

#### *Phenolics in epidermal tissue*

Phenolics in some plants from the Cape Floristic Region were studied by Glyphis & Puttick (1988). They concluded that mean seasonal values for all assays increase from lowest concentrations in winter to highest concentrations in autumn. Total phenols for *Passerina vulgaris* range from 5.2% of dry weight in leaf material in winter to 9.8% in autumn. This increase in phenols from winter to autumn correlates well with the dry warm summers of the Mediterranean climate of the Cape. Ormrod, Landry & Conklin (1995), working on *Arabidopsis thaliana* (L.) Heynh., showed that the presence of UV-absorptive substances in the epidermal cells of leaves protects mesophyll tissue from the harmful effects of UV-B radiation. Hence it is speculated that in *Passerina* the large quantities of phenols in the vacuoles of the epidermal cells (Figs 1–16) may well be a response to UV-B radiation which is high during the dry warm summers of the Cape (Musil & Bhagwandin, 1992).

### *Speculations on functions of mucilaginous epidermis in* Passerina

A four-fold mechanism for the protection of the mesophyll tissue in *Passerina*, a response to the Mediterranean climate of the Cape, is proposed. The hydrophobic cuticle protects the leaves against desiccation. The convex outer periclinal epidermal cell wall focuses light rays onto the mesophyll. Large vacuoles filled with phenols and the mucilage formed by the cellulose-slimes (inner periclinal walls) protect the mesophyll from UV-B radiation. The mucilaginous inner periclinal wall forms excessive quantities of mucilage, resulting in a gelatinous layer or 'slime cushion' with the rupture of adjacent anticlinal layers of inner epidermal periclinal cell walls. A primary function of this mucilage is probably to serve as a regulator of hydration within the leaf, protecting the leaf against water loss at certain times and also to serve as a water-accumulating environment for the development and function of the leaf in times of drought.

### *Ecology*

In *Passerina*, formation of the hydrophilic mucilaginous epidermis is apparently genetically determined and it is, to a greater or lesser extent, present in all species. The modification of the abaxial epidermis, whether strongly mucilaginous or mostly tanniniferous with a few mucilaginous cells, may depend on the humidity of the environment. We suggest that the hydrophilic mucilaginous epidermis allows the accumulation of water, when available, for later use by the plant. This may account for the observation that in *Passerina* increased mucilagination occurs in species of which the plants grow at the sea shore (*P. ericoides*, *P. paleacea*), in high rainfall areas (*P. filiformis*, *P. galpinii*, *P. pendula* and *P. rubra*), on mountain slopes (*P. falcifolia*) and at high altitudes on the Drakensberg Mountains (*P. drakensbergensis*). On the other hand, in species occurring in the arid western Karoo and Namaqualand (*P. glomerata* and *P. comosa*), the abaxial epidermis has cells with large vacuoles almost completely filled with tannin and few cells containing mucilage.

## *Systematic value*

In *Passerina* mucilaginous epidermal cell walls cannot be used as a taxonomic character at species level as the character is present to varying degrees in all species, irrespective of their environment. At the family level, mucilaginous cell walls are regarded as common in the Thymelaeaceae (Solereder, 1908; Metcalfe & Chalk, 1979). It is therefore concluded that mucilagination, as a taxonomic character, is useful at the family level only. In Thymelaeaceae mucilaginous epidermal cell walls have already been reported in species of the genera *Arthrosolen* C.A. Mey., *Chymococca* Meisn., *Cryptadenia* Meisn., *Daphne* L., *Diarthron* Turcz., *Dicranolepis* Planch., *Edgeworthia* Meisn., *Gnidia* L., *Lachnaea* L., *Lagetta* Juss., *Lasiadenia* Benth., *Lasiosiphon* Fresen., *Linodendron* Griseb., *Linostoma* Endl., *Lophostoma* Meisn., *Ovidia* Meisn., *Passerina* L., *Peddiea* Harv., *Phaleria* Jack, *Pimelea* Gaertn., *Struthiola* L., *Synaptolepis* Oliv., *Thymelaea* Endl. and *Wikstroemia* Endl. (Solereder, 1908; Beyers, 1992).

## CONCLUSIONS

Although mucilagination (also referred to as 'gelatinization') of cell walls has been reported by many authors, up to now it has been grossly confused with the process of mucilage formation in specialized mucilage-secreting cells. Moreover, epidermal cells with mucilaginous inner tangential walls have frequently been interpreted erroneously as a biserial epidermis. Our study has shown that the periclinal as well as anticlinal walls of epidermal cells in *Passerina* are conspicuously mucilaginous, positively confirming the authenticity of mucilaginous cell walls, especially in epidermal tissue. The development of mucilagination of epidermal cell walls is probably an advanced state, especially, in *Passerina* where this phenomenon is considered an adaptation to survive the dry warm summers typical of the Mediterranean climate of the Cape Floristic Region. The character is present in all species of *Passerina*, irrespective of their environment. Mucilaginous epidermal cell walls are also well known in other families and genera in the Cape Floristic Region and in the Mediterranean flora.

## ACKNOWLEDGEMENTS

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## APPENDIX: SPECIMENS EXAMINED AND VOUCHER SPECIMENS CITED

Fresh material collected for the TEM study of the wall structure is marked with an asterisk (*). All specimens are housed at PRE.

*Passerina burchellii* Thoday, *Bolus* 684, Baviaanskloof, Genadendal, Western Cape.

*P. comosa* C.H.Wright, *Andreae 1288*, Seweweekspoort, Western Cape.

*P. comosa* C.H. Wright, ***Bredenkamp 1034***, Seweweekspoort, Western Cape.

*P. drakensbergensis* Hilliard & B.L.Burtt, ***Edwards 974***, Royal Natal National Park, KwaZulu-Natal.

*P. drakensbergensis* Hilliard & B.L. Burtt, *Bredenkamp 1018*, Ndedema Gorge, Cathedral Peak Forest Reserve, KwaZulu-Natal.

*P. drakensbergensis* Hilliard & B.L.Burtt, *Bredenkamp 1019*, Ndedema Gorge, Cathedral Peak Forest Reserve, KwaZulu-Natal.

*P. drakensbergensis* Hilliard & B.L.Burtt, *Bredenkamp 1020*, Ndedema Gorge, Cathedral Peak Forest Reserve, KwaZulu-Natal.
*P. ericoides* L., *Taylor 4042*, Pearly Beach, Western Cape.
**P. ericoides* L., *Bredenkamp 956*, Milnerton, Cape Town, Western Cape.
**P. ericoides* L., *Bredenkamp 962*, Cape Maclear, Cape Town, Western Cape.
*P. falcifolia* C.H. Wright, *Tysson 1449*, Knysna, Western Cape.
**P. falcifolia* C.H. Wright, *Bredenkamp 915*, Tsitsikamma, Western Cape.
**P. falcifolia* C.H. Wright, *Bredenkamp 917*, Gouna, Western Cape.
*P. filiformis* L., *Killick 238*, Table Mountain, Pietermaritzburg, KwaZulu-Natal.
*P. filiformis* L., *Bredenkamp 1016*, Oribi Gorge, KwaZulu-Natal.
*P. filiformis* L., *Bredenkamp 896*, Kiwane, Eastern Cape.
*P. filiformis* L., *Bredenkamp 1036*, Steenbras River Mouth, Western Cape.
*P. filiformis* L., *Van Wyk & Bredenkamp 1*, Umtamvuna River Bridge, KwaZulu-Natal.
*P. galpinii* C.H. Wright, *Galpin 4491*, Melkhoutfontein, Western Cape.
*P. galpinii* C.H. Wright, *Bredenkamp 923*, Mossel Bay, Western Cape.
*P. galpinii* C.H. Wright, *Bredenkamp 932*, Riethuiskraal, Western Cape.
*P. galpinii* C.H. Wright, *Bredenkamp 933*, Still Bay, Western Cape.
*P. galpinii* C.H. Wright, *Bredenkamp 946*, De Hoop Nature Reserve, Western Cape.
*P. glomerata* Thunb., *Bredenkamp 973*, Tulbagh, Western Cape.
*P. glomerata* Thunb., *Bredenkamp 977*, Groenfontein, Western Cape.
*P. glomerata* Thunb., *Bredenkamp 984*, Citrusdal, Western Cape.
*P. glomerata* Thunb., *Bredenkamp 994*, Cedarberg Mountains, Western Cape.
*P. glomerata* Thunb., *Bredenkamp 1002*, Cedarberg Mountains, Western Cape.
*P. montana* Thoday, *W. Gies 13136*, Auas Mountains, Namibia.
*P. montana* Thoday, *Bredenkamp 1028*, Marikele Nature Reserve, Northern Province.
*P. montana* Thoday, *Bredenkamp 889*, Golden Gate, National Park, Free State.
*P. montana* Thoday, *Bredenkamp 890*, Golden Gate, National Park, Free State.
*P. montana* Thoday, *Bredenkamp 893*, Ladybrand, Free State.
*P. sp. nov.*, *Bredenkamp 1044*, Waboomberg, Ceres, Western Cape.
*P. obtusifolia* Thoday, *Bredenkamp 919*, Perdepoort, Oudtshoorn, Western Cape.
*P. obtusifolia* Thoday, *Bredenkamp 929*, Rooiberg, Western Cape.
*P. obtusifolia* Thoday, *Bredenkamp 967*, Jonaskop, Western Cape.
*P. obtusifolia* Thoday, *Bredenkamp 971*, Karoo National Botanical Garden, Western Cape.
*P. obtusifolia* Thoday, *Bredenkamp 1033*, Seweweekspoort, Western Cape.
*P. paleacea* Wikstr., *Bredenkamp 940*, Puntjie, Western Cape.
*P. paleacea* Wikstr., *Bredenkamp 950*, De Hoop Nature Reserve, Western Cape.
*P. paleacea* Wikstr., *Bredenkamp 952*, Harold Porter National Botanical Garden, Western Cape.
**P. paleacea* Wikstr., *Bredenkamp 960*, Kommetjie, Cape Town, Western Cape.
**P. paleacea* Wikstr., *Bredenkamp 961*, Cape Maclear, Cape Town, Western Cape.
*P. paludosa* Thoday, *Thoday 100*, Riet Valley, Cape Flats, Western Cape.
*P. paludosa* Thoday, *Bredenkamp 1035*, Rondevlei Nature Reserve, Western Cape.
*P. pendula* Eckl. & Zeyh., *Fourcade 3040*, Zuur Anys, Eastern Cape.
*P. pendula* Eckl. & Zeyh., *Bredenkamp 908*, Groendal Nature Reserve, Eastern Cape.
*P. pendula* Eckl. & Zeyh., *Bredenkamp 909*, Groendal Nature Reserve, Eastern Cape.
*P. rigida* Wikstr., *Bredenkamp 1013*, Umtamvuna River Mouth, KwaZulu-Natal.
*P. rigida* Wikstr., *Bredenkamp 897*, Kleinmond West, Eastern Cape.
*P. rigida* Wikstr., *Bredenkamp 898*, Port Alfred Eastern, Cape.
*P. rigida* Wikstr., *Bredenkamp 899*, Kenton-on-Sea, Eastern Cape.
*P. rigida* Wikstr., *Bredenkamp 911*, Jeffrey's Bay, Eastern Cape.
*P. rubra* C.H. Wright, *Bredenkamp 900*, Grahamstown, Eastern Cape.
*P. rubra* C.H. Wright, *Bredenkamp 914*, Kareedouw, Eastern Cape.
*P. vulgaris* Thoday, *Bredenkamp 901*, Grahamstown, Eastern Cape.
*P. vulgaris* Thoday, *Bredenkamp 907*, Groendal Nature Reserve, Eastern Cape.
*P. vulgaris* Thoday, *Bredenkamp 924*, Kleinbrak, Western Cape.
*P. vulgaris* Thoday, *Bredenkamp 926*, Riversdale, Western Cape.
*P. vulgaris* Thoday, *Bredenkamp 943*, Bontebok National Park, Western Cape.

## 4.3 Epidermis

BREDENKAMP, C.L. & VAN WYK, A.E. 2000. The epidermis in *Passerina* (Thymelaeaceae): structure, function and taxonomic significance. *Bothalia* 30: 69–86.

CONTENTS

Bothalia 30,1: 69–86 (2000)

# The epidermis in *Passerina* (Thymelaeaceae): structure, function and taxonomic significance

C.L. BREDENKAMP* and A.E. VAN WYK**

**Keywords:** anatomy, cuticle, epicuticular waxes, epidermis, *Passerina*, southern Africa, stomata, taxonomy, Thymelaeaceae

## ABSTRACT

Epidermal features were studied in all 17 species of *Passerina*, a genus endemic to southern Africa. Leaves in *Passerina* are inversely ericoid, the adaxial surface concave and the abaxial surface convex. Leaves are inversely dorsiventral and epistomatic. The adaxial epidermis is villous, with unicellular, uniseriate trichomes and relatively small thin-walled cells, promoting flexibility of leaf margins owing to turgor changes. In common with many other Thymelaeaceae, abaxial epidermal cells are large and tanniniferous with mucilaginous cell walls. The cuticle is adaxially thin, but abaxially well developed, probably enabling the leaf to restrict water loss and to tolerate high light intensity and UV-B radiation. Epicuticular waxes, present in all species, comprise both soft and plate waxes. Epidermal structure proves to be taxonomically important at family, genus and species levels. Interspecific differences include arrangement of stomata and presence or absence of abaxial epidermal hair. Other diagnostic characters of the abaxial epidermal cells are arrangement, size and shape, cuticular ornamentation and presence or absence of wax platelets. Two groups of species on the basis of abaxial epidermal cell orientation are recognised. Many leaf epidermal features in *Passerina* are interpreted as structural adaptations to the Mediterranean climate of the Cape.

## CONTENTS

## INTRODUCTION

The genus *Passerina* L. comprises about 17 species, all endemic to southern Africa (Thoday 1924; Bond & Goldblatt 1984). Despite the now outdated revision by Thoday (1924), taxonomic boundaries in *Passerina* remain a problem, mainly owing to the apparent lack of marked morphological differences between the species. The present paper emanates from a comparative leaf-anatomical survey of the genus, undertaken as part of a monographic study of the group. This survey highlighted the importance of the epidermis as a source of taxonomic evidence.

The combined distribution of all the *Passerina* species is shown in Figure 1. Most species of *Passerina* are

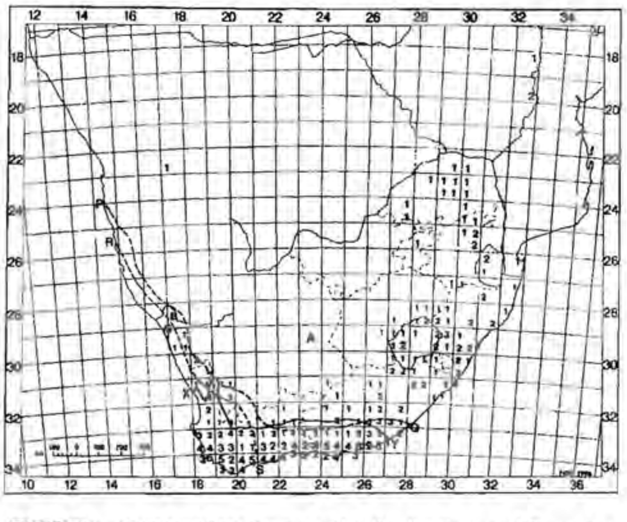

FIGURE 1—Number of species per grid in the distribution of *Passerina*. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops.

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TABLE 1.—*Passerina* specimens examined and housed at PRE

| 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 | *Andreae *1288; MacDonald *2125* | WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (–AD). |
| *drakensbergensis* Hilliard & B.L.Burtt | *Edwards 974* | KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB). |
| | *Bredenkamp *1018, 1019, *1020* | KWAZULU-NATAL.—2829 (Harrismith): Ndedema Gorge, Cathedral Peak Forest Reserve, (–CD). |
| *ericoides* L. | *Bredenkamp *962* | WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD). |
| | *Bredenkamp *+956* | WESTERN CAPE.—3318 (Cape Town): Milnerton, (–CD). |
| | *Taylor 4042* | WESTERN CAPE.—3419 (Caledon): Pearly Beach, (–CB). |
| *falcifolia* C.H.Wright | *Bredenkamp *+917* | WESTERN CAPE.—3323 (Willowmore): Gouna, (–CC). |
| | *Bredenkamp *915* | WESTERN CAPE.—3324 (Steytlerville): opposite Tsitsikamma Lodge, (–CD). |
| | *Tyson 1449* | WESTERN CAPE.—3423 (Knysna): Knysna, (–AA). |
| *filiformis* L. | *Killick 238* | KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (–CB). |
| | *Bredenkamp *1016, *1017* | KWAZULU-NATAL.—3030 (Port Shepstone): Oribi Gorge, (–CB). |
| | *Bredenkamp *1012; Van Wyk & Bredenkamp 1* | KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (–AA). |
| | *Bredenkamp 896* | EASTERN CAPE.—3327 (Peddie): Kiwane, (–BA). |
| | *Bredenkamp 1036* | WESTERN CAPE.—3418 (Simonstown): Steenbras River Mouth, (–BB). |
| *galpinii* C.H.Wright | *Bredenkamp *946* | WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD). |
| | *Galpin 4491* | WESTERN CAPE.—3421 (Riversdale): Melkhoutfontein, (–AD). |
| | *Bredenkamp *932* | WESTERN CAPE.—3421 (Riversdale): Riethuiskraal, (–AD). |
| | *Bredenkamp 933* | WESTERN CAPE.—3421 (Riversdale): Still Bay, (–AD). |
| | *Bredenkamp 923* | WESTERN CAPE.—3422 (Mossel Bay): Mossel Bay, (–AA). |
| *glomerata* Thunb. | *Bredenkamp *988, 994, 1002* | WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, near Algeria, (–AC). |
| | *Bredenkamp 984* | WESTERN CAPE.—3219 (Wuppertal): Citrusdal, (–CA). |
| | *Bredenkamp 977* | WESTERN CAPE.—3219 (Wuppertal): Ceres, Karoo, Farm Groenfontein, (–DC). |
| | *Bredenkamp *973* | WESTERN CAPE.—3319 (Worcester): Tulbagh, (–AC). |
| *montana* Thoday | *Giess 13136* | NAMIBIA.—2217 (Windhoek): Auas Mountains, (–CA). |
| | *Bredenkamp 1028* | NORTHERN PROVINCE.—2427 (Thabazimbi): Marikele Nature Reserve, (–BC). |
| | *Bredenkamp *1024* | MPUMALANGA.—2430 (Pilgrim's Rest): World's View, (–DD). |
| | *Bredenkamp *1025* | MPUMALANGA.—2430 (Pilgrim's Rest): God's Window, (–DD). |
| | *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 CAPE.—3319 (Worcester): Karoo National Botanical Garden, (–CB). |
| | *Bredenkamp 967* | WESTERN CAPE.—3319 (Worcester): Jonaskop, (–CD). |
| | *Bredenkamp 1033, *1034* | WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (–AD). |
| | *Bredenkamp *929* | WESTERN CAPE.—3321 (Ladismith): Rooiberg, (–CB). |
| | *Bredenkamp *919* | WESTERN CAPE.—3322 (Oudtshoorn): Perdepoort, (–CD). |
| *paleacea* Wikstr. | *Bredenkamp 960* | WESTERN CAPE.—3418 (Simonstown): Kommetjie, (–AB). |
| | *Bredenkamp *+961* | WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD). |
| | *Bredenkamp 952* | WESTERN CAPE.—3418 (Simonstown): Harold Porter National Botanical Garden, (–BD). |
| | *Bredenkamp 950* | WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD). |
| | *Bredenkamp *949* | WESTERN CAPE.—3420 (Bredasdorp): Waenhuiskrans, (–CA). |
| | *Bredenkamp 940* | WESTERN CAPE.—3421 (Riversdale): Puntjie, (–AC). |
| *paludosa* Thoday | *Bredenkamp *1035; Jungle *156* | WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (–BA). |
| | *Thoday 100* | WESTERN CAPE.—3418 (Simonstown): Riet Valley, Cape Flats, (–BA). |
| *pendula* Eckl. & Zeyh. | *Fourcade 3040* | EASTERN CAPE.—3324 (Steytlerville): Suuranys, (–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 *1013* | KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Mouth, (–AA). |
| | *Bredenkamp *899* | EASTERN CAPE.—3326 (Grahamstown): Kenton-on-Sea, (–DA). |
| | *Bredenkamp 898* | EASTERN CAPE.—3326 (Grahamstown): Port Alfred, (–DB). |
| | *Bredenkamp 897* | EASTERN CAPE.—3327 (Peddie): Kleinmond West, (–CA). |
| | *Bredenkamp 911* | EASTERN CAPE.—3424 (Humansdorp): Jeffreys Bay, (–BB). |
| *rubra* C.H.Wright | *Bredenkamp 914* | EASTERN CAPE.—3324 (Humansdorp): Kareedouw, (–CD). |
| | *Bredenkamp *905* | EASTERN CAPE.—3325 (Port Elizabeth): Colchester, (–DB). |
| | *Bredenkamp *900* | EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD). |
| *vulgaris* Thoday | *Bredenkamp *926* | WESTERN CAPE.—3321 (Ladismith): foot of Gysberg Pass, (–CC). |
| | *Bredenkamp 907* | EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB). |
| | *Bredenkamp 901* | EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD). |
| | *Bredenkamp 943* | WESTERN CAPE.—3420 (Bredasdorp): Bontebok National Park, (–AB). |
| | *Bredenkamp *924* | WESTERN CAPE.—3422 (Mosselbaai): Kleinbrak, (–AA). |
| sp. nov. 1 | *Bredenkamp *1044, *1046, *1047* | WESTERN CAPE.—3319 (Worcester): Waboomberg, (–AD). |
| sp. nov. 2 | *Esterhuysen *12189, *26859* | WESTERN CAPE.—3218 (Clanwilliam): northern Cederberg Mountains, (–BB). |
| sp. nov. 3 | *Stokoe *9302* | EASTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, Prince Albert area, (–AC). |
| | *Esterhuysen *28006* | EASTERN CAPE.—3324 (Steytlerville): Cockscomb, (–BD). |
| sp. nov. 4 | *Schlechter *9302* | EASTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–AC). |
| | *Esterhuysen *10734* | EASTERN CAPE.—3323 (Willowmore): Kouga Mountains, (–DA). |

* Material used for the SEM study of the ad- and abaxial epidermises. +Fresh material collected for the TEM study.

endemic to the Cape Floristic Region. From here the distribution of *P. filiformis* and *P. montana* extends east and north along the eastern mountains and Great Escarpment of southern Africa. In the Cape the climate is for the most part Mediterranean or semi-Mediterranean. In the west, it rains in winter; along the south coast, winter rainfall is complemented by some summer rain which increases eastwards. The western Karoo and Namaqualand (Succulent Karoo Biome) are characterised by winter precipitation and summer drought. KwaZulu-Natal and the eastern mountains of southern Africa are predominantly summer rainfall areas. Distribution of the species of *Passerina* coincides with the geography and climate along the whole distribution area. *P. ericoides*, *P. paleacea*, *P. paludosa*, *P. galpinii* and *P. burchellii* are endemic to Western Cape. The first three species are found along beaches and salt marshes only, *P. galpinii* grows mainly on calcrete in the Agulhas Plain area (Goldblatt & Manning in press) and *P. burchellii* is found on the high mountains at Genadendal and Villiersdorp. *P. comosa* grows on mountain slopes and summits in the Kamiesberg, Great Winterhoek and Klein Swartberg Ranges. *P. glomerata* is found from Worcester to Tulbagh, in the Clanwilliam area and extends to the Witteberg south of Matjiesfontein. *P. obtusifolia* is ubiquitous in the Cape, distributed from Worcester in Western Cape to Alice in Eastern Cape and on some of the mountain ranges in and around the Little Karoo. A new species, of which the plants are often buried under snow during winter, grows at high altitudes in the Ceres Karoo. *P. vulgaris* is a pioneer with a wide distribution from Western Cape to East London in Eastern Cape. *P. falcifolia* is found on mountain ranges between George and Uitenhage and *P. pendula* is endemic to the KwaZunga Catchment Basin and the Zwartkops River area of Eastern Cape. *P. rubra* is common in the Port Elizabeth to Uitenhage area, with outliers in the Swellendam and Bredasdorp Districts. *P. drakensbergensis* is endemic to the high Drakensberg in the Bergville District of KwaZulu-Natal and *P. rigida* is distributed all along the coast, from northern KwaZulu-Natal to the Cape Peninsula. *Passerina* sp. nov. 2 is found on the northern Cederberg Mountains, *P.* sp. nov. 3 at mountain tops in the Uitenhage area and the Swartberg Pass and *P.* sp. nov. 4 on the Kouga Mountains and the Montagu Pass.

The most important studies applying the 'anatomical method' for the delimitation of the Thymelaeaceae were published by Van Tieghem (1893) and Supprian (1894). The presence of mucilaginous epidermal cells in *P. ericoides* (= *Chymococca empetroides* Meisn.) as opposed to the total lack thereof in the other species, was also mentioned by Supprian (1894). Subsequently, Gilg (1894) critically discussed the 'anatomical method' as applied by Van Tieghem (1893) and Supprian (1894) for the delimitation of the Thymelaeaceae and concluded that certain characters would not uphold criticism. He regarded former systems based on floral morphology as more suitable for a taxonomic grouping of the Thymelaeaceae.

The twentieth century yielded very little anatomical work on the Thymelaeaceae. Standard works were those of Solereder (1908) and Metcalfe & Chalk (1950, 1979). Thoday (1921) described the structure and behaviour in drought of the ericoid leaves of *P. filiformis* and *P.* cf. *falcifolia*; he also supplied some notes on their anatomy. In a discussion of inversely dorsiventral leaves, Kugler (1928) included a description of the leaves of *P. filiformis* (= *P. pectinata* Hort.). More recently, leaf anatomy of the genera *Lachnaea* L. and *Cryptadenia* Meisn. was treated by Beyers (1992) and leaf and involucral bract characters of systematic use in *Gnidia* L. were studied by Beaumont *et al.* (1994). The scanty information on leaf anatomy in Thymelaeaceae calls for further research in this field, especially in the genus *Passerina*.

Previous leaf anatomical studies identified mucilagination of the epidermal cells as being of possible taxonomic importance. Recently Bredenkamp & Van Wyk (1999) clarified the structure of the epidermal cells and origin of the mucilage, concluding that mucilagination of epidermal cells is of taxonomic importance mainly at the family level.

The wide distribution of *Passerina* in the Cape Floristic Region, along the southern and eastern coastline and along the Great Escarpment of southern Africa as far north as Zimbabwe, illustrates the adaptation of these plants to a wide range of habitats, including Mediterranean and summer rainfall regimes. Decreasing rainfall from the eastern Escarpment to the northwestern Cape is reflected by adaptive changes in the leaf structure of the group. The present paper provides a description of epidermal characters in *Passerina* as well as an assessment of their taxonomic significance. It also speculates on the possible adaptive value of the observed structural features of the leaf.

## MATERIAL AND METHODS

Fresh leaf material of 17 species of *Passerina* (Table 1) was collected, 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 collected, fixed and air-dried for each species and herbarium specimens were made.

### Light microscope (LM) studies

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

The following three methods were followed in the study of the cuticles:

1. GMA transverse sections of leaves were stained for 10 minutes in 1% Sudan Black B dissolved in 70% ethanol. Sections were rinsed twice in 70% ethanol for a few seconds and mounted in glycerine jelly.

2. Cuticular mounts were obtained by maceration according to the method of Kiger (1971). Specimens were slightly over-stained in a 1% acqueous safranin solution, dehydrated in methyl cellusolve and mounted in Entellan.

3. Epidermal mounts were obtained by removing small pieces of ad- and abaxial epidermis manually and by paradermal hand sections. Epidermises were stained in 1% safranin dissolved in 50% ethanol, dehydrated in a graded ethanol series and mounted in Entellan.

### Scanning electron microscope (SEM) studies

The SEM was used to study the epidermal surface features (including epicuticular waxes), as well as to verify the structure of the cuticle. Leaves from air-dried material were used for all species. Whole leaves were used as they are small and ericoid, but trichomes were manually removed adaxially to reveal the stomata. Leaves were mounted onto aluminium stubs with silver paint, exposing the ad- and abaxial surfaces separately and sputter-coated with gold. For the purpose of studying epicuticular waxes, the sputter-coating process was modified to prevent high temperatures from changing the wax surfaces. Specimens were sputter-coated for 30 seconds and left to retain their normal temperature for one minute. This was repeated five times after which the specimens were viewed with a Jeol 840 SEM.

For the verification of the authenticity of epicuticular wax droplets and small round protrusions observed in certain species of *Passerina*, leaves were washed in chloroform for one minute, before they were pasted onto aluminium stubs. The procedure described above was used for sputter-coating and viewing.

### Transmission electron microscope (TEM) studies

The TEM was used for the study of the structure of mucilaginous epidermal cell walls in *Passerina*. The second, fifth and tenth leaf from the growing points of *P. ericoides*, *P. falcifolia* and *P. paleacea* were used to study the structure of the cell wall. Leaf segments of ± 1 mm$^2$ were fixed in a modified Karnovsky fixative (Karnovsky 1965). Fixed material was rinsed in 0.075 M phosphate buffer, pH 7.4–7.5, post-fixed for one hour in 0.25% aqueous $OsO_4$, washed in three changes of water, dehydrated in a graded acetone series and embedded in Quetol 651 resin (Van der Merwe & Coetzee 1992). Ultrathin sections were contrasted in 4% aqueous uranyl acetate for 10 minutes and rapidly rinsed in water three times. The sections were then contrasted with lead citrate (Reynolds 1963), rinsed in water and examined with a Phillips 301 TEM.

For the verification of wettability and possible absorption of water by laminar epidermal hairs, we follow Alvin (1987). He proposed a mechanism through which water is absorbed by the specialised abaxial epidermal trichomes of *Androstachys johnsonii* Prain. This process involves the wettability of the hairs which he investigated by spraying the glabrous adaxial surfaces of the leaves with water. Water seeped round the leaf margins to the abaxial surface, wetting approximately 50% of the abaxial surface within 5 minutes. In the present study, the glabrous abaxial surfaces of five cymbiform leaves (from dried herbarium specimens) were pasted onto a sticky surface, exposing the villous concave adaxial surface. A drop of water was placed in the adaxial groove at the base of each leaf (average leaf size 2.5 × 4.0 mm) and left overnight. This experiment was repeated using 0.5% aqueous safranin, followed after 20 minutes by a rinse with water.

### Terminology

#### *Trichome structure*

We have followed the terminology of Stace (1965) and Theobald *et al.* (1979).

#### *Cuticle*

Although the interpretation proposed by Martin & Juniper (1970) for the cuticle of plants has been widely followed by many workers, Holloway (1982) reviewed the historical perspective of the plant cuticle and attempted to adopt the most workable interpretation of the cuticular membrane (CM) in practice. In response, we follow Jeffree (1986), whose uncomplicated and pragmatic interpretation distinguishes three main zones, namely the cuticle proper, the cuticular layer and the cell wall. The cuticular membrane comprises the cuticle proper plus the cuticular layer and is bonded to the outer periclinal walls of the epidermal cells by a pectin-rich layer, which is equivalent to the continuous middle lamella. A layer of epicuticular wax generally coats the cuticle proper.

#### *Cuticular ornamentation (LM and SEM)*

We follow Wilkinson (1979) in our choice of terminology to describe cuticular ornamentation.

#### *Epicuticular wax*

The recognition of soft waxes in the present study is based on the criteria proposed by Amelunxen *et al.* (1967), Wilkinson (1979) and Barthlott *et al.* (1998).

## RESULTS

### Macromorphology of the leaf

*Leaf arrangement* decussate, sometimes imbricate, closely adherent to stem or spreading at angle of 5°–20°(–60°); spreading of leaves often prominent in juvenile plants. *Lamina* inversely ericoid; adaxial surface concave, often forming a groove facing stem and lined with woolly hairs; 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 (boat-shaped), falcate or cigar-shaped; plane shape linear, oblong, lanceolate, ovate or trullate. *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) × (0.8–)1.2–2.0(–3.0) mm.

### Anatomy of the leaf

*Transverse section* (LM): *leaves* epistomatic. *Adaxial epidermis* concave, villous, with unicellular, uniseriate trichomes; cuticle relatively thin, 2–5 µm; epidermal cells uniserial, relatively small (10–)15–25(–35) × 10–17(–20) µm; vacuoles large with tanniniferous substances, cell walls thin; stomata present, with guard cells at same level, sunken below, or raised above adjacent epidermal cells. *Abaxial epidermis* convex, glabrous or sparsely hairy; cuticle relatively thick (10–)20–40(–70) µm; epidermal cells relatively large, periclinal diam. of cells (20–)30–60(–65) µm, anticlinal diam. (25–)30–75 (–105) µm (Table 2), tanniniferous, often with mucilaginous cell walls. *Mesophyll* inversely dorsiventral (Kugler 1928); spongy parenchyma situated adaxially and palisade parenchyma abaxially. *Main vascular bundle* collateral, surrounded by parenchymatous bundle sheath with ample amounts of tanniniferous substances; bundle sheath adaxially irregularly biseriate, abaxially strengthened by sclerenchyma. *Secondary vascular bundles* ± 6; bundle sheaths irregular, parenchymatous and tanniniferous. Figure 2A, B.

### Adaxial (dorsal) epidermis

#### *Cuticle*

*Transverse section* (LM): cuticular membrane 2–5 µm thick, smooth, ridged along boundaries of guard cells (Figure 2G), gradually thickening close to leaf margins, equalling abaxial cuticle in thickness and sculpturing at margins.

*Surface view* (LM and SEM): smooth (Figure 2C), except in *Passerina* sp. nov. 1, where markings on epicuticular wax are most probably caused by snow (Figure 3D, E).

#### *Epidermal cells*

*Transverse section* (LM): cells uniserial, irregularly shaped, relatively small with periclinal diam. (10–)15–25(–35) µm, anticlinal diam. 10–17(–20) µm; cell walls thin, outer periclinal wall convex; vacuoles large, containing tanniniferous substances (Figure 2A, F–H). Margin formed by a few rows of conically shaped or anticlinally elongated cells.

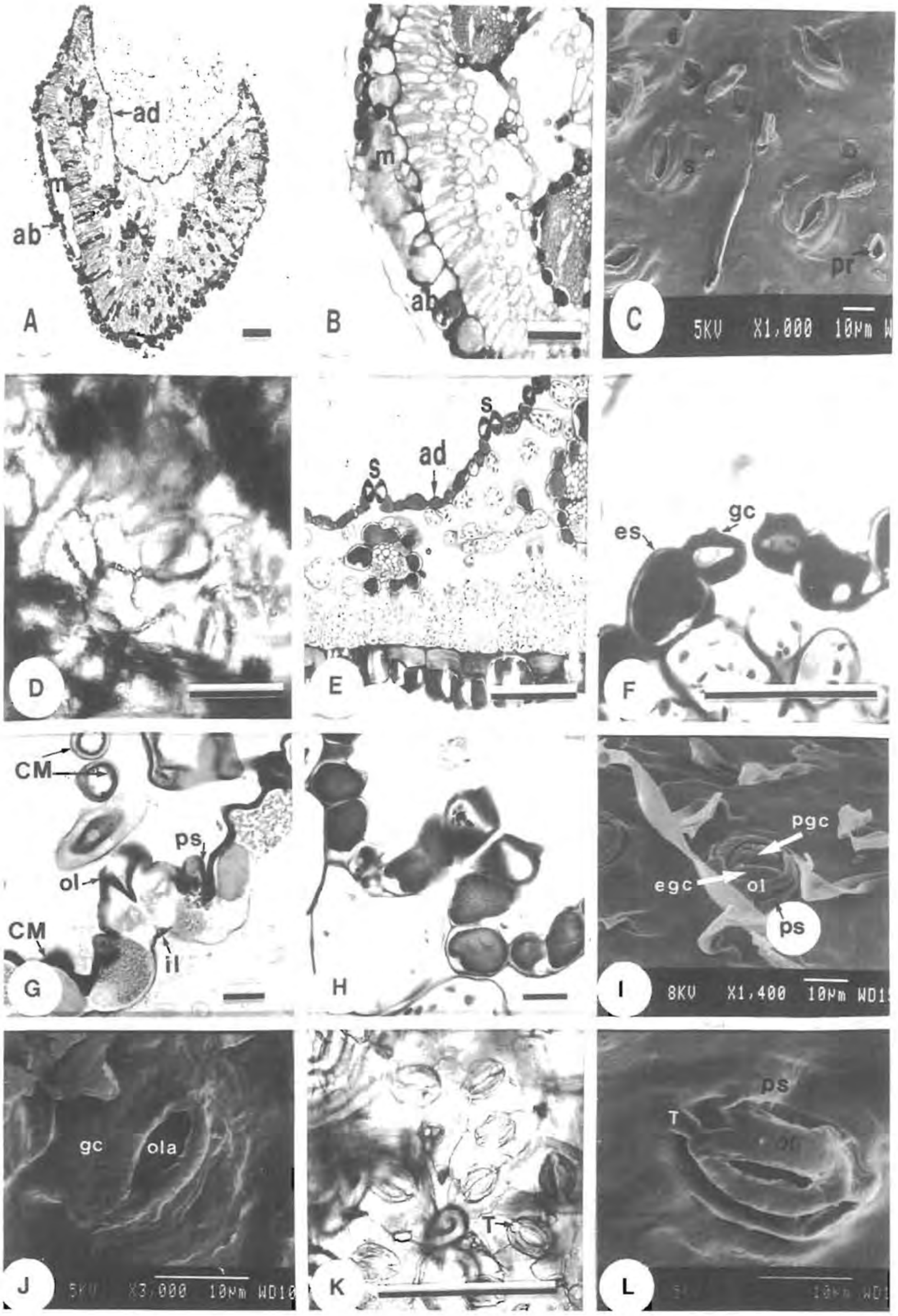
*Surface view* (LM and SEM): cells polygonal, 4–many-sided, walls usually undulate with loose, wide u-shaped curves of shallow amplitude (Figures 2D, K; 3C), arranged in rows and straight-walled in *Passerina* sp. nov. 1 (Figure 3D, E). Nodular walls observed in *P. falcifolia* (Figure 2D). Vacuoles with ample tanniniferous substances.

#### *Stomatal complex*

*Transverse section* (LM): *lamina* epistomatic; stomata dispersed randomly over adaxial surface, but absent from edges of leaf margin; raised or at same level as other epidermal cells (Figure 2E–H); dispersed in two columns in adaxial epidermal folds, with ± 3–5 rows of epidermal cells in between; raised, sunken or arranged in stomatal crypts in *Passerina* sp. nov. 1 (Figure 3F). *Guard cell* outline in all species varying between widely obtrullate, very widely obtrullate or widely depressed obtrullate, with angles slightly rounded; cell walls thick-

TABLE 2.—Dimensions of abaxial epidermal cells and cuticular membrane (CM) in *Passerina*. Measurements in µm in cross section and surface view

| Name | Width of CM | Periclinal diam. | Anticlinal diam. | Length × width | Shape of cell |
|---|---|---|---|---|---|
| *comosa* (Figure 4B, C) | 10–40 | 30–60 | 70–75 | 45–55 × 35–40 | slightly oblong |
| *glomerata* | (20–)30–40(–50) | (20–)30–35(–40) | (25–)30–55(–60) | 30–40 × 30–35 | isodiametric |
| *ericoides* (Figure 4D–F) | 20–32 | 35-60 | 40–60 | 35–50 × 40–50 | ± isodiametric |
| *obtusifolia* (Figure 4G–I) | 20–30 | 40–55 | 55–75(–105) | (30–)40–55(–60) × (45–)50–70(–95) | transversely oblong |
| *burchellii* (Figure 4J–L) | 60(–70) | 45 | 75 | (65–)85(–125) × 45–50 | angles rounded, oblong |
| *drakensbergensis* (Figure 5A–C) | 20 | 30–35 | 50–55 | 50–65 × 30–40 | oblong |
| *montana* | 30–35 | 30–45 | 45–65 | 40–60 × 35–40 | isodiametric to slightly oblong |
| sp. nov. 1 (Figure 5D–F) | 20 | 35 | 40 | 45–55 × 35–40 | oblong |
| *vulgaris* | (10–)20–30 | 30–45 | 35–45(–70) | 35 × 30–40 | transversely oblong |
| *filiformis* | 20–35 | 35(–65) | 55–75(–90) | 35–55 × 25–30 | oblong |
| *falcifolia* | 20 | 40 | 40 | 60–75 × 35–50 | oblong |
| *pendula* | 30 | 45–55 | 60–65 | 50–65 × 30–40 | oblong |
| *rigida* (Figure 5G–I) | 20–30 | 35–50 | 35–55 | 35–45 × 35–40 | isodiametric to slightly oblong |
| *galpinii* | 40–50 | 30–35 | (40–)55–60(–70) | 30–40 × 30 | isodiametric to slightly oblong |
| *rubra* | 20–30 | 30–50 | 45 | (30–)35(–55) × 35–40 | isodiametric to slightly oblong |
| *paleacea* | 20(–40) | 35(–65) | 50–60 | 45–50 × 30–35 | slightly oblong |
| *paludosa* (Figure 5J–L) | 20 | 35–45 | 60–70 | 95–100 × 45–50(–95) | oblong |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ened (Figure 2F, H); periclinal and anticlinal dimensions for individual guard cells 10.0–12.5(–15.0) × (10.0–) 12.5–15.0(–20.0) µm. *Cuticular membrane* (Figures 2G; 3B) covering outer periclinal walls of epidermal and guard cells, as well as poral epidermal walls of guard cells, smooth or slightly crenate when lining the pore (Figure 3B), contracted into a pair of ± continuous outer stomatal ledges above guard cells, thus forming an entire outer cavity (not divided into compartments); inner stomatal ledges and inner cavity present. *Epidermal cells* surrounding guard cells not different from other epidermal cells in size, shape or staining properties (Figure 2F). *Peristomatal cuticular rims* conspicuous on epidermal cells bordering guard cells (Figure 2G).

*Surface view* (LM and SEM): *stomata* anomocytic; outline elliptic to circular, dimensions (20–)26–30(–35) × (15–)24–30(–35) µm, circular in *Passerina* sp. nov. 1, dimensions 27.5 × 27.5 µm. *Epidermal cells surrounding guard cells* 3–5(6), irregularly shaped with sinuate walls and long axis parallel to guard cells, corresponding in orientation, size, shape and staining properties to other ± elongated epidermal cells (Figures 2D, K; 3C); pentagonal to heptagonal epidermal cells in *Passerina* sp. nov. 1, with walls slightly sinuate to straight, possibly nodular (Figure 3E). *Stomata* raised above or at same level as other epidermal cells in all species (Figure 2I, J, L); dispersed in two columns in adaxial epidermal folds, with ± 3–5 rows of epidermal cells in between, sunken or arranged in stomatal crypts in *Passerina* sp. nov. 1 (Figure 3D). *Guard cells* often conspicuously raised (Figure 2I, J). *Peristomatal cuticular rims* conspicuous on epidermal cells bordering guard cells (Figures 2I, L; 3A), rims also visible as 1–4 small semilunar protrusions bordering guard cells in cuticular preparations and epidermal peels (Figure 3C) (rims should not be confused with small subsidiary cells, an interpretation which could result in stomata being erroneously classified as paracytic or cyclocytic). *Outer stomatal ledges* ± continuous, present above guard cells (Figures 2I–L; 3A, C). *Stomatal poles* (where guard cells meet) retuse; T-pieces (cuticular thickenings of common walls between guard cells) well developed (Figures 2I, J, L; 3C).

*Trichomes*

LM and SEM: *adaxial surface* of leaf villous. *Trichomes* nonglandular, unbranched, devoid of surface features or constrictions, mostly strongly spiralled (Figure 3G, H), terete, with central lumen, covered by cuticle (Figures 2G; 3I). *Hair bases* with pore, poral rim somewhat thickened (Figures 2C; 3C, G); hair base cells mostly 4–6 and slightly radially elongated (Figure 3C, G). *Trichomes bordering leaf margin* conspicuous in *P. burchellii*, *P. paludosa* and *P. pendula* (Figure 3I, J). *Trichome foot* scarcely modified, inserted between epidermal cells (Figure 3I), usually straight, but with individual trichomes strongly spiralled (Figure 3J) in *P. pendula* (brown in dried material).

Wettability and the possible absorption of water by the laminar epidermal hairs in *Passerina* were assessed by means of laboratory tests. We found that water had formed a film over the felty layer of hair at the leaf base, whereas the adaxial surface had remained dry. A treatment with 0.5% aqueous safranin revealed that only the exposed parts of the spiralised hairs in the felty indumentum at the leaf bases stained pinkish. Although the longer hairs at the leaf margins were stained, those on the rest of the adaxial surface remained unstained.

**Abaxial (ventral) epidermis**

*Trichomes*

*Abaxial* surfaces of bracts and young leaves in *P. comosa*, *P.* sp. nov. 3 and *P.* sp. nov. 4 tomentose to sparsely hairy (Figure 4B), older leaves often glabrous. Description of trichomes as described under adaxial epidermis.

*Epidermal cells*

*Transverse section* (LM and TEM) (Figures 2A, B, E; 3K–L): epidermis uniserial. *Stomata* absent. *Epidermal cells* more or less oblong in outline; outer periclinal walls straight or convex, inner periclinal walls straight, convex or bulging towards mesophyll, often mucilaginous and then superficially resembling a multiple epidermis; periclinal diam. of cells (20–)30–60(–65) µm, anticlinal diam. (25–)30–75(–105) µm (Table 2). *Mucilaginous cell walls* increasing progressively from leaf margin to midrib (Figure 2B), affecting mainly inner periclinal but also anticlinal cell walls (Figure 3K, L); mucilage with a layered appearance (Figures 2E; 3K), eventually occupying about two-thirds of epidermal cell and separated from cytoplasm by innermost cellulose layer of inner periclinal cell wall (Figure 3L). *Cytoplasm* compressed by mucilage, remaining as a thin layer appressed to large, usually tanniniferous vacuole. *Anticlinal layer* of inner periclinal cell wall often plicate but gradually straightening and often disappearing as mucilagination increases, eventually breaking under pressure of accumulating

FIGURE 2.—LM photographs and SEM micrographs of epidermis of inversely ericoid leaf in *Passerina*. A, *P. falcifolia*, *Bredenkamp 917*, ad- and abaxial epidermis with mucilage accumulating abaxially; B, *P. galpinii*, *Bredenkamp 946*, mucilaginous abaxial epidermal cells; C, *P. filiformis*, *Bredenkamp 1016*, smooth adaxial cuticle, stomata and poral rims of hair bases; D, *P. falcifolia*, *Bredenkamp 915*, adaxial epidermal walls undulate, nodular; E, *P. ericoides*, *Taylor 4042*, stomata at different levels in relation to adaxial epidermis; F, *P. comosa*, *Bredenkamp 1034*, PAS staining of guard cell walls and surrounding epidermal cells, showing width; G, *P. pendula*, *Bredenkamp 909*, t/s adaxial epidermis stained with Sudan Black B, showing cuticular membrane; H, *P. pendula*, *Bredenkamp 909*, raised stomata stained with toluidine blue; I, *P. paleacea*, *Bredenkamp 961*, with peristomatal rim, raised epidermal and poral walls of guard cells, conspicuous outer stomatal ledges; J, *P. galpinii*, *Bredenkamp 946*, with distinct outer stomatal ledge aperture; K, *P. filiformis*, *Bredenkamp 1016*, and L, *P. pendula*, *Bredenkamp 909*, with T-pieces at stomatal poles. Abbreviations: ad, adaxial epidermis; ab, abaxial epidermis; CM, cuticular membrane; e, epidermal cell; egc, epidermal wall of guard cell; es, epidermal cell surrounding guard cell; gc, guard cell; ic, inner cavity; il, inner stomatal ledge; l, lumen of trichome; m, mucilage; oc, outer stomatal cavity; ol, outer stomatal ledge; ola, outer stomatal ledge aperture; p, pore; pgc, poral wall of guard cell; pr, trichome poral rim; ps, peristomatal rim; s, stomata; sc, stomatal crypt; t, trichome; T, T-piece at stomatal pole. Scale bars: A, B, D, E, F, K, 100 µm; C, G, H, I, J, L, 10 µm.

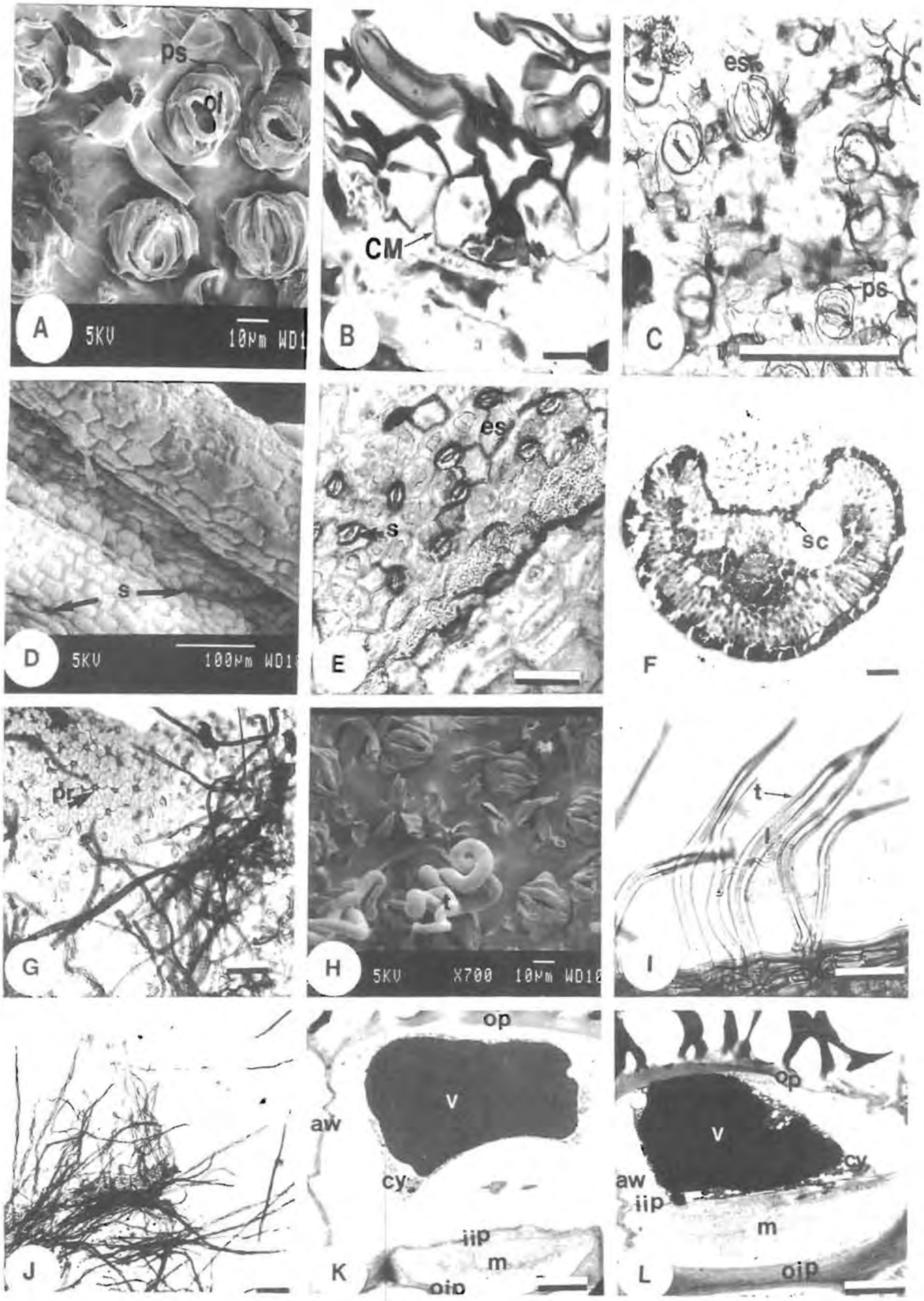
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TABLE 3.—Abaxial epidermal characters in *Passerina*

| Name | Epidermal cells | | Abaxial hair present | Ornamentation of CM | | | | | | Epicuticular wax | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Papillate | | | | | | | |
| | random | in rows | | Smooth | Molar-like crown | One dome per cell | Several domes per cell | Several globular papillae per cell | Striate | Soft wax | Platelets | Plates |
| **Group A** | | | | | | | | | | | | |
| *P. glomerata* (Figure 6C) | X | | | X | | | | | | | | X |
| *P. ericoides* (Figures 4D–F; 6D) | X | | | X | | | | | | X | | |
| *P. obtusifolia* (Figures 4G–I; 6E) | X | | | | | X | | | | X | | |
| *P. burchellii* (Figures 4J–L; 6F) | X | | | | | | X | | | X | | X |
| **Intermediate** | | | | | | | | | | | | |
| *P. comosa* (Figures 4B, C; 6A,B) | | X | X | | X | | | | | | X | X |
| *P.* sp. nov. 3 | | X | X | | | | X | | | | | X |
| *P.* sp. nov. 4 | | X | X | X | | | | X | | | X | |
| *P. drakensbergensis* (Figures 5A–C; 6G) | | X | | | | | | X | | | | X |
| *P. montana* | | X | | X | | | | X | | | | X |
| **Group B** | | | | | | | | | | | | |
| *P.* sp. nov. 1 (Figure 5D–F) | | X | | | | | X | | | | | X |
| *P.* sp. nov. 2 | | X | | | | | X | | | | X | |
| *P. vulgaris* | | X | | | | | | | X | | | X |
| *P. filiformis* (Figure 6H) | | X | | | | | | | X | | | X |
| *P. falcifolia* | | X | | | | | | | X | | | X |
| *P. pendula* (Figure 6I) | | X | | | | | | | X | | X | X |
| *P. rigida* (Figures 5G–I; 6J) | | X | | | | | | | X | | X | X |
| *P. galpinii* | | X | | | | | | | X | X | | |
| *P. rubra* | | X | | | | | | | X | X | | |
| *P. paleacea* (Figure 6K, L) | | X | | | | | | | X | X | | |
| *P. paludosa* (Figure 5J–L) | | X | | | | | | | X | X | | |

mucilage, resulting in a mucilage-filled cavity between remains of epidermal cells and adjacent mesophyll (Figure 2A) (Bredenkamp & Van Wyk 1999).

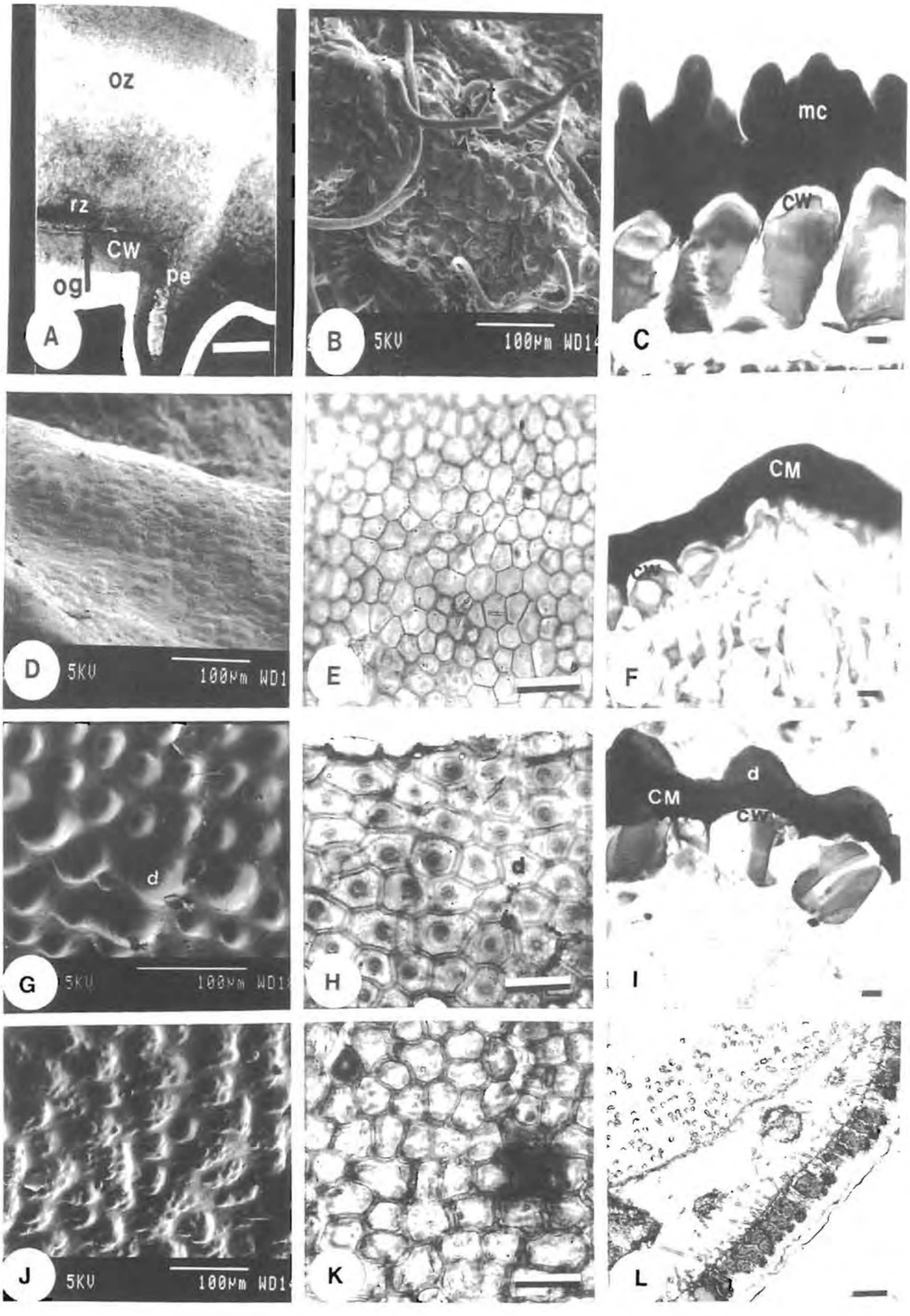
*Surface view* (SEM micrographs and cuticular preparations): *shape* pentagonal to heptagonal, cells mostly isodiametric or transversely oblong in *P. glomerata*, *P. ericoides* (Figure 4D, E) and *P. obtusifolia* (Figure 4G, H), but oblong in *P. burchellii* (Figure 4J, K); cells mostly slightly oblong or oblong in all other species of *Passerina* (Figure 5; Table 2). *Arrangement* random in *P. glomerata*, *P. ericoides*, *P. obtusifolia* and *P. burchellii* (Figure 4D–K), in rows in all other species of *Passerina* (Figure 5; Table 3).

### *Cuticle*

*Transverse section* (LM): *epicuticular wax* absent owing to chemical treatment during fixation, embedding and staining. *Cuticular membrane* (CM) well developed, (10–)20–30(–70) μm thick (Table 2); cuticle proper delineated by narrow, lightly stained outer zone and cuticular layer by wider, darker stained zone; cuticular pegs present, formed by layer projecting into grooves between anticlinal walls of adjacent epidermal cells. *Outer periclinal cell walls* not staining with Sudan Black B (Figures 4I; 5C, I, L).

TEM: cuticle structure corresponding to the cuticular structural type 3, described by Holloway (1982). Cuticle proper and CM not distinguishable. *Cuticular membrane* (Figure 4A) comprising a wide, mainly amorphous outer zone and narrow faintly reticulate inner zone; osmiophilic granules aligned on border of clearly defined cell wall; cuticular pegs with unknown (possibly pectinaceous) substance (stained light grey) between cell wall and peg, forming part of middle lamella.

FIGURE 3.—LM photographs and SEM micrographs in *Passerina*. A–F, structure of stomatal complex. A–C, *P. rigida*, *Bredenkamp 1013*, *Ward 7211*: A, surface view of stomata showing peristomatal rims, raised guard cells and pronounced outer stomatal ledges; B, t/s adaxial epidermis stained with Sudan Black B, with crenate surface of cuticular membrane lining poral walls of guard cells; C, epidermal maceration stained with safranin, showing structure of epidermal cells surrounding guard cells, peristomatal rims. D–F, *Passerina* sp. nov. 1, *Bredenkamp1046*: D, sunken stomata in cavity of cymbiform leaf; E, epidermal maceration stained with safranin, with structure of epidermal cells and sunken stomata; F, t/s leaf, with raised stomata as well as stomatal crypts. G–J, structure of trichomes. G, *P. rubra*, *Bredenkamp 905*, with poral rims in relation to adaxial epidermal cells. H, *P. falcifolia*, *Bredenkamp 915*, with unicellular, long, spiralised, pointed trichomes; I, *P. paludosa*, *Bredenkamp 1035*, with trichome foot and conspicuous lumen; J, *P. pendula*, *Bredenkamp 909*, trichomes strongly spiralised. K, L, TEM micrographs of abaxial leaf epidermal cells of *P. falcifolia*, *Bredenkamp 917*, in cross section: K, mucilage accumulated between innermost and outermost cellulose layers of inner periclinal cell wall; L, innermost cellulose layer of inner periclinal cell wall. Abbreviations: aw, anticlinal cell wall; cy, cytoplasm; iip, innermost layer of inner periclinal cell wall; oip, outer layer of inner periclinal cell wall; m, mucilage; op, outer periclinal cell wall; v, vacuole. Scale bars: K, L 5 μm; A, B, H, 10 μm; C–F, G, I, J, 100 μm.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### *Cuticular ornamentation*

In transections and surface view of leaves, LM and SEM studies showed that two groups of species, henceforth called Groups A, Intermediate and B (Table 3), can be distinguished on the basis of the arrangement and shape of epidermal cells as well as cuticular ornamentation.

#### Group A

*Epidermal cells* mostly isodiametric or transversely oblong in surface view; arranged randomly; cuticle mostly papillate; *outer periclinal walls* of cells convex in all species. *Cuticular membrane* (CM) smooth in *P. ericoides* and *P. glomerata* (Figures 4D–F; 6C); papillate in *P. obtusifolia*, with one dome per cell, situated ± centrally on outer periclinal wall of pentagonal or heptagonal cells (Figures 4G–I; 6E); with several domes per cell in *P. burchellii* (Figures 4J–L; 6F).

#### Group B

*Epidermal cells* mostly oblong in surface view, arranged in rows; concavities (depressions in centre region of cell) and convexities (roundish cells forming a low dome) more or less alternating (Figure 5G, J); cuticle with ridges at junction of epidermal cell walls mostly conspicuously raised, exhibiting a definite striate pattern (Figure 5D, G, J), otherwise ± plane.

*Cuticular membrane* pronounced at junctions of epidermal cell walls and grooved between anticlinal walls of adjacent cells (Figure 5I), more or less smooth in *P. vulgaris*, *P. filiformis*, *P. falcifolia*, *P. pendula*, *P. rigida*, and *P. galpinii*, except in *Passerina* sp. nov. 1, in which the presence of snow, at the time of collecting, seemed to have caused markings on the cuticular wax (Figure 5D, E). Small globular papillae visible between cuticular ridges in *Passerina* sp. nov. 1 (Figure 5D–E), *P. rubra*, *P. paleacea* and *P. paludosa* (Figure 5J–L).

#### Intermediate

*Epidermal cells* arranged in rows but CM less pronounced at junctions of epidermal cell walls and cuticular ridges less conspicuous, were recorded in *P. comosa* (Figures 4B; 6A, B), *P. drakensbergensis* (Figure 5A, B), *P. montana*, *P.* sp. nov. 3 and *P.* sp. nov. 4. CM smooth or with small globular papillae in *P. montana* and *P.* sp. nov. 4; domed with a 'molar'-like crown in *P. comosa* (Figure 4B, C), with several domes per cell in *P.* sp. nov. 3 and with 9 or 10 globular papillae per cell in *P. drakensbergensis* (Figures 5A–C; 6G).

### *Epicuticular waxes*

*Soft waxes* present, coating entire abaxial surface: wax protruding through amorphous layer of CM in a variety of configurations: droplets conspicuous in *P. comosa*, *P. ericoides* and *P. burchellii* (Figure 6A, D, F); droplets and small round protrusions forming flat, shapeless lumps in *P. paleacea* (Figure 6L). *Crystalloids*: wax platelets and plates present or absent (Table 3); thin wax platelets, with margins entire or non-entire, flaking from wax surface in *P. comosa* and *P. rigida* (Figure 6A, J) and changing to plates as margins become distinctly edged. Upright plates separating from surrounding wax in *P. filiformis* (Figure 6H). Platelets and plates varying from sparse to abundant; platelets ± square to irregularly shaped, plates ± square to oblong and usually arranged perpendicular to cell rows.

The authenticity of epicuticular wax droplets and small round protrusions, observed in *P. ericoides*, *P. obtusifolia* and *P. paleacea* (Figure 7), was verified by washing leaves in chloroform for one minute and comparing them to unwashed specimens under SEM. Epicuticular wax droplets were clearly discernible in unwashed *P. paleacea* (Figure 7A), while small pores appeared in the cleaned, de-waxed cuticle after washing (Figure 7B–E). Similar pores were also present in *P. ericoides* (Figure 7F). No pores were present in the papillate CM of *P. obtusifolia*, but the corroded apices of the papillae clearly showed an accumulation of epicuticular waxes at these points (Figure 7G–I).

## DISCUSSION

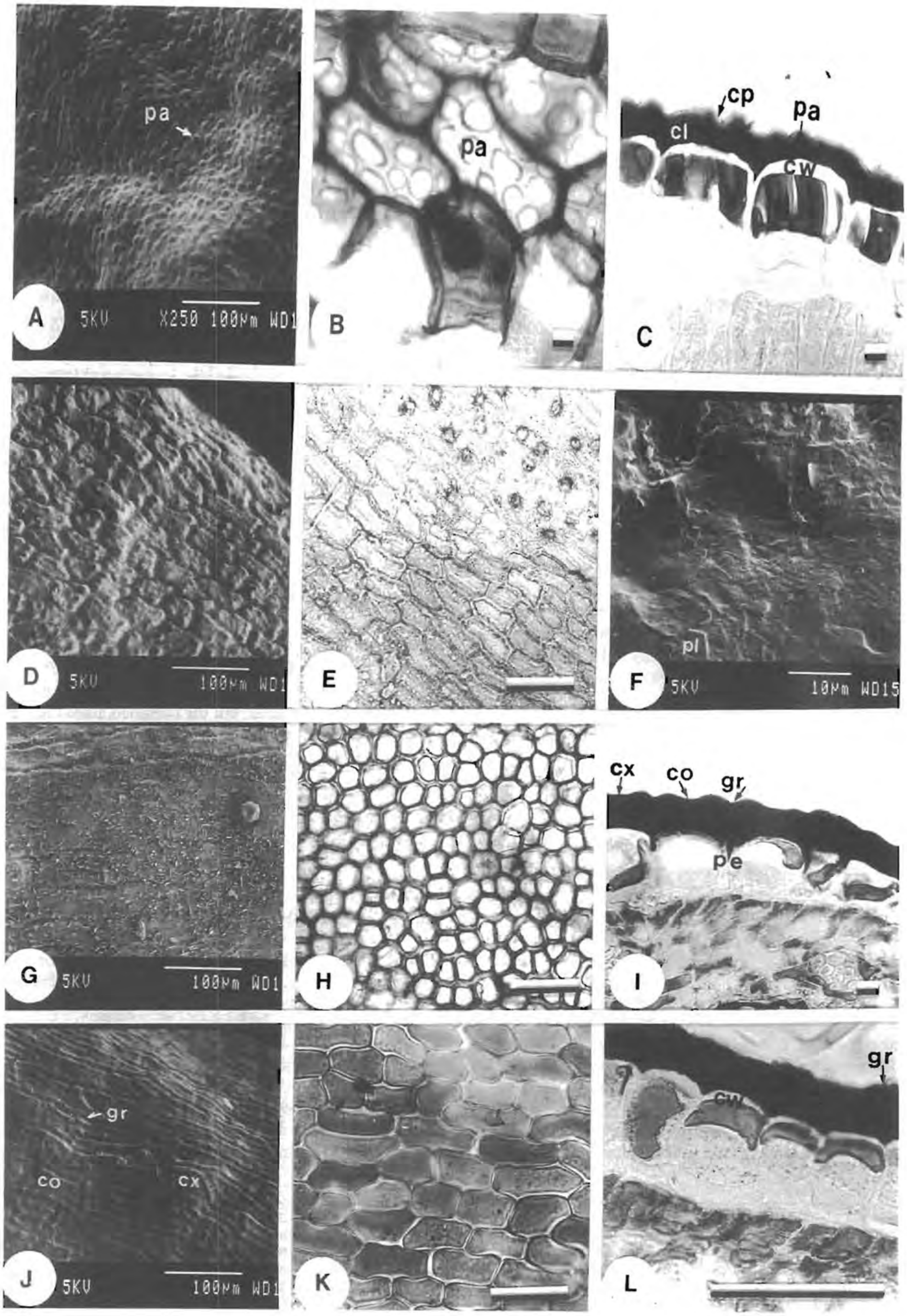
### Adaxial epidermis

Plants of high mountains in the tropics usually have straight to curved anticlinal epidermal cell walls, the percentage of species with undulated walls increasing as altitude decreases (Wilkinson 1979). The straight-walled arrangement of the cells in *Passerina* sp. nov. 1 (Figure 3D, E), a high-altitude montane species, seems to comply with this pattern.

### Stomatal complex

In all but one species of *Passerina* the stomata are usually raised or at the same level as other epidermal cells (Figure 2E, G, H), indicating that this character is of lim-

FIGURE 4.—A, TEM micrograph of cuticular membrane in *Passerina paleacea*, *Bredenkamp 961*, with wide, amorphous outside zone, narrow faintly reticulate inner zone, osmiophilic granules at border of cell wall and cuticular peg. B–L, LM photographs and SEM micrographs of abaxial leaf epidermis in *Passerina*. Epidermal macerations stained with safranin and t/s of epidermis stained with Sudan Black B. B, C, *P. comosa*, *MacDonald 2125*, *Andreae 1288*: B, trichomes present; C, CM domed, with 'molar-like' crown to each dome. D–F, *P. ericoides*, *Bredenkamp 956*, *962*, *Taylor 4042*: D, CM smooth, epidermal cells randomly arranged, ± isodiametric, outer periclinal cell walls convex; E, cells randomly arranged, ± isodiametric; F, convex outer periclinal walls and smooth CM. G–I, *P. obtusifolia*, *Bredenkamp 1034*: G, CM with one dome per cell; H, epidermal cells randomly arranged, transversely oblong with one dome per cell; I, convex outer periclinal cell wall and CM with one dome per cell. J–L, *P. burchellii*, *Bolus 687*, *Bredenkamp 1545*; J, CM with several domes per cell; K, randomly arranged cells, transversely oblong with rounded angles, several domes per cell; L, t/s epidermis in polarised light showing CM with several domes per cell. Abbreviations: CM, cuticular membrane; cw, outer periclinal cell wall; d, dome; mc, molar-like crown; og, osmiophilic granules; oz, amorphous outside zone; pe, cuticular peg; rz, narrow faintly reticulate inner zone; t, trichome. Scale bars: A, 5 µm; C, F, I, 10 µm; B, D, E, G, H, J–L, 100 µm.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ited taxonomic value at species level, except in *Passerina* sp. nov. 1, which has stomatal crypts or sunken stomata. Classification of the stomatal complex into stomatal types is often a problem owing to the subtle distinction of subsidiary cells (Wilkinson 1979; Van Wyk *et al.* 1982).

Patel (1978) considers subsidiary cells as morphologically and physiologically different from other epidermal cells and proposes a number of criteria to distinguish subsidiary cells in mature epidermis. Of these criteria we used the following in the distinction of subsidiary cells: size, shape, contents and position of cells. We found that the cells adjacent to the guard cells did not differ from other epidermal cells, except that they might be raised or sunken (Figures 2K; 3C). Furthermore, when stained with PAS, periclinal walls of subsidiary cells should be lightly stained compared with other epidermal cells, owing to less carbohydrates in these cell walls according to Patel (1978). In *Passerina* the periclinal walls of the cells adjacent to the guard cells stained homogenously with other cells in the stomatal complex (Figure 2F) and the anticlinal walls are not comparatively thinner than those of other epidermal cells, thus the cells adjacent to the guard cells cannot be considered subsidiary cells (Figure 2F, H). Stained with Sudan Black B, the contents of the cells surrounding the guard cells do not differ from those of other epidermal cells and no lipid bodies are present (Figure 2G).

We therefore conclude that the epidermal cells surrounding the guard cells in *Passerina* are not differentiated as subsidiary cells and we classify the stomatal apparatus in *Passerina* as anomocytic. This corresponds to the prevailing state in the Thymelaeaceae (Solereder 1908; Metcalfe & Chalk 1979). However, although we prefer to regard the epidermal cells surrounding the guard cells as similar to other epidermal cells, the presence of conspicuous peristomatal cuticular rims on the outer periclinal cell walls of epidermal cells around the guard cells may be used in support of a view that these cells are subsidiary cells. The stomatal apparatus could then be classified as staurocytic (Wilkinson 1979) or anomotetracytic (Dilcher 1974). As the number of epidermal cells surrounding the guard cells varies from 3–5(6), it would seem appropriate to classify the stomatal apparatus as anomostaurocytic (Van Wyk *et al.* 1982).

## Trichomes

*Passerina* leaves are often cymbiform with spiralised trichomes densely arranged in the concave ventral space. This indumentum is likely to play an important role in the water relations of the plant. Water droplets precipitating from the atmosphere, or running down from leaves directly above, would accumulate in the concave leaf space. Droplets would be repelled by the hydrophobic cuticle of the trichomes and owing to cohesion forces cause a moisture layer in the upper part of the dense trichomes. One may speculate that water vapour escaping through the stomata would not be drawn outwards by capillary forces because of the water-repelling nature of the cuticle surrounding the trichomes, thus retaining a high concentration of moisture in the vicinty of the stomata. The overall high concentration of water vapour over the adaxial surface of the leaf is likely to decrease the transpiration rate. Laboratory tests to assess the wettability and the possible absorption of water by the laminar epidermal hairs in *Passerina*, suggest that the wettability of the spiralised hairs is quite low and that absorption of water by these trichomes is highly improbable. However, our suggestion of an overall high concentration of water in the adaxial cavity of the leaf, which serves to decrease the transpiration rate, is supported by these tests.

## Cuticular ornamentation

Cuticular thickness may be affected by light, temperature, soil, atmospheric moisture and altitude (Wilkinson 1979). In *Passerina*, with many species adapted to the Cape Mediterranean climate, all members have a relatively thick cuticle, but it was the thickest in *P. comosa*, *P. glomerata*, *P. burchellii*, *P. galpinii* and *P. paleacea* (Table 2). The first two species grow in the northwestern parts of the Western Cape and on the mountains in and around the Little Karoo (= Karoo Mountain Centre *sensu* Weimarck 1941), areas with high light intensity, high temperature and low atmospheric moisture. *P. burchellii*, growing on high mountains at Villiersdorp and Genadendal, is exposed to high light intensity as well as high and low critical temperatures. *P. galpinii* grows on calcrete and *P. paleacea* is exposed to salt spray and wind. In *P. drakensbergensis*, *P. falcifolia*, *P. paludosa* and *P.* sp. nov. 1, the thickness of the CM is ± 20 µm. Of these species, *P. falcifolia*, from the mountains between George and Uitenhage, and *P. drakensbergensis*, from high altitudes in the Bergville District of KwaZulu-Natal, are exposed to relatively high atmospheric moisture. However, it is difficult to speculate on the functional significance of the relatively thin cuticles in *P. paludosa*, from salt marshes in the Cape Peninsula, and *P.* sp. nov. 1, a species from Waboomberg, one of the highest points in the Western Cape and often covered by snow in winter.

FIGURE 5.—Abaxial leaf epidermis and structure of CM in *Passerina*. Epidermal macerations stained with safranin and t/s of epidermis stained with Sudan Black B. A–C, *P. drakensbergensis*, *Bredenkamp 1018*, *1019*: A, cells arranged in rows with 9 or 10 globular papillae per cell; B, inner surface facing upwards, cells oblong in shape with 9 or 10 papillae per cell; C, CM layered, with cuticular layer and cuticle proper, also globular papillae. D–F, *Passerina* sp. nov. 1, *Bredenkamp 1044*, *1046*: D, several domes per cell, CM irregularly marked by ice crystals; E, cells arranged in rows, oblong in shape with CM irregularly marked by ice crystals; F, geometrical plates, flat or slightly raised. G–I, *P. rigida*, *Bredenkamp 1013*, *Ward 7211*: G, cells arranged in rows, plates abundant; H, cells arranged in rows, isodiametric to slightly oblong; I, CM pronounced at junctions of epidermal cell walls, grooved in midline of joining walls, concavities and convexities not conspicuous. J–L, *P. paludosa*, *Bredenkamp 1035*, *Thoday 100*: J, cells arranged in rows, CM pronounced at junctions of epidermal cell walls, grooved in midline of joining walls, concavities and convexities conspicuous; K, cells arranged in rows, cells oblong; L, CM pronounced at junctions of epidermal cell walls, grooved in midline of joining walls. Abbreviations: cl, cuticular layer; co, concavity; cp, cuticle proper; cw, outer periclinal cell wall; cx, convexity; gr, groove in CM; pa, papillae; pe, cuticular peg; pl, plates. Scale bars: A, D, E, G, H, J–L, 100 µm; B, C, F, I, 10 µm.

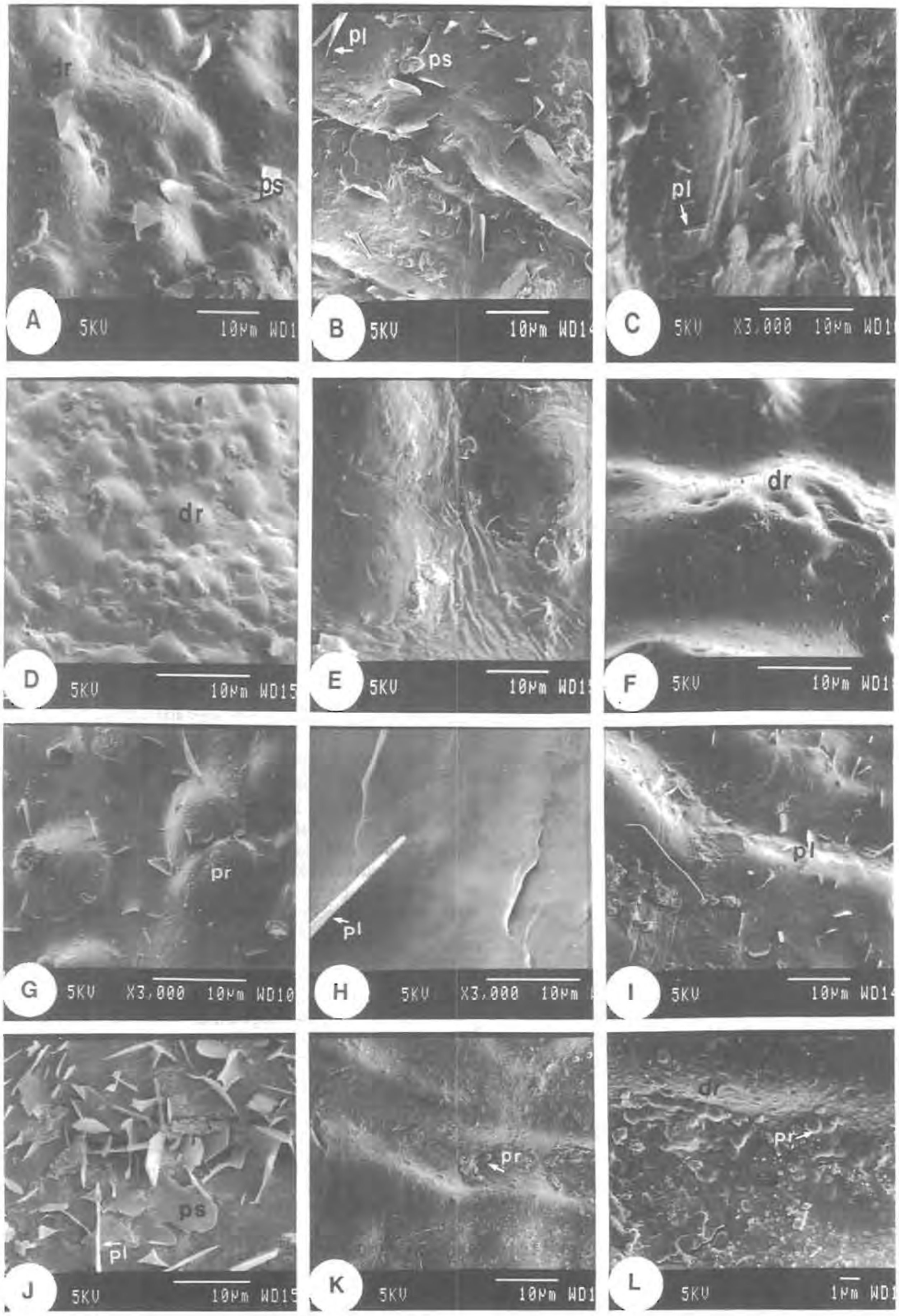

FIGURE 6.—SEM micrographs of abaxial leaf surfaces, the CM and epicuticular waxes in *Passerina*. A, B, *P. comosa, MacDonald 2125*: A, droplets present in epicuticular wax, platelets flaking from smooth wax coating; B, wax platelets flaking from smooth wax coating, plates present. C, *P. glomerata, Bredenkamp 973*, outer periclinal wall convex, plates scarce, square to oblong, raised 30°–90°; D, *P. ericoides, Bredenkamp 956*, droplets present in epicuticular wax; E, *P. obtusifolia, Bredenkamp 929*, smooth wax coating also covering domes. F, G, *P. burchellii, Stokoe 2542*: F, droplets at apices of domes; G, small round protrusions at apices of papillae. H, *P. filiformis, Bredenkamp 1016*, upright plates separate from surrounding wax, orientated at an angle to cell rows; I, *P. pendula, Bredenkamp 908*, plates frequent, perpendicular to cell rows, square to oblong, flat or raised; J, *P. rigida, Bredenkamp 1013*, platelets and plates ; K, L, *P. paleacea, Bredenkamp 961*, wax droplets, protrusions and flat shapeless lumps contributing towards soft wax coating or smooth layer. Abbreviations: dr, droplets in epicuticular wax; pl, plates; pr, small round protrusions of epicuticular wax; ps, platelets. Scale bars: A–K, 10 µm; L, 1 µm.

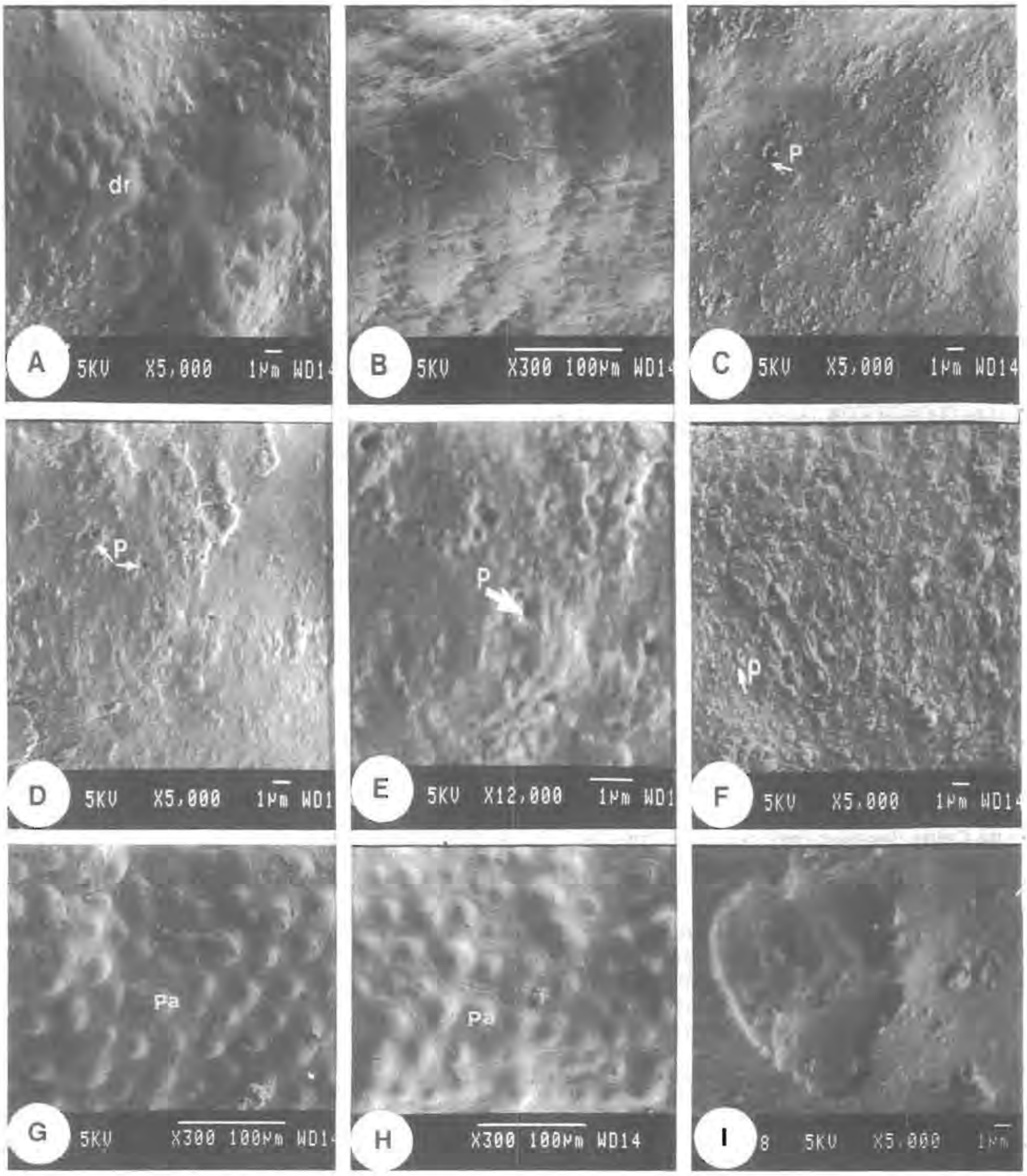

FIGURE 7.—SEM micrographs of abaxial leaf surfaces of *Passerina* washed in chloroform for one minute, compared to unwashed specimens. A–E, *P. paleacea*, *Bredenkamp 961*: A, unwashed leaf showing droplets in smooth wax coating; B, low magnification of washed leaf, showing CM devoid of epicuticular wax; C–E, higher magnifications showing pores in CM. F, *P. ericoides*, *Bredenkamp 956*, washed specimen showing pores in CM. G–I, *P. obtusifolia*, *Bredenkamp 929*: G, unwashed specimen; H, I, washed specimens showing corroded apices of papillae. Abbreviations: dr, droplets in epicuticular wax; p, pore; pa, papillae. Scale bars: A, C–F, I, 1 µm; B, G, H, 100 µm.

Haberlandt (1914), following a study of plants in tropical rain forests, considered the function of papillose epidermal cells as concentrating limited light by acting as lenses. Bredenkamp & Van Wyk (1999) speculate that, in *Passerina*, the convex outer periclinal epidermal cell wall may well focus light rays onto the mesophyll, whereas large vacuoles filled with phenols and the mucilage formed by the cellulose slimes (inner periclinal walls) protect the mesophyll from potentially dangerous UV-B radiation. According to Wilkinson (1979) the presence and prominence of papillae are diagnostically unreliable because they vary with the climate or distribution of the species; only morphologically distinct types can be used for diagnostic purposes. However, distinct epidermal cell papillae characterise *P. comosa*, *P. obtusifolia* *P. burchellii*, *P. drakensbergensis* and *P.* sp. nov. 2 (Figures 4B–C, G–L; 5A–C). The presence of these papillae could have been induced by the high light intensity of the areas in which these plants grow.

## Epicuticular waxes

In their study of the epicuticular waxes in the families of the Dilleniidae and Rosidae, Ditsch & Barthlott (1997) documented the numbers of genera, species and hybrids in which different wax types occur, without identifying the various taxa. The epicuticular waxes of 12 genera, 31 species and two hybrids were studied in the Thymelaeaceae. Of these, nine genera and 26 species have wax flakes, one species has angled platelets and four genera and five species have no crystalloids. Our observations indicate that the simple plate-type waxes found in *Passerina* correspond well to those described by Ditsch & Barthlott (1997) in the Thymelaeaceae. Of the 17 species in *Passerina*, two have wax flakes, eight have platelets or angled plates and seven are devoid of crystalloids (Figure 6, Table 3).

The mechanism of wax extrusion through the cuticle is highly controversial (Baker 1974; Jeffree *et al.* 1975; Hallam 1982). Baker (1982) discusses the extrusion of wax by means of 'pores and channels, the liquid extrusion theory, polymerization theory and the crystallization theory'. Hallam (1982) proposes that wax or wax precursors in their protein or glycoprotein 'shells' move through the cuticle and burst on the surface, liberating the wax from the 'package'; on crystallization, the protein coats stick to the surface as the wax crystals develop.

Our results indicate small pores in the cleaned, dewaxed cuticle of *P. paleacea* and *P. ericoides* (Figure 7B–F), after washing leaves in chloroform. Both Baker (1982) and Hallam (1982) are convinced that detailed investigations by many investigators have failed to confirm the presence of pores or microchannels in certain plant cuticles and that pores have not been shown to connect with the plasmalemma of the epidermal cytoplasm below. Although the presence of pores has been confirmed by our study, further research on the ultrastructure of the CM in *Passerina* could be most informative.

Freeman *et al.* (1979), working on *Citrus*, found amorphous wax layers on immature leaves and fruit, with small protrusions and isolated regions of upright platelets developing, eventually followed by cracks and irregular plates. Similarly in *Passerina*, wax droplets, protrusions and flat, shapeless lumps contribute towards a soft wax coating or a smooth layer. Species of *Passerina* with soft wax coatings, without platelets or plates, are summarised in Table 3. In *P. comosa*, *P. filiformis* and *P. rigida* (Figure 6B, H, J) platelets and plates are formed as a result of cracks developing on the outer wax surface, crystallising into irregularly shaped flakes, which gradually become square or oblong with 'entire' or 'non-entire' margins, often becoming distinctly edged. In *P. filiformis* (Figure 6H) upright plates separate from the surrounding wax, orientating themselves at an angle to the cell rows, eventually resulting in most plates being arranged more or less perpendicularly to the cell rows. Wax type, as well as the presence or absence of plates and platelets, is apparently genetically determined (Baker 1982). For example, *P. ericoides*, *P. rigida* and *P. paleacea* (Figure 6D, J, K) all grow along the sea shore, where they are subjected to wind, salt spray and high light intensity, and yet, *P. ericoides* and *P. paleacea* have coverings of soft waxes only, whereas platelets and plates are abundantly present in *P. rigida*. However, in plate waxes the number of platelets and plates, size, configuration and distribution of the surface wax structures can be considered as environmentally induced (Baker 1974, 1982).

### *Functions of epicuticular waxes*

Possible functions of epicuticular waxes are discussed by Jeffree (1986). In *Passerina*, large areas of the abaxial epidermis are exposed to the atmosphere because the inverse-ericoid leaves are usually closely appressed to the stem. In response to the warm, dry summers of the Mediterranean climate of the Cape, it is proposed that the CM, including the abaxial epicuticular waxes, has a water-proofing function, protecting the leaves against desiccation and limiting transpiration to the adaxial epidermis only. As the leaves are decussately arranged, the water-repelling function of the waxes would cause droplets of water to run off the abaxial epidermis, into the concave, hairy adaxial surface of the lower leaf, resulting in a decreased transpiration rate owing to the higher adaxial water concentration. According to Jeffree (1986) the wettability of the plant surface is determined by its microroughness. The presence of crystalloid platelets and plates, and especially their arrangement perpendicular to cell rows, may facilitate the retention of moisture.

### *Systematic value*

Epicuticular waxes have been proven taxonomically valuable, among others in the study of the Centrospermae (Engel & Barthlott 1988), Dilleniidae and Rosidae, including the Thymelaeaceae (Ditsch & Barthlott 1997), at sectional level in *Eucalyptus* L'Hér. (Hallam & Chambers 1970) and at species level in *Hordeum* L. (Baum *et al.* 1989). In *Passerina* the presence or absence of crystalloid platelets or plates combined with characteristics of the CM and the outer periclinal cell walls of the abaxial epidermis, makes it possible to distinguish between two groups in the genus. This distinction is species-specific for most of the 17 species examined (Table 3).

## Ecological aspects of leaf epidermis

The structure and function of the epidermis should be considered in context with gross leaf morphology and arrangement. Leaf arrangement is of vital importance to the physiology of the plant. The epidermis serves as an envelope, physically protecting the mesophyll, the largest part of the abaxial epidermis forming a multifunctional barrier to the environment. The thin adaxial epidermis is concealed in the groove of the cymbiform leaf in most cases; it is almost covered by dense, long, spiralised uniserial trichomes and contains the stomata, which are often raised. This arrangement is likely to reduce the rate of transpiration, especially if moisture can be retained by the indumentum. The abaxial epidermis is probably multifunctional. The whole of the CM has a waterproofing function and the epicuticular waxes also have a water-repelling function. At the same time the CM may play a major part in focusing light rays onto the palisade parenchyma. Large tanniniferous vacuoles may play a role in the possible absorption of UV-B radiation, and mucilage formed by the cellulose slimes (inner periclinal walls) possibly protects the mesophyll from desiccation (Bredenkamp & Van Wyk 1999).

The expansion and inrolling of the leaf margins in *Passerina*, as a result of changing turgor pressure in the epidermal cells, were described by Thoday (1921). He regards the main mechanism involved as the co-ordination between the turgor pressure and the difference in size and thickness of cell walls of the ad- and abaxial epidermis, whereas the plicate anticlinal cell walls of the abaxial epidermis protect the cells against bending stress. Stomata (or at least the indumentum) are exposed when the leaf margins expand and are protected in a villous groove when the leaf margins are rolled inwards, thus regulating the rate of transpiration.

## CONCLUSIONS

Leaf shape and structure in Thymelaeaceae exhibit a transformation series from mainly dorsiventral, the prevailing family feature, to isobilateral or centric in *Diarthron* Turcz., *Pimelea* Banks & Soland. and *Thymelaea* Juss. (Metcalfe & Chalk 1950). All the mentioned states are present in *Lachnaea* and *Cryptadenia* (Beyers 1992) and, as the most advanced state, inversely dorsiventral leaves in *Passerina*. A transformation series can also be illustrated by the presence of amphistomatic, hypostomatic and epistomatic leaves in the Thymelaeaceae (Metcalfe & Chalk 1950), the epistomatic state in *Passerina* considered to be the most advanced (the collateral vascular bundles of the leaves, with xylem arranged adaxially and phloem abaxially, rule out the possibility of resupination of the leaves).

The most pronounced epidermal characters of the Thymelaeaceae are anomocytic stomata (Metcalfe & Chalk 1950), unicellular trichomes and mucilagination of epidermal cells. In the present study the presence or absence, distribution of or changes in the above-mentioned structures, were used as distinguishing characters at both generic and species levels. Mucilagination of epidermal cells is often found both ad- and abaxially in the leaves of Thymelaeaceae. In *Passerina*, mucilagination takes place in the abaxial epidermis only. At species level the sunken stomata and stomatal crypts of *Passerina* sp. nov. 1 are used in the delineation of the new taxon and *P. comosa* is distinguished by the presence of unicellular trichomes on the abaxial surface of the leaves.

On the basis of abaxial cuticular characters, it has been possible to distinguish two groups of species in the genus. Group A comprises *P. burchellii* Thoday, *P. comosa* C.H.Wright, *P. ericoides* L., *P. glomerata* Thunb. and *P. obtusifolia* Thoday. Group B comprises *P. drakensbergensis* Hilliard & B.L.Burtt, *P. falcifolia* C.H.Wright, *P. filiformis* L., *P. galpinii* C.H.Wright, *P. montana* Thoday, *P. paleacea* Wikstr., *P. paludosa* Thoday, *P. pendula* Eckl. & Zeyh., *P. rigida* Wikstr., *P. rubra* C.H.Wright, *P. vulgaris* Thoday, *P.* sp. nov. 1, *P.* sp. nov. 2, *P.* sp. nov. 3 and *P.* sp. nov. 4. Certain species in each of the two groups seem to be naturally allied. Distribution patterns of *P. obtusifolia* and *P. glomerata* coincide at Worcester and transitional types can be clearly distinguished. Transitional types are similarly present in *P. filiformis* and *P. vulgaris* in the Cape Peninsula and in *P. filiformis* and *P. falcifolia* near Knysna.

Hence it can be concluded that the conspicuous differences as well as the concise characters of the ad- and abaxial epidermis, critically described and discussed in this paper, can be used as taxonomic tools at the family, genus and species levels. Furthermore, the leaf epidermis in *Passerina* is probably most valuable to the plant in terms of ecological adaptation, considering the wide distribution of the genus in southern Africa as well as the accompanying geographical and climatic variation. The gross leaf morphology and the ad- and abaxial epidermal characters have been most useful in the interpretation of the possible functioning of the leaves and are of vital importance in the survival strategies of the plant.

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## 4.4 Leaf anatomy

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CONTENTS

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

C.L. BREDENKAMP* and A.E. VAN WYK**

**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 | *P.* sp. nov. 1 | High altitudes, Ceres Karoo | Rocky areas, often covered by snow in winter |
| B1 | *P. burchellii* | High mountains of Genadendal and Villiersdorp | South-facing rocky outcrops on mountain summits |
| B1 | *P. pendula* | KwaZunga Catchment Basin and Zwartkops River area of Eastern Cape | On moutain slopes, zone between valley bushveld and fynbos, also on plains and roadsides |
| B2 | *P. comosa* | Kamiesberg, Great Winterhoek and Klein Swartberg Ranges | Mountain slopes and summits |
| B2 | *P. paludosa* | E of Muizenberg | Rare in salt marshes on lowland flats |
| B2, B3 | *P. galpinii* | Agulhas Plain area | Calcrete, in stony areas, fields, disturbed areas and roadsides |
| B3 | *P. drakensbergensis* | 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 | *P. ericoides* | Beaches of Western Cape | In salt spray, on cliff faces overhanging sea, on primary dunes |
| B3 | *P.* sp. nov. 2 | Northern Cederberg Mountains | Between large rocks at mountain tops |
| B3 | *P.* sp. nov. 3 | Mountain tops of Uitenhage area and Swartberg Pass, Kouga Mountains and Montagu Pass | In rocky areas and rock crevices |
| B4 | *P. rubra* | Port Elizabeth to Uitenhage with outliers in Swellendam and Bredasdorp Dist. | In rocky areas, on flatter areas, roadsides and disturbed areas |
| B3, B4 | *P. filiformis* L. subsp. *filiformis* | 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 | *P. filiformis* L. subsp. nov. | From Malmesbury NE to Vredendal | Deep acid sands |
| B2, B3, B4, B5 | *P. obtusifolia* | 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 | *P. glomerata* subsp. *glomerata* | Worcester to Tulbagh, in Clanwilliam area, extending to Witteberg S of Matjiesfontein | Large range of Karoo habitats, mostly dry rocky areas |
| B6 | *P. glomerata* subsp. nov. | From Cederberg Mountains, along mountain summits to Cape Peninsula | Rocky crevices on mountain tops and slopes |
| C | *P. falcifolia* | Mountainous areas between George and Uitenhage | On rocky slopes, on mountain passes, roadsides and in flatter field areas |
| C | *P.* sp. nov. 4 | 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 | *P. montana* | 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 | *P. paleacea* | Beaches and salt marshes of Western Cape | On primary and secondary dunes as well as rocky areas near sea shore |
| B3, B6, D2 | *P. rigida* | 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 | *P. vulgaris* | From Western Cape to East London in Eastern Cape | In rocky places on mountain slopes and valleys, pioneer in disturbed places, along roads, even on secondary dunes on coast |

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

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

### *Thickness of the main vascular bundle*

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

### *Leaf width*

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

## Terminology

### *Epidermal structure*

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

### *Cuticle*

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

### *Cuticular ornamentation (LM and SEM)*

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

### *Epicuticular wax*

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

### *Leaf anatomy*

The definitions of dorsiventral and isobilateral leaves (Eseau 1965; Metcalfe 1979; Fahn 1982; Mauseth 1988) are accepted in the present study. However, we follow Kugler (1928) who coined the term 'inverse-dorsiventral' for leaves where the palisade parenchyma develops abaxially, because the abaxial epidermis is exposed to the environment. In addition to leaf symmetry, the works of the above-mentioned authors as well as those of Solereder (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 trullate. *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 | Inverse-dorsiventral | | | | arranged randomly | arranged in rows | | | |
| | Type A | Type B | Type C | Type D | | Group A | Group B | Smooth | Papillate | Striate |
| *P.* sp. nov. 1 (Figure 3A) | A | | | | | | X | | X | |
| *P. burchellii* | | B1 | | | | X | | | X | |
| *P. pendula* (Figure 3B) | | B1 | | | | | X | | | X |
| *P. comosa* | | B2 | | | X | | X | | X | |
| *P. paludosa* (Figure 3C) | | B2 | | | | | X | | | X |
| *P. galpinii* (Figure 2C) | | B2, B3 | | | | | X | | | X |
| *P. drakensbergensis* | | B3 | | | | | X | | X | |
| *P. ericoides* (Figure 3D) | | B3 | | | | X | | X | | |
| *P.* sp. nov. 2 | | B3 | | | | | X | | X | |
| *P.* sp. nov. 3 | | B3 | | | X | | X | X | X | |
| *P. rubra* | | B4 | | | | | X | | | X |
| *P. filiformis* subsp. *filiformis* (Figure 3E) | | B3, B4 | | | | | X | | | X |
| *P. filiformis* subsp. nov. | | B4, B6 | | | | | X | | | X |
| *P. obtusifolia* (Figure 3G) | | B2, B3, B4, B5 | | | | X | | | X | |
| *P. glomerata* subsp. *glomerata* (Figure 3F) | | B2, B3, B5 | | | | X | | X | | |
| *P. glomerata* subsp. nov. | | B6 | | | | X | | | X | |
| *P. falcifolia* (Figure 4A) | | | C | | | | X | | | X |
| *P.* sp. nov. 4 (Figure 4B) | | | C | | | | X | | | X |
| *P. montana* (Figure 4C) | | B2, B3 | | D1 | | | X | X | X | |
| *P. paleacea* (Figure 4D) | | B2, B3, B4 | | D2 | | | X | | | X |
| *P. rigida* (Figures 3H, 4E) | | B3, B6 | | D2 | | | X | | | X |
| *P. vulgaris* (Figure 4F) | | | | D2 | | | X | | | X |

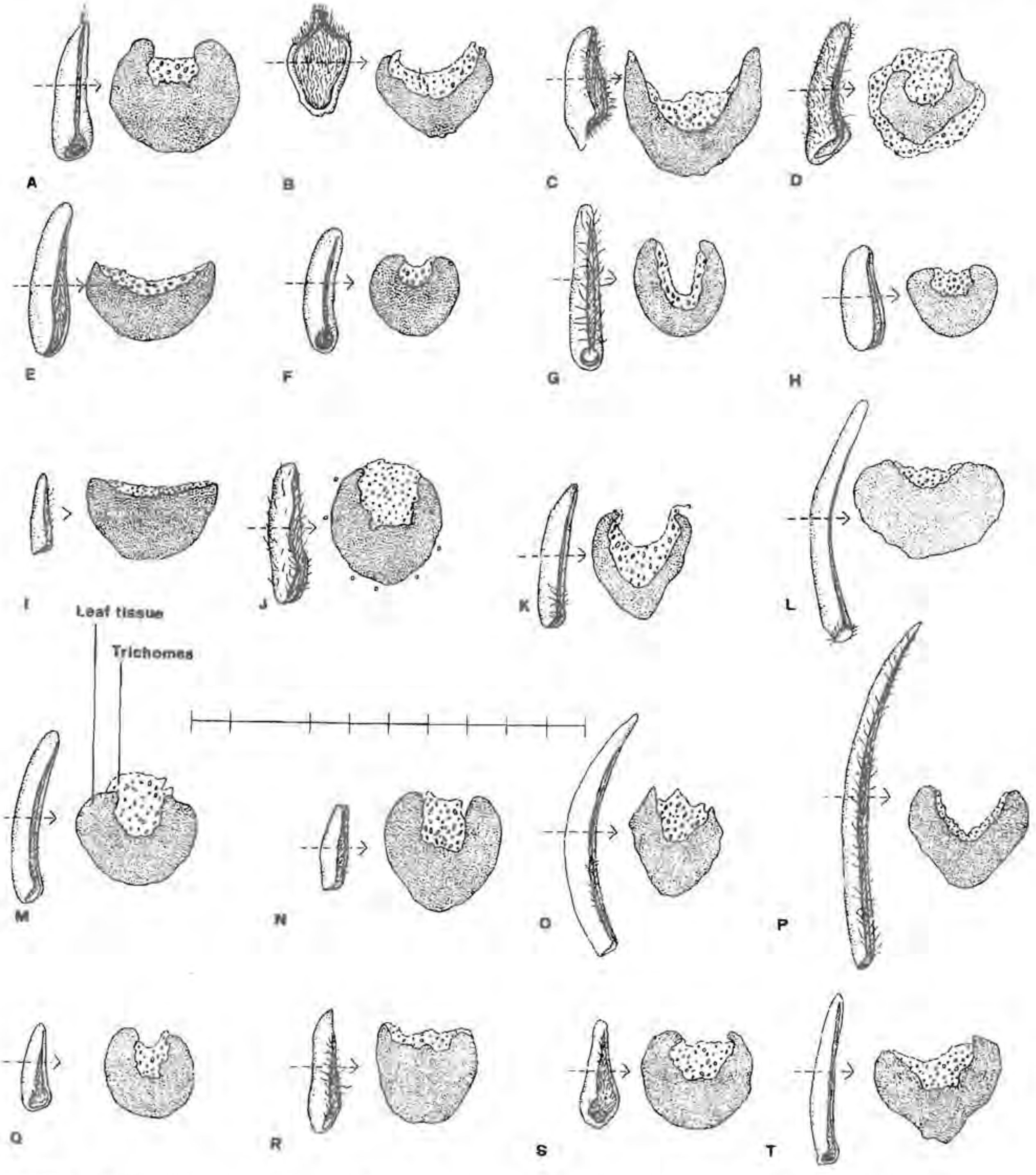

FIGURE 1.—Camera lucida drawings of leaves of *Passerina* species arranged according to leaf structural type (Table 3), correlating leaf shape to outline of leaves in t/s: A, *P.* sp. nov. 1, *Bredenkamp 1044*; B, *P. burchellii, Bolus 684*; C, *P. pendula, Bredenkamp 908*; D, *P. comosa, Andreae 1288*; 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. obtusifolia, Bredenkamp 919*; N, *P. glomerata* subsp. *glomerata, Bredenkamp 984*; O, *P. falcifolia, Bredenkamp 917*; P, *P. sp. nov. 4, Bredenkamp 1016*; Q, *P. montana, Bredenkamp 889*; R, *P. paleacea, Bredenkamp 960*; S, *P. rigida, Bredenkamp 911*; T, *P. vulgaris, Bredenkamp 901*. Leaf size A–T × 20. Scale bar: 10 mm; leaves in t/s not to scale.

### *Tanniniferous substances*

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

### *Crystals*

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

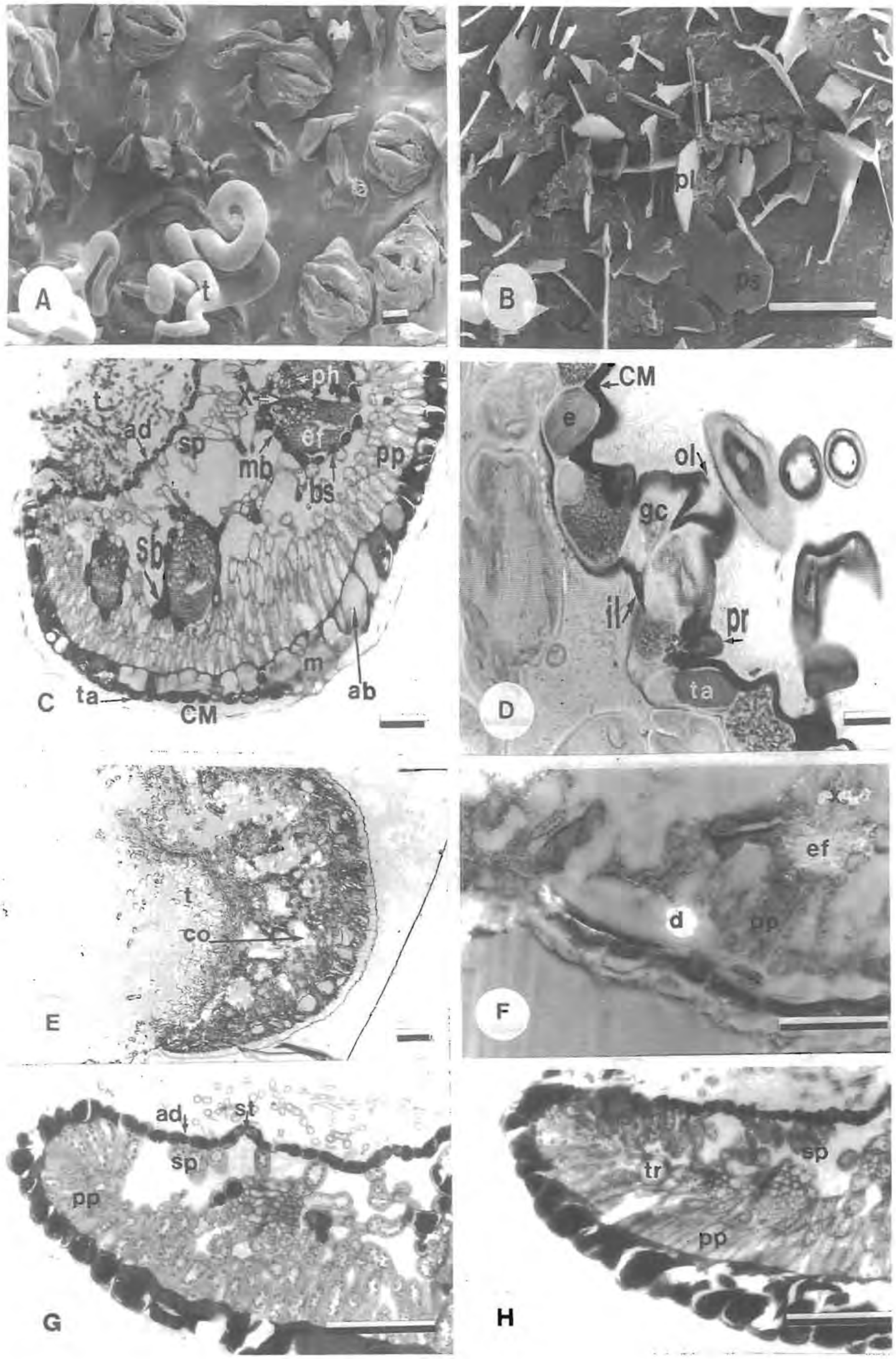

FIGURE 2.—A, B, SEM micrographs of trichomes and epicuticular waxes: A, *P. falcifolia*, *Bredenkamp 915*; B, *P. rigida*, *Bredenkamp 1013*. C–H, LM photographs of leaf: C, *P. galpinii*, *Bredenkamp 946*; D, *P. pendula*, *Bredenkamp 909*, stomatal apparatus in adaxial epidermis stained with Sudan Black B; E, *P. paleacea*, *Pillans 3783*, calcium oxalate crystals and druses in polarized light; F, *P. falcifolia*, *Tyson 1449*, cluster crystal from ruptured palisade parenchyma in polarized light; G, *P. drakensbergensis*, *Bredenkamp 1019*, mesophyll in leaf margin; H, *P. glomerata* subsp. *glomerata*, *Bredenkamp 977*, mesophyll and tracheid in leaf margin. ab, abaxial epidermis; ad, adaxial epidermis; bs, bundle sheath; c, cambial cells; CM, cuticular membrane; co, calcium oxalate crystals; cy, collenchyma; d, druse; e, epidermal cell; ef, extraxylary 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, tanniniferous compounds; tr, tracheid; X, xylem. Scale bars: A, B, D, 10 µm; C, E–H, 100 µm.

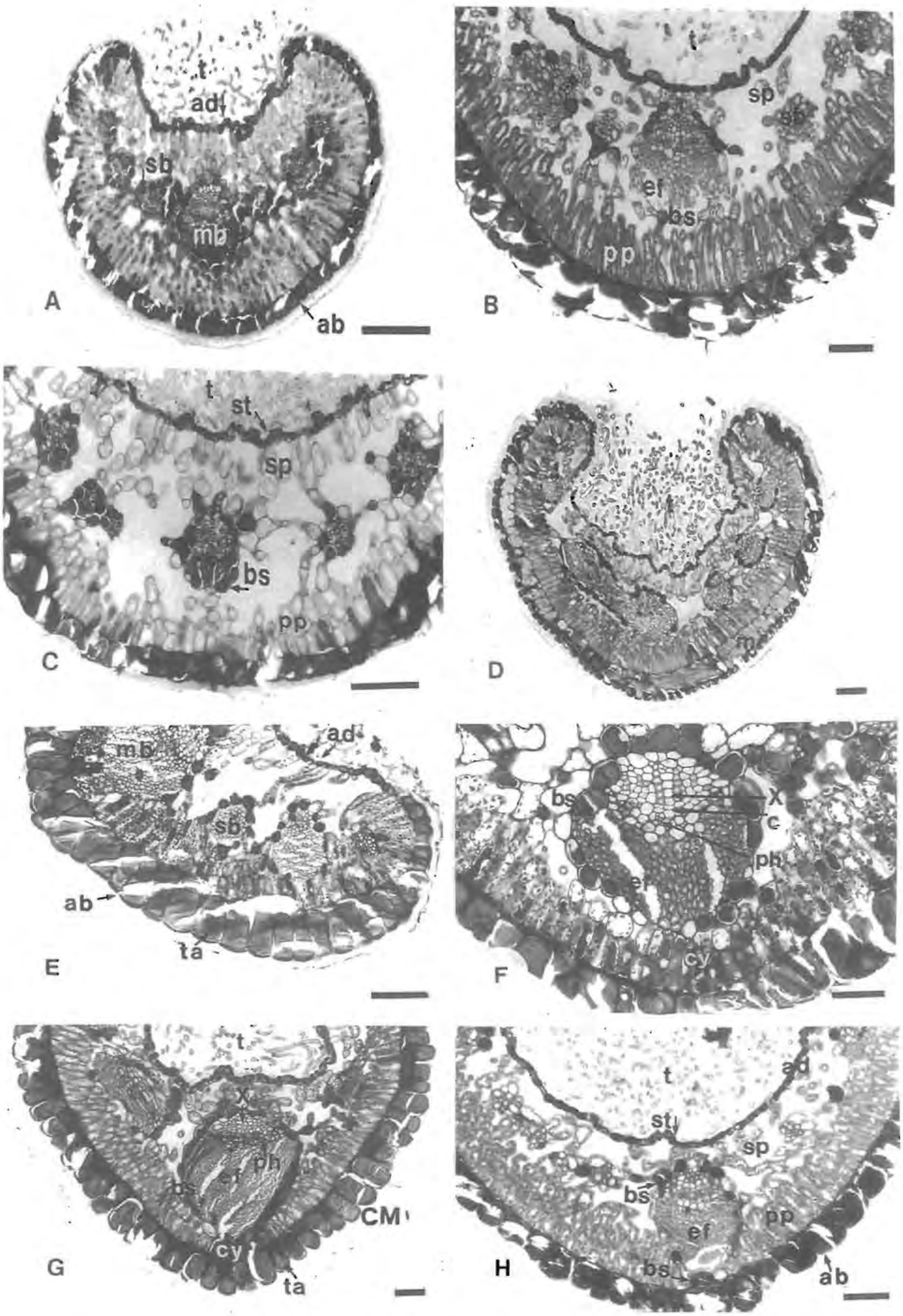

FIGURE 3.—LM photographs of leaf structural types A and B. Type A: A, *P.* sp. nov. 1, *Bredenkamp 1044.* Type B1: B, *P. pendula, Bredenkamp 908.* Type B2: C, *P. paludosa, Bredenkamp 1035.* Type B3: D, *P. ericoides, Bredenkamp 962.* Type B4: E, *P. filiformis* subsp. *filiformis, Bredenkamp 1039.* 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 µm.

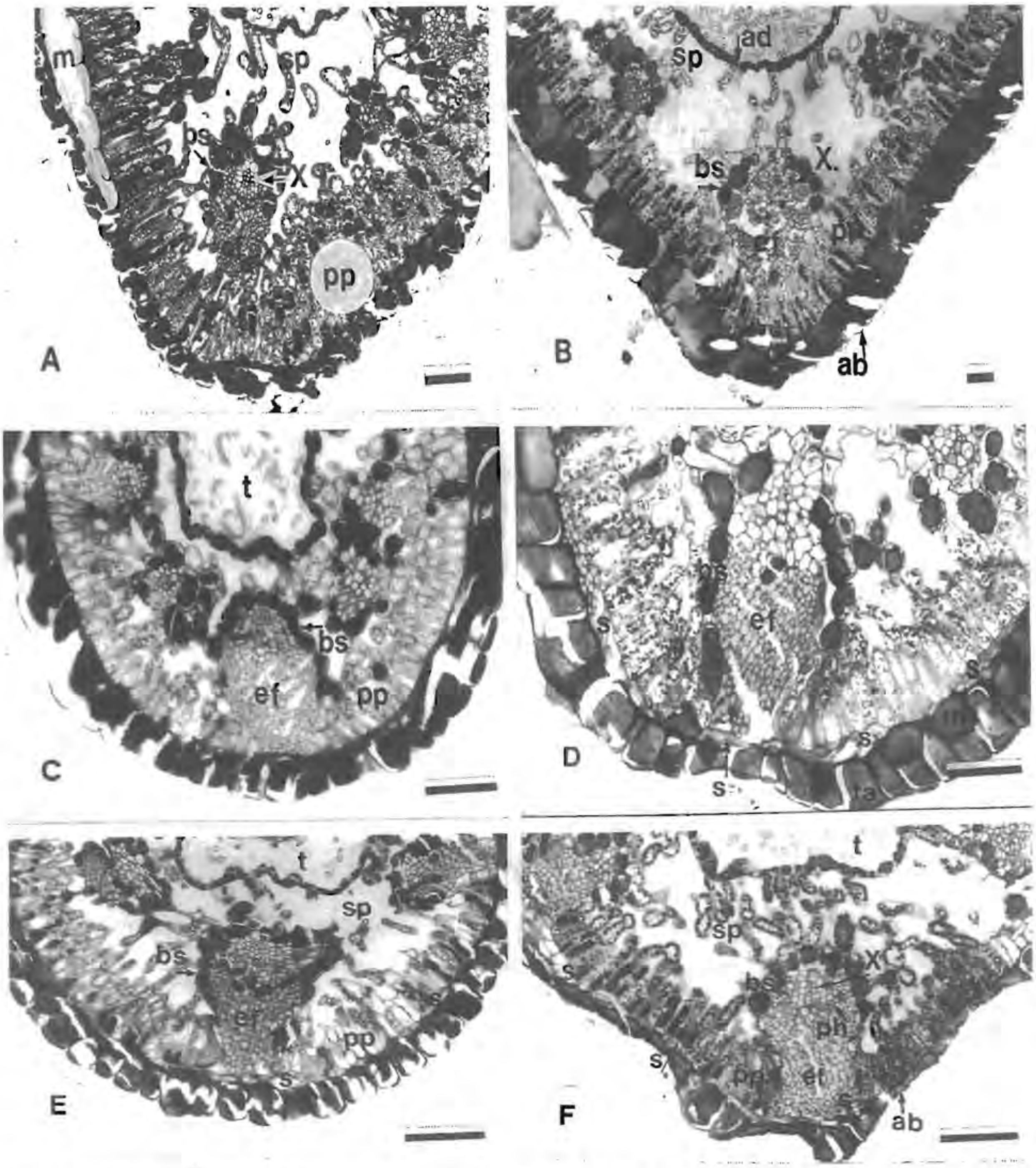

FIGURE 4.—LM photographs showing leaf structural types C and D. Type C: A, *P. falcifolia*, *Bredenkamp 917*; B, *P.* sp. nov. 4, *Bredenkamp 1016*. Type D1: C, *P. montana*, *Bredenkamp 889*. Type D2: D, *P. paleacea*, *Bredenkamp 960*; E, *P. rigida*, *Bredenkamp 962*; F, *P. vulgaris*, *Bredenkamp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

### *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) µm. *Midrib* often raised below owing to supporting sclerenchyma fibres, cymbiform leaf folding along reinforced midrib; thickness of main vein (260–)440(–560) µm. *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 µm; cells narrowly elliptic to elliptic in isobilateral leaves or elongated in inverse-dorsiventral leaves, containing chloroplasts, tanniniferous deposits and druse crystals. *Spongy parenchyma* in isobilateral leaves ± 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-dorsiventral 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 × anticlinal dimensions in t/s 30–65 × (–35)55–60 (–70) µm:
9a Palisade parenchyma U-shaped . . . . . . . . . . . . . . . . *P. paleacea*
9b Palisade parenchyma horseshoe-shaped . . . *P. galpinii*, *P. drakensbergensis*, *P. ericoides* (Figure 3D), *P. rigida*, *P. montana*
8b Abaxial epidermal cells exceptionally large, abundantly tanniniferous, mucilagination minimal, periclinal × anticlinal dimensions in t/s (20–)30–45(–50) × (25–)30–75(–105) µm:
10a Outline of leaf in t/s transversely elliptic to cordiform . . . . . . . . . . . . . . . . *P. obtusifolia* (Figure 1M), *P. glomerata* subsp. *glomerata* (Figure 1N), *P. filiformis* subsp. *filiformis* (Figures 1L)
10b Outline of leaf in t/s not transversely elliptic, depressed obovate or canaliculate respectively . . . . . . . . . . . . . . . . *P.* sp. nov. 2 (Figure 1I), *P.* sp. nov. 3 (Figure 1J)
7b Main vascular bundle sunken into palisade parenchyma, causing specialization of, or extending beyond palisade parenchyma:
11a Palisade parenchyma indented because of sunken main vascular bundle . . . type B4:
12a Abaxial epidermal cells strongly mucilaginous, periclinal × anticlinal diam. in t/s 30–65 × 45–60 µm:
13a Leaf outline in t/s canaliculate; secondary vascular bundles ± 6 on each side of main bundle . . . *P. rubra* (Figure 1K)
13b Leaf outline in t/s transversely oblong, margins erect; secondary vascular bundles 3 or 4 on each side of main bundle . . . . . . . . . . . . . . . . *P. paleacea* (Figure 1R)
12b Abaxial epidermal cells strongly tanniniferous, periclinal × anticlinal cell diam. in t/s (35–)40–45 × 45–75 (–105) µm . . . . . . . . . . . . . . . . *P. filiformis* subsp. *filiformis* (Figure 3E), *P. filiformis* subsp. nov., *P. obtusifolia*
11b Palisade parenchyma abaxial of main vascular bundle specialized, or main vascular bundle extending beyond palisade parenchyma:
14a Main vascular bundle separated from abaxial epidermis by collenchyma containing ample amounts of 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, ± 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, ± 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 epidermal 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 xeromorpic 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 tanniniferous 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 | Main vascular bundle | Bundle sheath enveloping main vascular bundle | | | Secondary vascular bundles | Palisade parenchyma | | | Spongy parenchyma |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Structural type | Outline | Width µm | | Width µm | Shape | Completely | Adaxial cap | No. cells | No. (each side of main bundle) | Shape | No. layers | No. cells per 50 µm | |
| *P.* sp. nov. 1 (Figure 3A) | A | transversely elliptic | ± 850 | | ± 450 | widely ovate | X | | 19–25 | 3 or 4 | | adaxial 3<br>abaxial 4 | 3 | |
| *P. burchellii* | B1 | narrowly transversely elliptic | ± 1480 | | ± 540 | widely ovate | X | | ± 20 | 4 | horseshoe | 1 or 2 | 4 | aerenchymatic |
| *P. pendula* (Figure 3B) | B1 | canaliculate | 780–860 | | ± 340 | widely ovate | X | | 17–19 | 4–9 | horseshoe | 1 or 2 | 4 or 5 | aerenchymatic |
| *P. comosa* | B2 | transversely elliptic | ± 940 | | ± 460 | oblate | X | | ± 22 | 3–5 | horseshoe/V | 3 or 4 | 4 or 5 | mesomorphic |
| *P. paludosa* (Figure 3C) | B2 | narrowly transversely elliptic | 990–1140 | | 410–460 | ovate | X | | 19–20 | 3–5 | horseshoe | 1 | 3 or 4 | aerenchymatic |
| *P. galpinii* (Figure 2C) | B2, B3 | transversely elliptic | 1000–1150 | | 520–550 | widely ovate | X | | 18–25 | 3 | horseshoe | 1 or 2 | 3 or 4 | aerenchymatic |
| *P. drakensbergensis* | B3 | canaliculate | 720–830 | | 370–400 | widely ovate | X | | 17–19 | 3 or 4 | horseshoe | 1 or 2 | 3 or 4 | aerenchymatic |
| *P. ericoides* (Figure 3D) | B3 | transversely elliptic | 910–1100 | | 390–470 | oblate | X | | ± 22 | 3 | horseshoe | 2 or 3 | 3 | aerenchymatic |
| *P.* sp. nov. 2 | B3 | depressed obovate | ± 720 | | 300–360 | widely ovate | X | | 23–28 | 2 or 3 | horseshoe | 1 or 2 | 4 or 5 | mesomorphic |
| *P.* sp. nov. 3 | B3 | canaliculate | 810–880 | | 380–430 | very widely ovate | X | | 18–27 | 3 | horseshoe | 1 or 2 | 4 or 5 | aerenchymatic |
| *P. rubra* | B4 | canaliculate | 800–920 | | 330–400 | widely ovate | X | | 23–28 | 6 | horseshoe | 1 or 2 | 4 or 5 | aerenchymatic |
| *P. filiformis* subsp. *filiformis* (Figure 3E) | B3, B4 | cordiform | 780–860 | | 350–420 | widely ovate | X | | 13–15 | 3 or 4 | horseshoe | 1 or 2 | 3–5 | aerenchymatic |
| *P. filiformis* subsp. nov. | B4, B6 | transversely elliptic | ± 820 | | ± 400 | widely ovate | X | | ± 27 | 2 or 3 | horseshoe | 2 | 5 | aerenchymatic |
| *P. obtusifolia* (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 |
| *P. glomerata* subsp. *glomerata* (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 |
| *P. glomerata* subsp. nov. | B6 | canaliculate | 770–830 | | 420–430 | ovate | X | | 22–25 | 2–4 | horseshoe | 2 | 3 or 4 | mesomorphic |
| *P. falcifolia* (Figure 4A) | C | carinate | 900–960 | | 520–550 | obovate | | X | 12–14 | 3 or 4 | V | 1 or 2 | 3 or 4 | aerenchymatic |
| *P.* sp. nov. 4 (Figure 4B) | C | carinate | 820–1280 | | 400–700 | obovate | | X | ± 21 | 3 or 4 | V | 2 | 3 or 4 | aerenchymatic |
| *P. montana* (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 |
| *P. paleacea* (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 |
| *P. rigida* (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 |
| *P. vulgaris* (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 vasular bundle adaxially or centrally arranged. An increase in the density, the number of cells and layers and specialization of tissues takes place in types B3 and B4, with B5 and B6 representing the most xeromorphic forms. A similar increase in xeromorphism can be shown in structural types C and D1 and D2, with the abaxial arrangement of the main vascular bundle, the increase in sclerenchyma tissue and the ultimate formation of the sclerenchymatous hypodermal sheath, in type D2, as the most xeromorphic state.

### *Ecological significance*

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

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

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

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

Type B5: xeromorphism is enhanced in *P. glomerata* subsp. *glomerata* and *P. obtusifolia* (Figure 3F, G), both growing in the warm, arid Karoo. The main vascular bundle is abaxially embedded in palisade parenchyma which differentiates into collenchyma and the spongy parenchyma surrounding the main vascular bundle which is more densely arranged with smaller intercellular spaces. This more xeromorphic arrangement mechanically strengthens the leaf, allows moisture for physiological processes but possibly retards loss of water.

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

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

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

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

### Sclerenchyma

#### *Prevailing characters in Thymelaeaceae*

Van Tieghem (1893) described extraxylary fibres, specially mentioning those without lignification in *Daphne mezereum* L. and with lignification in *D. cneorum* L. Supprian (1894), mentioned the presence of fibres in the mesophyll of the leaves, which he called 'Spicularzellen' and regarded as a constant taxonomic character. In a subsequent paper, Gilg (1894), critically discussed the anatomical method applied by the two previous workers, doubting the constant taxonomic value of 'Spicularzellen'. Thoday (1921) described a sclerenchymatous hypodermal sheath extending to the margins of the leaves in *P. filiformis* and *P.* cf. *falcifolia*, introducing the term 'wandering fibres'. Metcalfe & Chalk (1950) acknowledged the previous works, also mentioning the presence of bundles of sclerenchymatous elements supporting leaf margins in species of *Daphnopsis* C.Mart., *Dicranolepis* Planch. and *Passerina*.

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

### Less important taxonomic characters

#### *Leaf width*

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

#### *Crystals*

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

#### *Tanniniferous substances*

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

## Phylogenetic considerations

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

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

### *Mesophyll*

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

### *Sclerenchyma*

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

## Taxonomic significance

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

### *Family level*

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

### *Genus level*

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

### *Species level*

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

BREDENKAMP, C.L. & VAN WYK, A.E. 2001b. Taxonomic significance of inflorescences, floral morphology and anatomy in *Passerina* (Thymelaeaceae). *Bothalia* 31: 213–236.

### CONTENTS

Bothalia 31,2: 213–236 (2001)

# 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

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 rbc*L* 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 | Thymelaearum | | | | | | |
| Class | | Thymelaeae | | | | | |
| Order | | Daphnoideae | Thymelaeaceae | Thymelaeaceae | | | |
| Family | | | | | Thymelaeaceae | Thymelaeaceae | Thymelaeaceae |
| Subfamily | | | | | Thymelaeoideae | | Thymelaeoideae |
| Tribe | | Thymelinae | Gnidieae | Euthymelaeceae | Daphneae | Thymelaeoideae | Gnidieae |
| Subtribe | | Passerineae | Diplostemoneae | | Passerininae | Passeriniinae | Passerininae |
| 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 cylindric, 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, micropyle beak-like |

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 | Thymelaeales | | | | | | |
| Class | | | | | 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 | Thymelaeeae (= *Gnidieae)* | | | | | | |
| Subtribe | | | | | | | |
| Series | | | | | | | |
| Division | | | | | | | |
| Relationships | Myrtales: perianth tube<br>Malvales: pollen morphology | placed between Bixales and Proteaceae | placed between Dillenianae (including Malvales) and Myrtanae | 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 hypanthium | | | calyx tube cylindric |
| 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) | | diplostemonous | diplostemonous | diplostemonous | | | diplostemonous |
| Gynoecium (G) | pseudomonomerous | ovary superior | unilocular; ovules pendulous, epitropous, bitegmic, crassinucellate; endosperm nuclear | pseudomonomerous; ovules pendulous | pseudomonomerous; ovules solitary | | 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 *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, *Muntingia* |
| 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 |

* 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 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.

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

| 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* | WESTERN CAPE.—3320 (Montagu): Montagu District, near Concordia, (–CD). |
| | *Andreae 1288**, *MacDonald 2125* | WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (–AD). |
| *drakensbergensis* Hilliard & B.L.Burtt | *Edwards 974* | KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB). |
| | *Bredenkamp 1018, 1019, 1020, 1021** | KWAZULU-NATAL.—2829 (Harrismith): Ndedema Gorge, Cathedral Peak Forest Reserve, (–CD). |
| *ericoides* L. | *Bredenkamp 956*• | WESTERN CAPE.—3318 (Cape Town): Milnerton, (–CD). |
| | *Bredenkamp 962*•* | 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). |
| | *Tyson 1449* | WESTERN CAPE.—3423 (Knysna): Knysna, (–AA). |
| *filiformis* L. subsp. *filiformis* | *Boucher 2833* | WESTERN CAPE.— 3118 (Van Rhynsdorp): Clanwilliam Dist., Diepkloof S of Verlorevlei, (–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 Cave, (–CC). |
| *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). |
| | *Bredenkamp 923* | WESTERN CAPE.—3422 (Mossel Bay): Mossel Bay, (–AA). |
| *glomerata* Thunb. subsp. *glomerata* | *Bredenkamp 988* | WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Eikeboom, (–AC). |
| | *Bredenkamp 994* | WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Kromrivier, (–AC). |
| | *Bredenkamp 1002* | WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, Algeria, (–AC). |
| | *Bredenkamp 984, 985** | WESTERN CAPE.—3219 (Wuppertal): Citrusdal, Piekenierskloof Pass, (–CD). |
| | *Bredenkamp 977* | WESTERN CAPE.—3219 (Wuppertal): Groenfontein, (–DC). |
| | *Bredenkamp 973** | WESTERN CAPE.—3319 (Worcester): Tulbagh, (–AC). |
| *glomerata* Thunb. subsp. nov. | *Stokoe 8040* | WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains. |
| | *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* | MPUMALANGA.—2430 (Pilgrim's Rest): God's Window, (–DD). |
| | *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 CAPE.—3319 (Worcester): Karoo National Botanical Garden, (–CB). |
| | *Bredenkamp 967* | WESTERN CAPE.—3319 (Worcester): Jonaskop, (–CD). |
| | *Bredenkamp 1033, 1034* | WESTERN CAPE.—3321 (Laingsburg): Seweweekspoort, (–AD). |
| | *Bredenkamp 929* | WESTERN CAPE.—3321 (Ladismith): Rooiberg, (–CB). |
| | *Bredenkamp 919** | WESTERN CAPE.—3322 (Oudtshoorn): Perdepoort, (–CD). |
| *paleacea* Wikstr. | *Bredenkamp 960** | WESTERN CAPE.—3418 (Simonstown): Kommetjie, (–AB). |
| | *Bredenkamp 961* | WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD). |
| | *Bredenkamp 952* | WESTERN CAPE.—3418 (Simonstown): Harold Porter National Botanical Garden, (–BD). |
| | *Bredenkamp 950* | WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD). |
| | *Bredenkamp 949* | 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). |
| | *Jangle 156** | WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (–BA). |
| | *Thoday 100* | WESTERN CAPE.—3418 (Simonstown): Riet Valley, Cape Flats, (–BA). |
| *pendula* Eckl. & Zeyh. | *Fourcade 3043* | EASTERN CAPE.—3324 (Steytlerville): 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 1013** | KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Mouth, (–AA). |
| | *Bredenkamp 899* | EASTERN CAPE.—3326 (Grahamstown): Kenton-on-Sea, (–DA). |
| | *Bredenkamp 898* | EASTERN CAPE.—3326 (Grahamstown): Port Alfred, (–DB). |
| | *Bredenkamp 897* | EASTERN CAPE.—3327 (Peddie): Kleinmond West, (–CA). |
| | *Bredenkamp 911* | EASTERN CAPE.—3424 (Humansdorp): Jeffreys Bay, (–BB). |
| *rubra* C.H.Wright | *Bredenkamp 914** | EASTERN CAPE.—3324 (Steytlerville): en route to Kareedouw, (–CD). |
| | *Bredenkamp 905* | EASTERN CAPE.—3325 (Port Elizabeth): Colchester, (–DB). |
| | *Bredenkamp 900* | EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD). |
| *vulgaris* Thoday | *Bredenkamp 926* | WESTERN CAPE.—3321 (Ladismith): en route to Korenthe River Dam, (–CC). |
| | *Bredenkamp 907* | EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB). |
| | *Bredenkamp 901* | EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD). |
| | *Bredenkamp 951*• | 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). |
| | *Bredenkamp 1044, 1046, 1047* | WESTERN CAPE.—3319 (Worcester): Waboomberg, Ceres, (–AD). |
| | *Oliver 9281** | |
| sp. nov. 2 | *Esterhuysen 12189, 26859** | WESTERN CAPE.—3218 (Clanwilliam): Northern Cederberg Mountains, (–BB). |
| sp. nov. 3 | *Stokoe 9302* | WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, Prince Albert area, (–AC). |
| | *Schlechter 5846* | WESTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–CD). |
| | *Esterhuysen 10734** | EASTERN CAPE.—3323 (Willowmore): Kouga Mountains, (–DA). |
| | *Esterhuysen 28006** | EASTERN CAPE.—3324 (Steytlerville): Cockscomb, Uitenhage area, (–BD). |
| sp. nov. 4 | *Killick 238* | KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (–CB). |
| | *Bredenkamp 1016, 1017* | KWAZULU-NATAL.—3030 (Port Shepstone): Oribi Gorge, (–CB). |
| | *Van Wyk & Bredenkamp 1, 1012* | KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (–AA). |
| | *Bredenkamp 1327** | KWAZULU-NATAL.—3130 (Port Edward): Mkambati Nature Reserve, (–AC). |
| | *Gillett 4537* | WESTERN CAPE.—3422 (Mossel Bay): en route to Knysna from George, (–BB). |
| | *Keet s.n.* | WESTERN CAPE.—3423 (Knysna): Knysna, Redlands, (–AA). |

* Illustrated specimens; • specimens used for light microscopy.

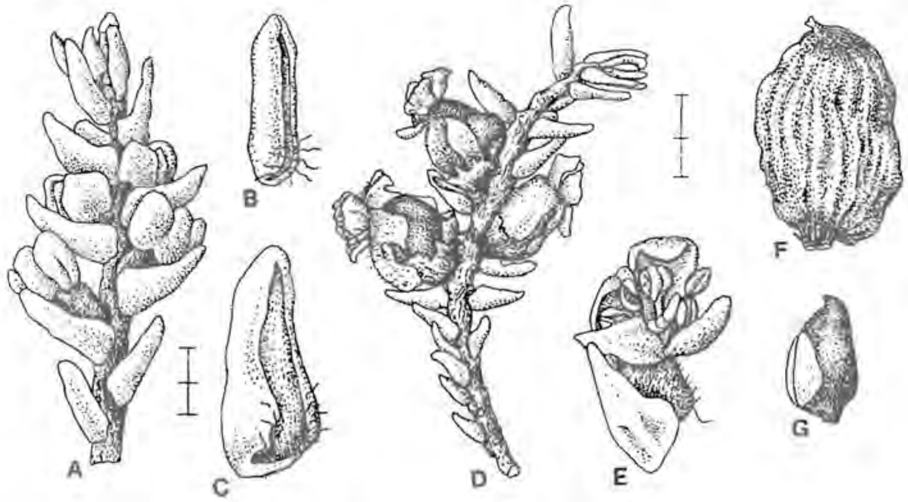

FIGURE 1.—*Passerina ericoides*. A–G, *Bredenkamp 962*. A, young inflorescence; B, leaf exposing adaxial surface; C, bract exposing adaxial surface; D, fruiting branchlet; E, flower enveloped by bract; F, fleshy one-seeded berry; G, seed with black tegmen and white fragment of endocarp. A, D, × 10; B, 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 (boat-shaped) 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 × $^1/_2$ width (2.5–)3.5–4.5(–5.5) × (0.9–)1.0–1.5(–2.4) mm; bracts with leaf-like point, length × $^1/_2$ width (4.0–)5.1–6.3(–7.3) × (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 ± 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-tinged. *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*).

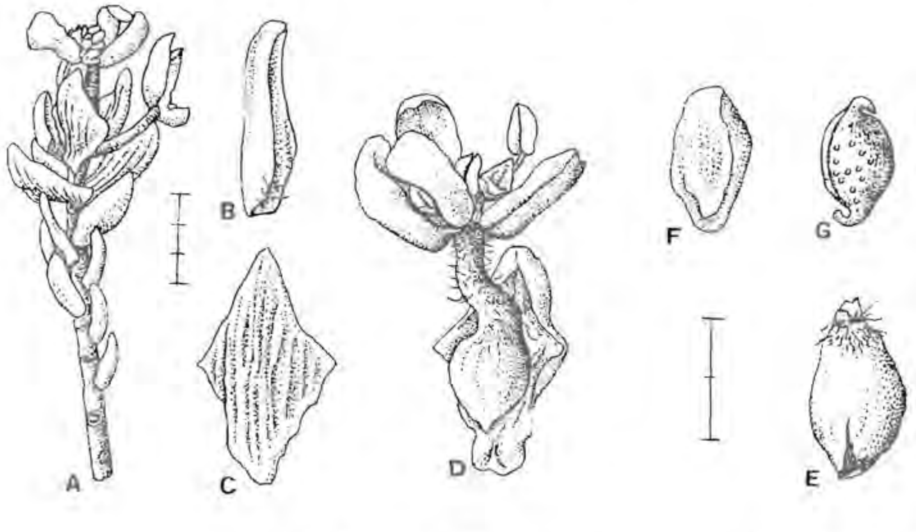

FIGURE 2.—*Passerina vulgaris*, *Bredenkamp 944*. A, inflorescence; B, leaf exposing adaxial surface; C, bract exposing abaxial surface; D, flower enveloped by bract; E, fruit enveloped by hypanthium, with fragmentation at neck base; F, achene; G, seed with black tegmen and white spots. A, × 10; B–G, × 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 obtrullate, 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. paludosa* (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 obtrullate, 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 ± 4-ribbed ...................... *P. falcifolia* (Figure 4J)
19b Midrib shortly extended into a short point, apex acute; wings ± 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) × (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) × (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) × 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-

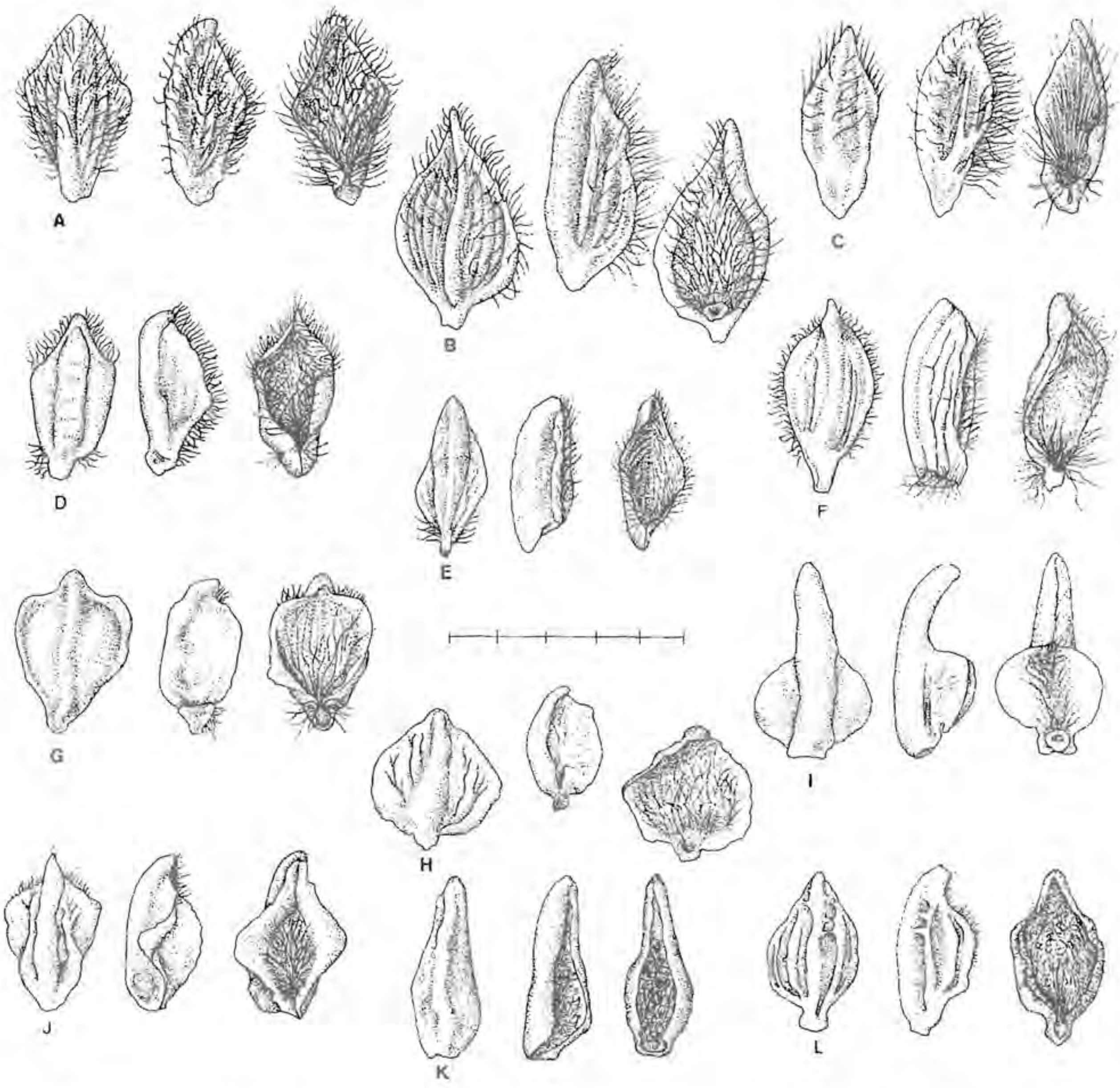

FIGURE 3.—Camera lucida drawings of abaxial, lateral and adaxial views of bracts of *Passerina* taxa, arranged according to sequence in key. A, *P. comosa*, *Andreae 1288*; B–C, *P.* sp. nov. 3, *Esterhuysen 10734, 28006*; D, *P. burchellii*, *Bolus 687*; E, *P. pendula*, *Bredenkamp 908*; F, *P. montana*, *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-

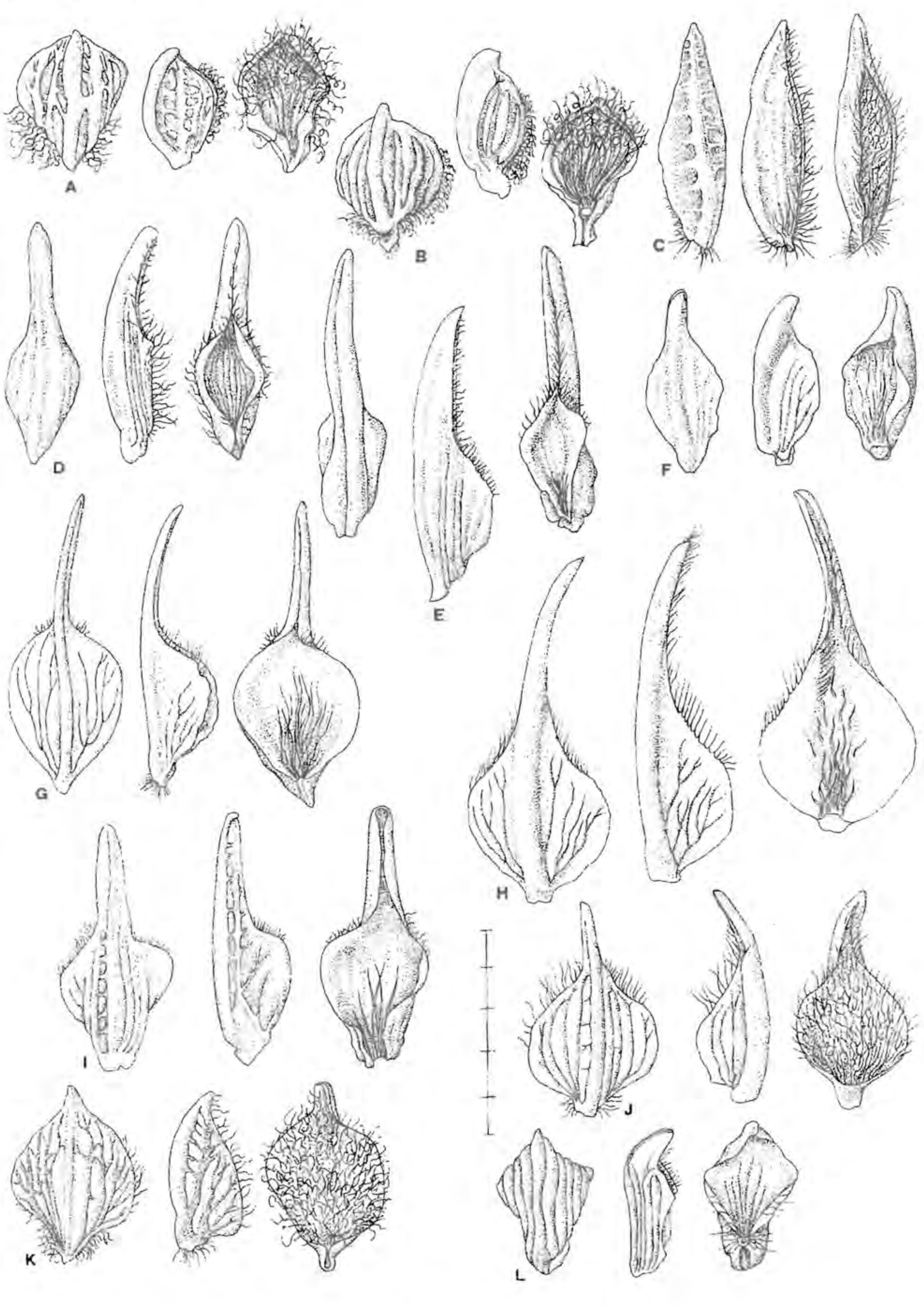

FIGURE 4.— Camera lucida drawings of abaxial, lateral and adaxial views of bracts of *Passerina* taxa, arranged according to sequence in key. A. *P. glomerata* subsp. *glomerata*, *Bredenkamp 973*; B, *P. glomerata* subsp. nov., *Esterhuysen 28587*; C, *P. drakensbergensis*, *Bredenkamp 1012*; D, *P. 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.

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 | | Multi-flowered main and co-florescences | Indumentum | | Size length × $^{1}/_{2}$ width (mm) | Plane shape | Lamina (per side of main vein) | Wings (per side of main vein) |
| | subcapitulate | reduced | | abaxial | adaxial | | | | |
| *comosa* | | | 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 |
| *burchellii* | | X | | | villous | (3.2–)3.5 × 1.5 | rhombic, apex involute, acute | coriaceous, smooth | smooth |
| *pendula* | | | X | | comose | (3.0–)4.2 × 1.0(–1.5) | rhombic, apex obtusely angled | softly coriaceous, smooth | margins membranous |
| *montana* | X | | | | villous | (3.2–)4.0 × 0.9(–1.6) | ovate to obovate, apex subacute | thinly coriaceous, obscurely ribbed | margins membranous |
| *paleacea* | X | | | | villous, wing borders glabrous | (2.5–)2.7 × 1.2(–1.9) | widely ovate, apex obtuse | chartaceous, smooth | membranous, obscurely veined |
| *galpinii* | | | 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 |
| sp. nov. 2 | | | X | | setose | 3.1 × 1.4 | helmet-shaped, widely obovate, apex subacute | thinly chartaceous, smooth | smooth, membranous rims |
| *ericoides* | | | X | | villous | 3.6 × 1.5 | leaf-like, oblong, obtuse | smooth, slightly succulent | absent |
| *rigida* | | | X | | villous | (2.6–)3.4 × 1.4(–1.9) | widely ovate, distinct, short, acute point | coriaceous, 2 or 3 shallow folds | absent |
| *glomerata* subsp. *glomerata* | X | | | | villous | 4.0 × 1.4(–2.4) | obovate to widely obovate, point obtuse | thickly coriaceous, ribbed and reticulately viened | absent |
| *glomerata* subsp. nov. | X | | | | villous | (2.5–)2.9 × 1.5 | obovate to widely obovate, point obtuse to acute | thickly coriaceous, ribbed | absent |
| *drakensbergensis* | | | X | | villous | 5.5 × 1.5 | lanceolate, apex obtuse to acute | coriaceous, obsurely ribbed and reticulately veined | absent |
| *obtusifolia* | | | X | | setose | (4.0–)5.8 × 1.5(–1.7) | narrowly obtrullate, point leaf-like, apex obtuse | coriaceous, closely 2-ribbed at margins | absent |
| *paludosa* | | | 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 |
| *filiformis* subsp. nov. | | | X | | centrally setose, wings glabrous | 4.6 × 1.5 | ovate acuminate, gradually narrowing to point | coriaceous | membranous with distinct venation |
| *filiformis* subsp. *filiformis* | | | 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 |
| *falcifolia* | | | X | | villous | (5.3–)5.8 × 1.7(–2.0) | widely ovate, narrowing into falcate point | coriaceous | coriaceous, ± 4-ribbed, reticulately veined |
| *rubra* | | | X | | villous | (4.3–)5.1 × 1.8(–2.0) | widely ovate, with short, acute point | coriaceous | coriaceous, ± 5-ribbed, reticulately veined |
| *vulgaris* | | | 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 t/s (Figures 5; 7; 10)

| Floral part | *P. ericoides* (fruit fleshy) | *P. vulgaris* (fruit dry) |
|---|---|---|
| Hypanthium | Lobed.<br>Outer and inner epidermis hairy (Figure 5E–G). | Scalloped.<br>Outer epidermis hairy, inner epidermis glabrous (Figure 5F, H). |
| Ovary wall | Independent of hypanthium.<br>Outer and inner epidermal wall strongly developed, containing tanniniferous substances.<br>Mesophyll of densely arranged parenchyma cells.<br>Dorsal carpellary bundle strongly developed (Figure 5G).<br>Commissural bundles densely arranged, often fused (Figure 5E, G). | Loosely adhering to hypanthium distally away from placenta (Figure 5F).<br>Epidermal walls less sturdy with less tanniniferous substances.<br>Mesophyll aerenchymatic.<br>Dorsal carpellary bundle rudimentary or absent (Figure 5F, H).<br>Commissural bundles closely arranged, often separate (Figure 5F, H). |
| Style | Four-lobed.<br>Vascular bundles 4, 1 per lobe (Figure 7C). | Elliptic.<br>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

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 |
| *ericoides* | B3 | X | | X | | | X | | | 5.0 | 2.1 × 1.7 | 0.5 | 1.3 | 0.9 × 0.7 |
| *rigida* | B3, B6, D2 | X | | | X | | | X | | 4.0 | 2.2 × 1.4 | 0.5 | 1.5 | 0.8 × 0.4 |
| *paleacea* | 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 |
| *galpinii* | B2, B3 | | X | | | X | | | X | 5.3 | 2.0 × 1.1 | 1.4 | 2.1 | 0.6 × 0.5 |
| *glomerata* subsp. *glomerata* | B2, B3, B5 | | X | | | X | | | X | 6.4 | 2.4 × 0.9 | 0.9 | 1.4 | 0.8 × 0.4 |
| *glomerata* subsp. nov. | B6 | | X | | | X | | | X | 4.9 | 2.5 × 0.9 | 1.2 | 1.4 | 0.9 × 0.4 |
| *obtusifolia* | B2, B3, B4, B5 | | X | | | X | | | X | 6.8 | 2.5 × 1.1 | 1.2 | 2.2 | 1.1 × 0.5 |
| *burchellii* | B1 | | X | | | X | | | X | 4.7 | 1.6 × 0.6 | 0.7 | 1.5 | 0.5 × 0.3 |
| *pendula* | B2 | | X | | | X | | X | | 6.5 | 2.0 × 0.7 | 1.5 | 2.0 | 0.8 × 0.4 |
| *comosa* | B2, B3, D1 | | X | | | X | | | X | 7.3 | 2.7 × 1.0 | 0.7 | 1.5 | 0.7 × 0.4 |
| *paludosa* | B2 | | X | | | X | | | X | 7.2 | 2.3 × 1.0 | 1.2 | 2.4 | 0.7 × 0.5 |
| *montana* | 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 |
| *drakensbergensis* | B3 | | X | | | X | | | X | 5.9 | 2.4 × 0.9 | 1.2 | 2.0 | 0.9 × 0.3 |
| *rubra* | B4 | | X | | | X | | | X | 8.4 | 2.7 × 1.1 | 0.7 | 1.7 | 0.9 × 0.3 |
| *filiformis* subsp. *filiformis* | B3, B4 | | X | | | X | | | X | 6.0 | 2.3 × 0.5 | 1.1 | 2.2 | 0.8 × 0.3 |
| *filiformis* 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 |
| *falcifolia* | C | | X | | | X | | | X | 8.4 | 2.5 × 0.7 | 1.4 | 2.1 | 1.0 × 0.4 |
| *vulgaris* | 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.

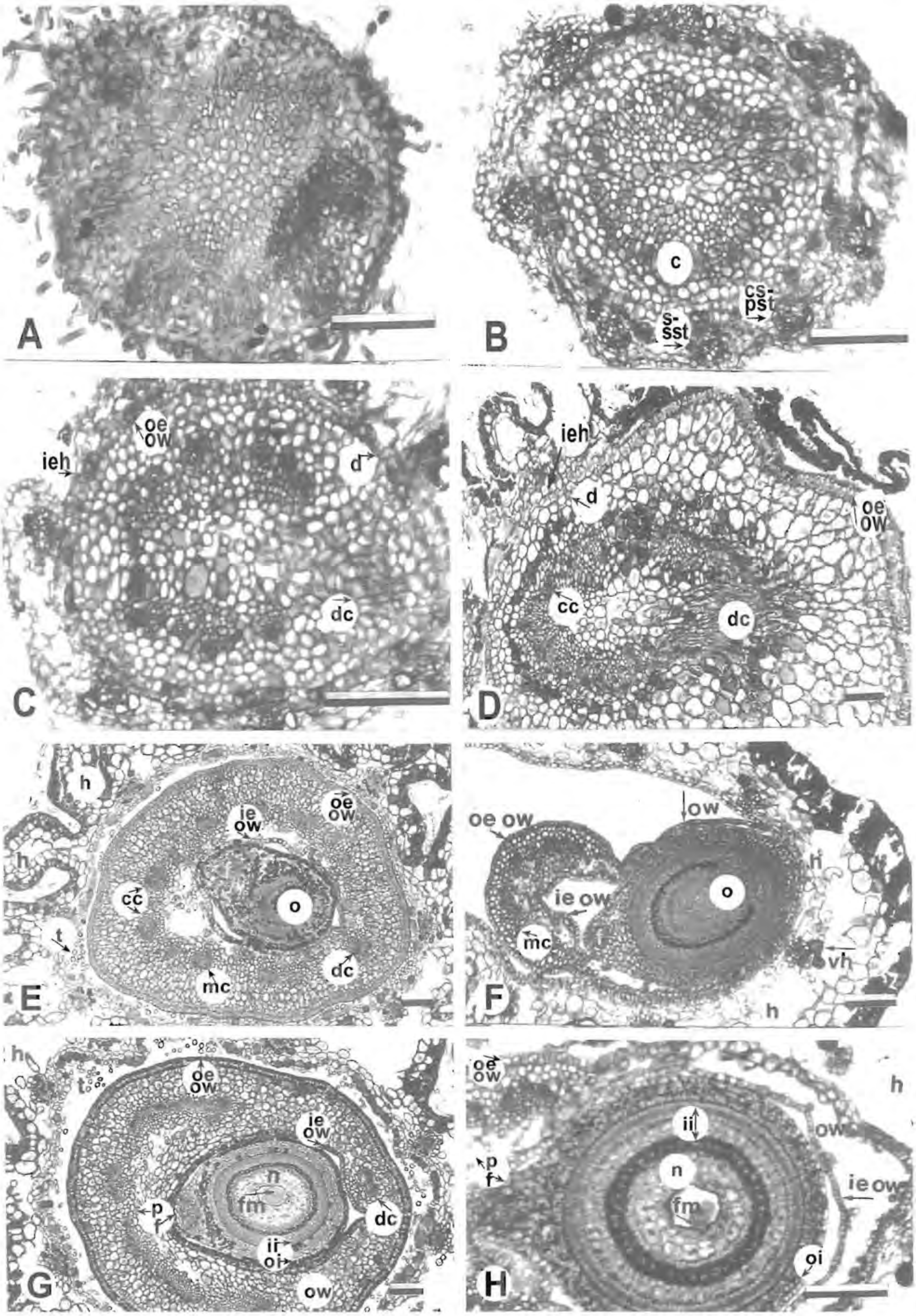

FIGURE 5.—LM photographs of *P. ericoides*, *Bredenkamp 956*, with fleshy fruit, and *P. vulgaris*, *Bredenkamp 951*, with dry fruit, showing structure of receptacle and base of ovary. A–D, t/s at different levels of receptacle. A–C, *P. vulgaris*: A, departure of eight traces from central stele; B, 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 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; cc, commissural carpellary bundles; cs-pst, fused commissural sepal and antipetalous stamen bundles; d, area of tissue differentiation; dc, dorsal carpellary bundle; f, funiculus; fm, functional macrospore; h, hypanthium; ieh, 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; 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 µm.

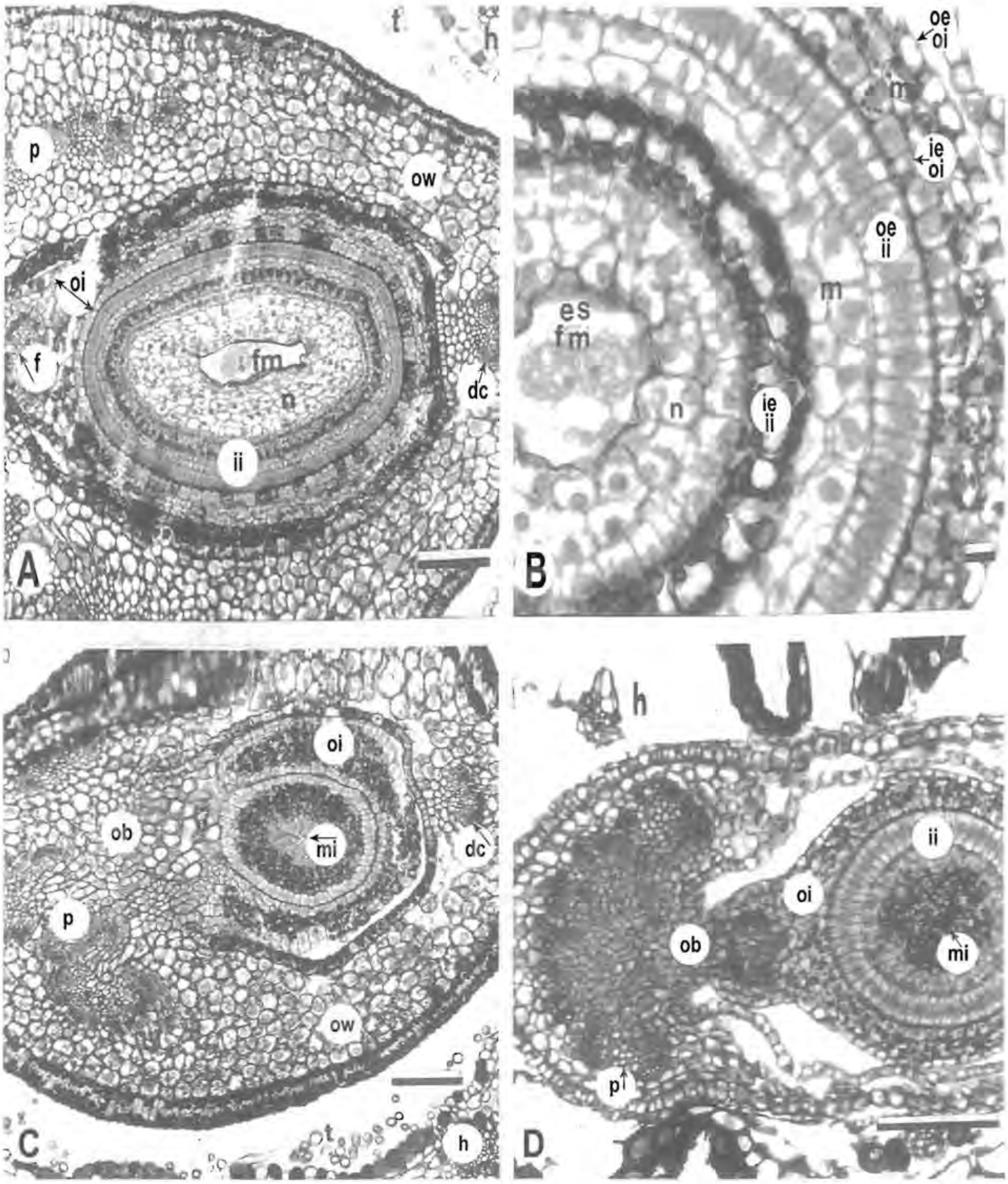

FIGURE 6.—LM photographs of *P. ericoides*, *Bredenkamp 956*, with fleshy fruit, and *P. vulgaris*, *Bredenkamp 951*, with dry fruit, showing structure of ovary and ovule. A, B, t/s in median position of ovary: A, *P. ericoides*, embryo sac and two cells of functional macrospore; B, higher magnification of similar stage in *P. vulgaris*. C, D, t/s 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

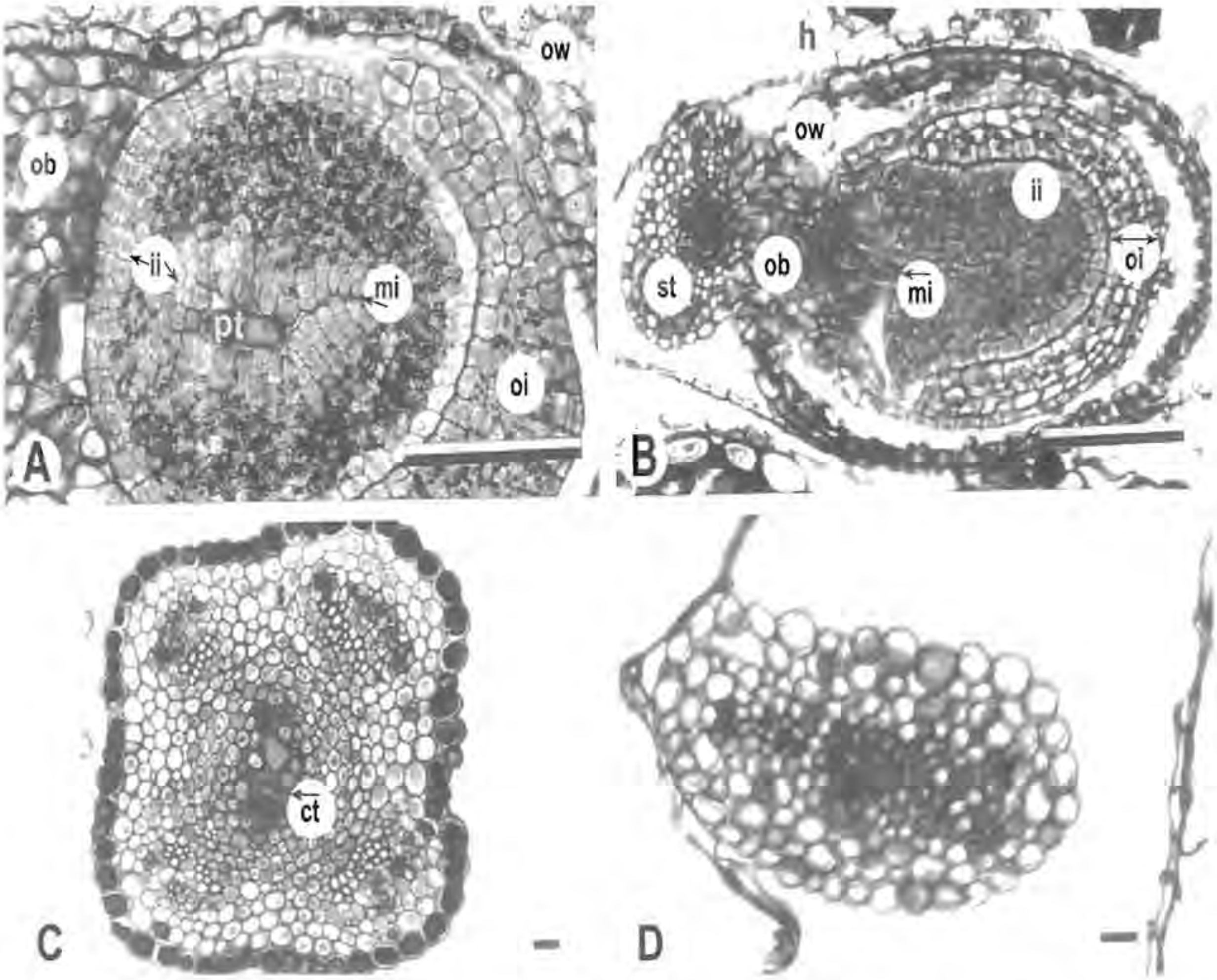

FIGURE 7.—LM photographs of *P. ericoides*, *Bredenkamp 956*, with fleshy fruit, and *P. vulgaris*, *Bredenkamp 951*, with dry fruit, showing structure of micropyle and style. A, *P. ericoides*, obturator, pollen tube penetrating micropyle, opening of outer integument towards micropyle. B, similar stage 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.

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 | outer lobe surface abaxial | inner lobe surface adaxial | inner lobe surface abaxial | | | outer | inner |
| sp. nov. 1 | A | X | | 1.2 | tomentose | tomentose | glabrous | apex setose | glabrous | glabrous | 1.9 × 1.2 | | cymbiform | widely ovate |
| *ericoides* | B3 | | X | 0.6 | strigose | strigose | puberulent | glabrous | puberulent | glabrous | 1.6 × 2.0 | concave, widely obovate | | |
| *rigida* | B3, B6, D2 | | X | 0.8 | glabrous | tomentose | midrib tomentose | glabrous | tomentose | glabrous | 1.8 × 0.9 | | cymbiform | obovate |
| *paleacea* | B2, B3, B4, D2 | | X | 0.3 | glabrous | glabrous | glabrous | glabrous | glabrous | glabrous | 1.8 × 1.5 | concave, elliptic or subrotund | | |
| sp. nov. 2 | B3 | | X | 0.7 | tomentose | tomentose | apex tomentose | apex setose | glabrous | apex setose | 1.8 × 1.0 | | concave, oblong | concave, obovate |
| *galpinii* | B2, B3 | | X | 1.0 | pubescent | pubescent | glabrous | glabrous | apex margin tomentose | glabrous | 2.4 × 1.6 | | concave, elliptic | obovate |
| *glomerata* subsp. *glomerata* | B2, B3, B5 | | X | 0.8 | glabrous | tomentose | scantily pubescent | glabrous | scantily pubescent | glabrous | 2.3 × 0.8 | | cymbiform | oblong-elliptic |
| *glomerata* subsp. nov. | B6 | | X | 0.7 | apex tomentose | tomentose | apex tomentose | glabrous | tomentose | glabrous | 2.6 × 1.6 | | concave, ovate | widely obovate |
| *obtusifolia* | B2, B3, B4, B5 | | X | 1.8 | glabrous | tomentose | tomentose | glabrous | tomentose | glabrous | 2.8 × 0.9 | | cymbiform | narrowly oblong |
| *burchellii* | B1 | X | | 0.8 | glabrous | tomentose | midrib setose | apex setose | tomentose | apex setose | 2.3 × 0.6 | | cymbiform | obovate |
| *pendula* | B2 | X | | 0.6 | glabrous | tomentose | scantily tomentose | glabrous | scantily tomentose | glabrous | 2.9 × 1.5 | | cymbiform | oblong |
| *comosa* | B2 | X | | 0.9 | glabrous | tomentose | glabrous | tomentose | glabrous | tomentose | 2.8 × 1.0 | | cymbiform | elliptic |
| *paludosa* | B2 | X | | 2.6 | shortly tomentose | strigose | glabrous | apex setose | apex margin tomentose | apex setose | 2.2 × 1.2 | | cymbiform | oblong |
| *montana* | B2, B3, D1 | X | | 1.3 | glabrous | tomentose | scantily tomentose | glabrous | tomentose | glabrous | 2.1 × 1.0 | | cymbiform | obovate |
| sp. nov. 3 | B3 | X | | 1.4 | glabrous | scantily tomentose | glabrous | apex setose | glabrous | apex tomentose | 2.7 × 1.5 | | concave, ovate | obovate |
| *drakensbergensis* | B3 | X | | 1.7 | scantily tomentose | tomentose | glabrous | tomentose | tomentose | tomentose | 2.4 × 0.8 | concave, lanceolate | | |
| *rubra* | B4 | X | | 2.0 | glabrous | pubescent | glabrous | glabrous | scantily tomentose | glabrous | 2.9 × 1.7 | | cymbiform | obovate |
| *filiformis* subsp. *filiformis* | B3, B4 | X | | 1.7 | tomentose | tomentose | glabrous | apex setose | glabrous | apex setose | 2.2 × 1.4 | | concave, obovate | obovate |
| *filiformis* subsp. nov. | B6 | X | | 1.5 | scantily tomentose | scantily tomentose | glabrous | apex setose | glabrous | apex setose | 2.5 × 1.5 | concave, obovate | | |
| sp. nov. 4 | C | X | | 2.3 | upper half tomentose | tomentose | glabrous | apex setose | glabrous | apex setose | 2.1 × 1.3 | | cymbiform | obovate |
| *falcifolia* | C | X | | 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 |

X, character present; * average in mm.

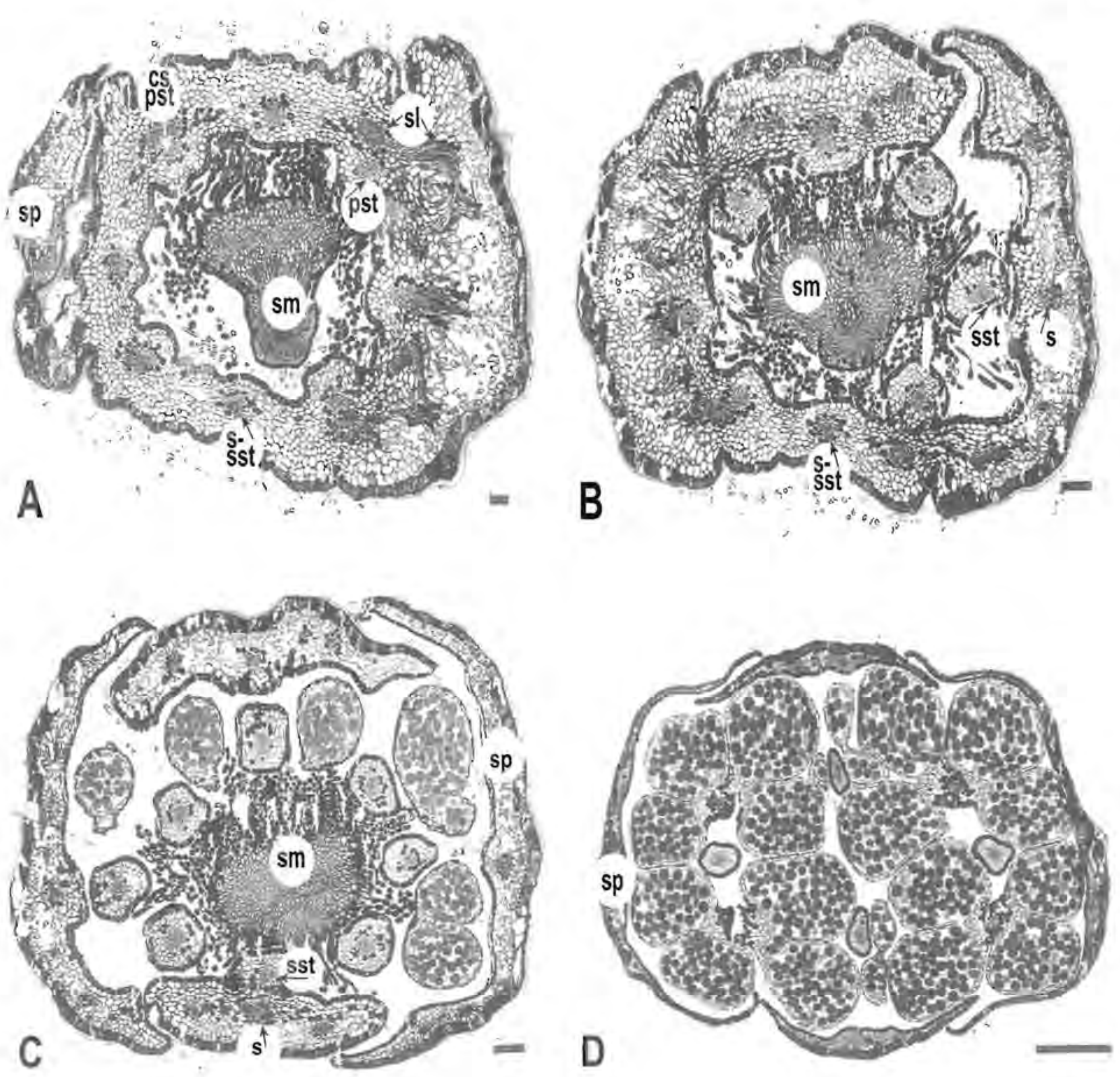

FIGURE 8.—LM photographs of *P. ericoides*, *Bredenkamp 956*, with fleshy fruit, and *P. vulgaris*, *Bredenkamp 951*, with dry fruit, showing structure of androecium. A–D, serial t/s of sepals and two anther whorls. A–C, *P. ericoides*: A, each of fused commissural sepal and antipetalous stamen bundles 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

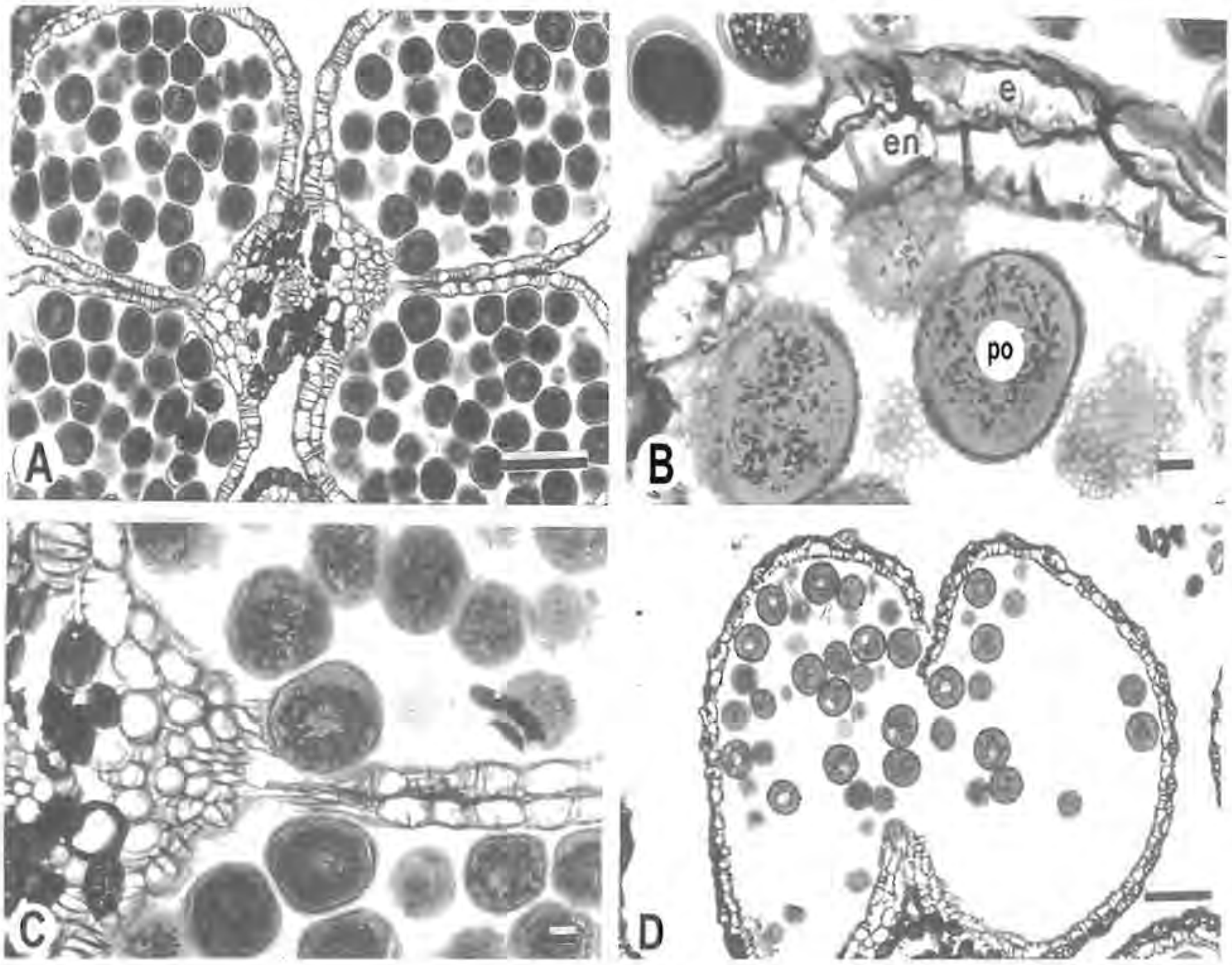

FIGURE 9.—LM photographs of *P. ericoides*, *Bredenkamp 956* and *P. vulgaris*, *Bredenkamp 951*, showing structure of anther loculae in t/s: A, *P. vulgaris*, 4-locular anther; B, *P. ericoides*, cell wall thickenings of endothecium rib-like; C, *P. vulgaris*, rupturing of partition between loculi; 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

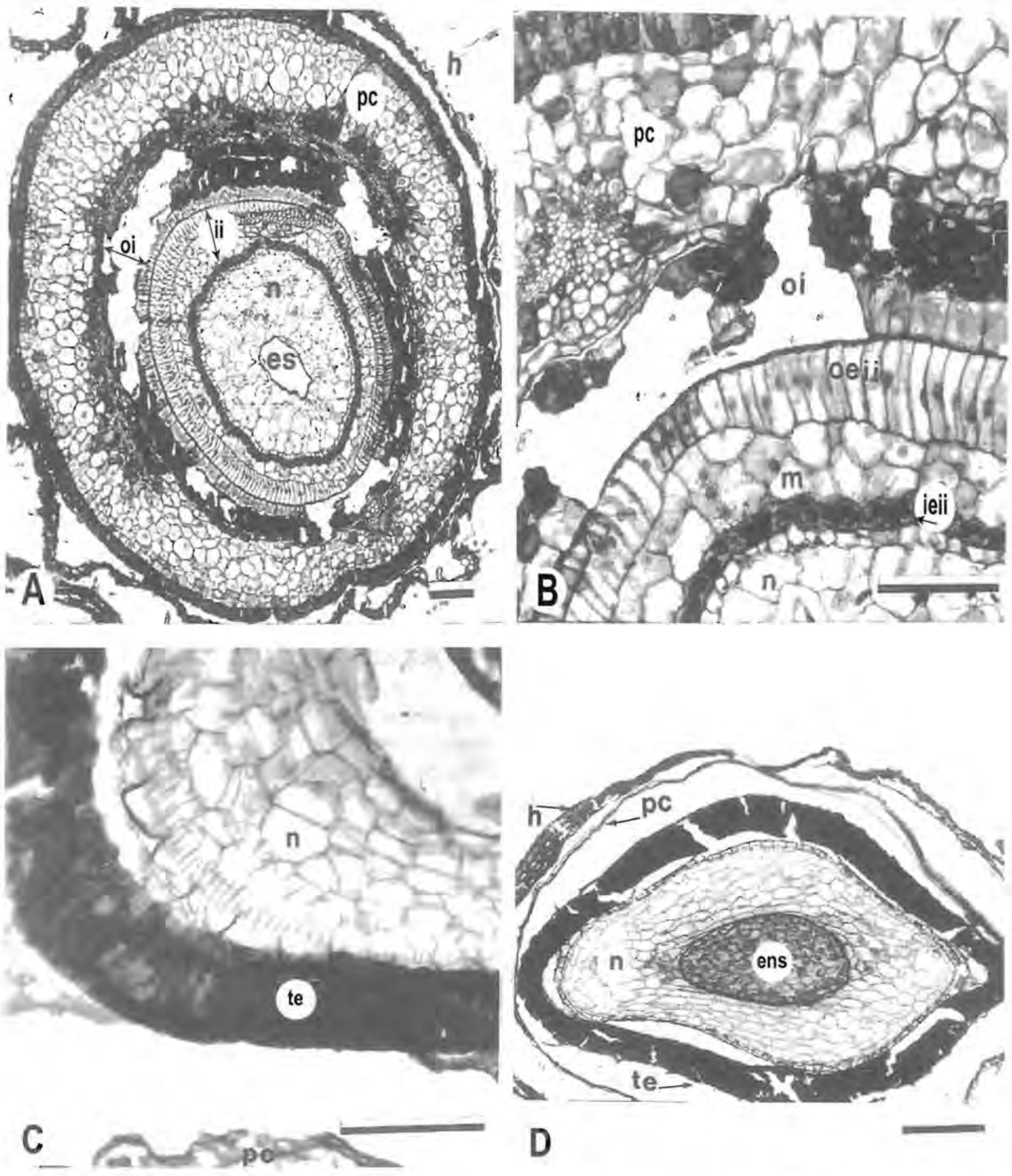

FIGURE 10.—LM photographs of *P. ericoides*, *Bredenkamp 956*, with fleshy fruit, and *P. vulgaris*, *Bredenkamp 951*, with dry fruit, showing structure of young fruit and developing seed in t/s. A, B, *P. ericoides*: A, pericarp fleshy, atrophy of outer integument; B, higher magnification, outer epidermis 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

(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 ± twice the length of the antipetalous ones. Both *P.* sp. nov. 1 and *P.* sp. nov. 2 have short antisepalous filaments of ± 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) × 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 → Violales → 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 exotegmic 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. 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), 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 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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# CHAPTER 5

# PHYTOGEOGRAPHY

## 5.1 Introduction

*Passerina* L. comprises 20 species and four subspecies. Endemism within the genus is highest in the Cape Floristic Region, with ten species and four subspecies endemic (Table 5.1) and four species near-endemic (Table 5.2). Three species are endemic to, but variously distributed in, the Northern, Western and Eastern Cape Provinces, as well as KwaZulu-Natal (Table 5.3). Two species are near-endemic to the Great Escarpment of southern Africa and *P. drakensbergensis* is endemic to the Bergville District of KwaZulu-Natal (Table 5.5).

Taking the most southerly distribution of *P. montivaga* into consideration, 18 *Passerina* species occur in the Cape Floristic Region (CFR), which has been extensively described by many authors (Good 1974; Goldblatt 1978; Takhtajan 1986; Cowling 1992; Cowling & Richardson 1995; Cowling *et al.* 1997; Goldblatt & Manning 2000; Van Wyk & Smith 2001). Beyers (2001) discusses the recognition of local centres of endemism within the CFR, from the initial descriptions by Weimarck (1941) up to those of Goldblatt & Manning (2000). In this thesis the interpretation of Goldblatt & Manning (2000), which identifies six local centres of endemism, is followed: the Northwestern (NW), Southwestern (SW), Agulhas Plain (AP), Karoo Mountain (KM), Langeberg (LB) and Southeastern (SE) Centres.

*Passerina* species endemic to the CFR (Table 5.1) are morphologically and anatomically adapted to the winter rainfall and dry warm summers of the Mediterranean or semi-Mediterranean climate in the region (Bredenkamp & Van Wyk 1999, 2000, 2001a). Most *Passerina* species in fynbos vegetation occur on oligotrophic soils derived from the orthoquartzites of the Cape Supergroup. These species are adapted to a variety of habitats, e.g. high-mountain peaks above the snowline, where plants are often surrounded by mist (throughout the year) or covered by snow especially during the winter months; forests and mountain fynbos; vleis and marshes; coastal limestone deposits and limestone hills; coastal fynbos, where the plants grow on sand dunes and in sandy areas. Many species are pioneers growing along roadsides and in disturbed places.

TABLE 5.1.—Taxa of *Passerina* endemic to the CFR

| **Taxa** | **Centres of endemism** | | | | | |
|---|---|---|---|---|---|---|
| | NW | SW | AP | KM | LB | SE |
| *burchellii* | | X | | | X | |
| *ericoides* | | X | X | | | |
| *esterhuyseniae* | Y | | | | | |
| *filiformis* subsp. *filiformis* | X | X | | | X | |
| *filiformis* subsp. *glutinosa* | X | X | | | | |
| *galpinii* | | | Y | | | |
| *paleacea* | | X | X | | X | |
| *paludosa* | | Y | | | | |
| *pendula* | | | | | | Y |
| *quadrifaria* | | | | X | X | X |
| *truncata* subsp. *monticola* | X | X | | | | |
| *truncata* subsp. *truncata* | X | X | | X | | X |
| Total number of species | 3 | 6 | 3 | 2 | 4 | 3 |

X, taxa endemic to more than one centre; Y, taxa endemic to one centre; NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern.

TABLE 5.2.—*Passerina* species that are near-endemic to the CFR

| **Species** | **Provinces adjacent to CFR** | **Centres of endemism within the CFR** | | | | | |
|---|---|---|---|---|---|---|---|
| | | NW | SW | AP | KM | LB | SE |
| *comosa* | Northern Cape | X | X | | X | | |
| *falcifolia* | Eastern Cape | | X | | | | X |
| *nivicola* | Northern Cape | X | X | | | | |
| *rubra* | Eastern Cape | | | | X | X | X |
| Total number of species | | 2 | 3 | | 2 | 1 | 2 |

X, taxa endemic to more than one centre; NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern.

TABLE 5.3.—Species of *Passerina* endemic to the Northern, Western and Eastern Cape Provinces and KwaZulu-Natal

| **Species** | **Distribution in provinces** | **Centres of endemism within the CFR** | | | | | |
|---|---|---|---|---|---|---|---|
| | | NW | SW | AP | KM | LB | SE |
| *obtusifolia* | Widespread in Northern, Western and Eastern Cape | X | X | X | X | X | X |
| *rigida* | Coastlines of KwaZulu-Natal, Western and Eastern Cape | X | X | X | | | X |
| *corymbosa* | Widespread in Western and Eastern Cape, with outliers in KwaZulu-Natal | X | X | X | X | X | X |
| Total number of species | | 3 | 3 | 3 | 2 | 2 | 3 |

X, taxa endemic to more than one centre; NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern.

TABLE 5.4.— Number and percentage of *Passerina* species present in each centre of endemism of the CFR

| **Species** | **Number of species in centres of endemism within CFR** | | | | | |
|---|---|---|---|---|---|---|
| | NW | SW | AP | KM | LB | SE |
| Endemic to CFR (Table 5.1) | 3 | 6 | 3 | 2 | 4 | 3 |
| Near-endemic to CFR (Table 5.2) | 2 | 3 | | 2 | 1 | 2 |
| Endemic at provincial level (Table 5.3) | 3 | 3 | 3 | 2 | 2 | 3 |
| TOTAL | 8 | 12 | 6 | 6 | 7 | 8 |
| Percentage | 40 | 60 | 30 | 30 | 35 | 40 |
| Percentage of species endemic to one centre | 5 | 5 | 5 | | | 5 |

NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern.

TABLE 5.5.—*Passerina* species endemic or near-endemic to the Great Escarpment of southern Africa

| **Species** | **Status** | **Country** | **Area** |
|---|---|---|---|
| *drakensbergensis* | Endemic | South Africa | KwaZulu-Natal, Bergville District in northern Drakensberg |
| *montana* | Near-endemic to Great Escarpment of southern Africa | High-mountain areas:<br>Angola | Huila Plateau, Lubango and Cheila Mountains |
| | | Zimbabwe | Nyanga |
| | | Mozambique | Manica and Sofala |
| | | Namibia | Moltkeblick on the Auas Mountains |
| | | South Africa | Limpopo Province, Mpumalanga, KwaZulu-Natal, Free State, and Eastern Cape |
| | | Swaziland | Mbabane |
| | | Lesotho | Widespread |
| *montivaga* | Near-endemic to Great Escarpment of southern Africa | Zimbabwe | Chimanimani Mountains |
| | | Mozambique | Manica and Sofala |
| | | South Africa | Limpopo Province, Mpumalanga, KwaZulu-Natal, Western and Eastern Cape |
| | | Swaziland | Mbabane |

Taxa near-endemic to the CFR are more widespread (Table 5.2). These species have adapted to a wider amplitude of environmental conditions: on the northern side of the southern Cape mountain ranges, they are often adapted to karroid and summer-rainfall conditions; certain species are adapted to forest conditions and others to snow at high altitudes. Three *Passerina* species are endemic to the Northern, Western and Eastern Cape Provinces and KwaZulu-Natal (Table 5.3). With the exception of *P. rigida* adapted to maritime conditions, the other two species are common within their widespread, inter-provincial distribution ranges.

*Passerina* species endemic to the northern Drakensberg or near-endemic to the Great Escarpment of southern Africa (Table 5.5) are usually adapted to the high moisture levels prevalent on the eastern escarpment and under summer-rainfall conditions. These plants are often found in a marginal belt between forest and grassland; they also grow along streams and riverbanks and on mountain slopes.

## 5.2 Observations

The combined distribution of all the *Passerina* species is shown in Figure 5.1. The number of species per degree and per quarter degree square (Edwards & Leistner 1971) is indicated in Figures 5.2 and 5.3. In *Passerina* the highest numbers of species per grid are concentrated in a belt including the 33° and 34° S latitude and between 18° to 27° E longitude. The highest number of species per grid (nine) occurs in each of the grids 3321 (Ladismith), 3322 (Oudtshoorn) and 3419 (Caledon) (Figure 5.2). The highest diversity of species (six) occurs in the False Bay area, from Seekoeivlei, including the Cape Flats, to De Mond at the Palmiet River (3418B) (Figure 5.3). Levyns (1938) was the first to show that the Caledon District is the centre of species richness with a reduction in numbers to the north and east. Oliver *et al.* (1983) regard the quarter degree 3418BB as the richest area in the CFR. Bredenkamp & Van Wyk (2001a) regard the Western Cape as the centre of diversity for *Passerina*, from where certain species extend to the west, north and east.

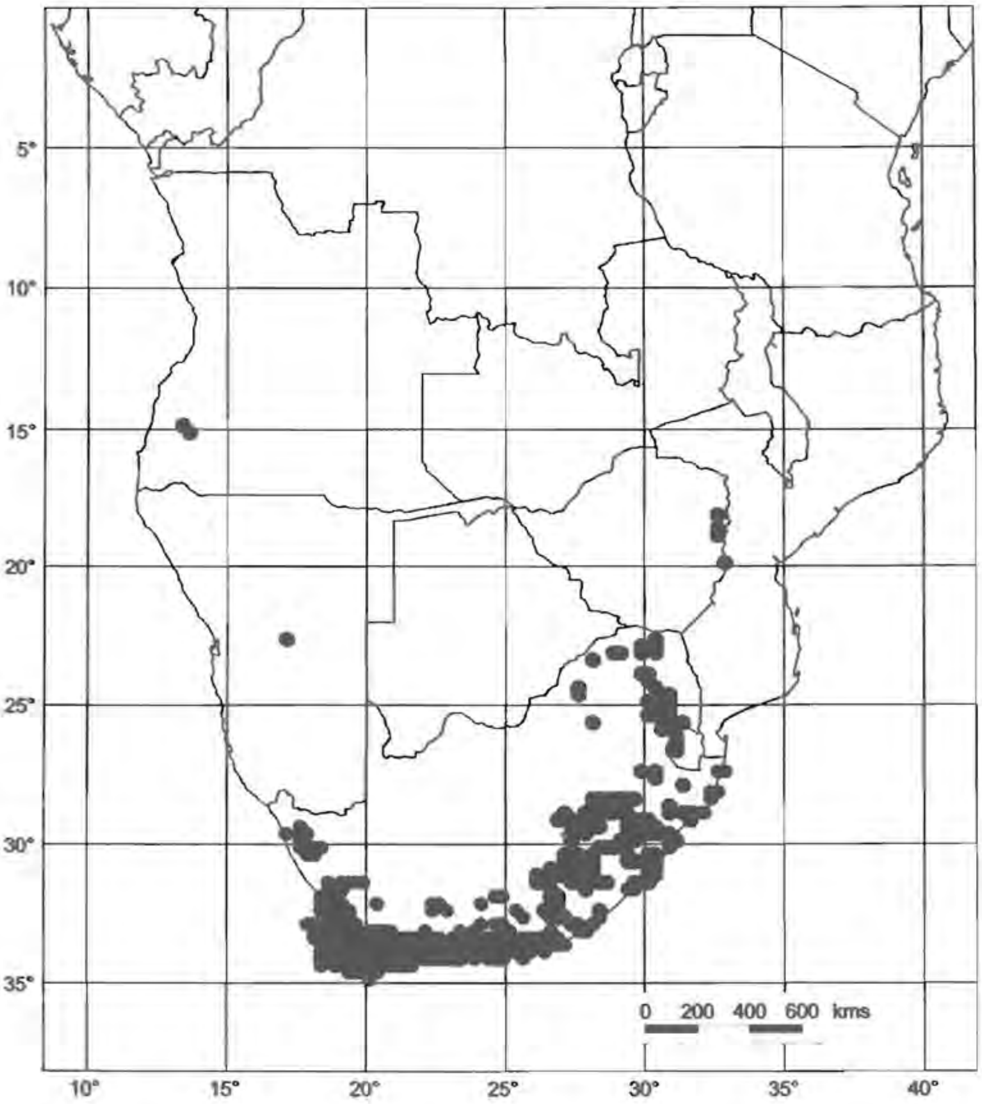


FIGURE 5.1.—Known distribution of genus *Passerina*.

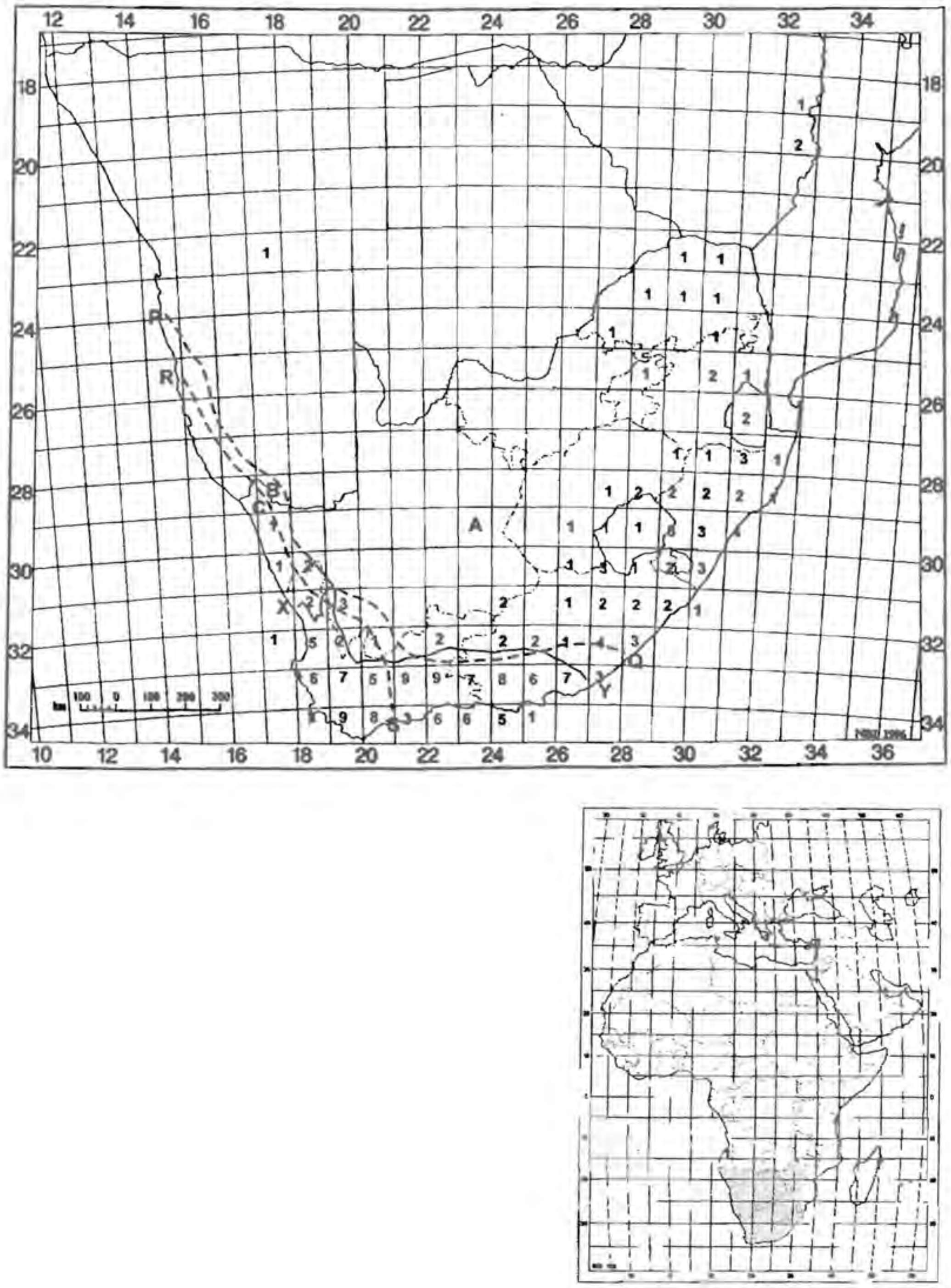


FIGURE 5.2.—Number of species per degree grid square in the distribution of *Passerina*. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops. Distribution outside South Africa shown in insert.

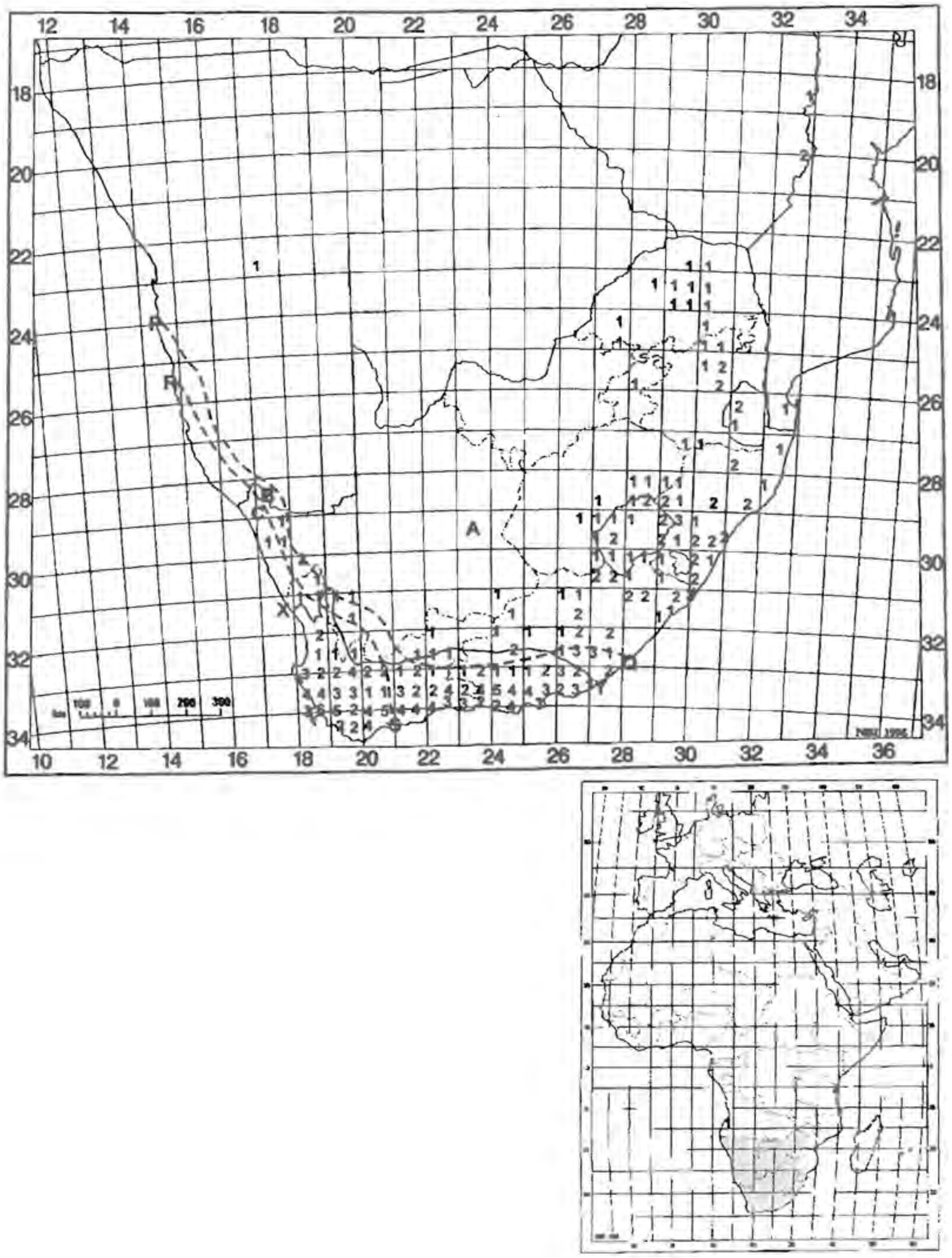


FIGURE 5.3.—Distribution of *Passerina*, with number of species per quarter degree grid square indicative of highest diversity of species. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops. Distribution outside South Africa shown in insert.

### *5.2.1 Species endemic to the CFR*

*Passerina* shows a high percentage of endemism within the CFR, as 10 species out of 20 (50%), as well as the four subspecies, are endemic to this region (Table 5.1). Of these 10 species, four are each endemic to one local centre of endemism within the CFR and will be discussed separately. Diverse types of distributions occur amongst the remaining species. *P. burchellii* is found on the high mountains at Genadendal and Villiersdorp. *P. ericoides* is distributed from Melkbosstrand along the coast of the Cape Peninsula to De Mond in the Bredasdorp District and *P. paleacea* from Langebaan, round the Cape Peninsula up to Stilbaai. The latter two species are both confined to beaches and salt marshes. *P. filiformis* subsp. *filiformis* is common in the Cape Peninsula, and is distributed from Piquetberg, across the Hex River Mountains, to Attaquaskloof in the southwestern Cape, growing in rocky areas, mostly on south-facing mountain slopes; subsp. *glutinosa* occurs in the Strandveld (Acocks 1988), from Doring Bay in the north to St. Helena Bay in the south. *P. pendula* is endemic to the KwaZunga Catchment Basin and the Zwartkops River area of the Eastern Cape. *P. quadrifaria* occurs on the Langeberg, Swartberg, Kouga, Outeniqua, Tsitsikamma and Great Winterhoek Mountains. Plants grow at high altitudes (1 500–1 670 m), often on southeast-facing rocky slopes, on rocky peaks and mountain summits. *P. truncata* subsp. *truncata* is distributed from Vanrhynsdorp, along the Cederberg Mountains, to Ceres, Tulbagh, Matjiesfontein and Seven Weeks Poort; the subsp. *monticola* is distributed from Clanwilliam, along the Cederberg Mountains, southwards to Table Mountain, Helderberg, Kogelberg, the Hex River Mountains and the Riviersonderend Mountains.

#### Local centres of endemism within the CFR

The Northwestern Centre has a relatively high concentration of *Passerina* species, as eight out of 20 (40%) species occur here (Tables 5.1, 5.3, 5.4). *P. esterhuyseniae* was collected in the northern Cederberg Mountains at Groenberg near Pakhuis and at Konpoort and is the only species that is endemic to the Northwestern Centre. This species grows in Mountain Fynbos (Rebelo 1998) at mountain summits and is possibly still under-collected.

As the grids 3419 (Caledon) and 3418 (Simonstown) are regarded as centres of species richness by Levyns (1938) and Oliver *et al.* (1983), it is not surprising that 12 out of 20 (60%) *Passerina* species occur in the Soutwestern Centre (Tables 5.1, 5.3, 5.4). *P. paludosa* is the only species in the genus endemic to this Centre. Because of urbanization and invasion by alien vegetation in the Cape Peninsula, it is currently confined to small marshy areas east of Muizenberg. The only three extant populations known are at the Rondevlei Nature Reserve, Zeekoevlei and along the Strandfontein Road (Smuts 1996). Recently two new populations of a taxon that appears to be *P. paludosa* were recorded in the grids 3419AD and 3419CB. Taking urbanization and invasion by alien vegetation into account, the specimens collected from these populations were not included in the distribution of *P. paludosa* as further field studies are needed. Consequently the Red List status of this species was not reassessed, but remains Critically Endangered (Species Survival Commission 2000).

Geology and soils play an important role in the species composition of the Agulhas Plain Centre, where limestones extensively outcrop along the southern coast from the Agulhas Peninsula to Mossel Bay (Goldblatt & Manning 2000). Six out of 20 (30%) of the *Passerina* species occur in this centre (Tables 5.1, 5.3, 5.4), with *P. galpinii* as the only endemic species. It is distributed on stony flats, coastal limestone deposits and limestone hills, from Elim to Bredasdorp, Arniston, Stilbaai, Melkhoutfontein, Albertinia and Mossel Bay, growing at altitudes of 0–290 m.

The number of *Passerina* species represented in the Karoo Mountain Centre is relatively low, with six out of 20 (30%) of the species occurring in this region (Tables 5.1, 5.3, 5.4). Seven out of 20 (35%) *Passerina* species are represented in the Langeberg Centre. There are no *Passerina* species endemic to either the Karoo Mountain or the Langeberg Centres.

The Southeastern Centre has a relatively high concentration of *Passerina* species, as eight out of 20 (40%) species occur here (Tables 5.1, 5.3, 5.4). *P. pendula* is the only species endemic to the Southeastern Centre. It is distributed from the Kouga Mountains in the Western Cape to the Langkloof Mountains and the Great Winterhoek Mountains in the Eastern Cape. The species occurs in the KwaZunga

Catchment Basin and on the banks of the Upper Swartkops River as well as the Boesmans River at Port Elizabeth. *P. pendula* grows at altitudes of (133–)383–600 m.

### *5.2.2 Species near-endemic to the CFR*

*Passerina comosa* occurs in the Northern Cape as well as in the Northwestern, Southwestern and Karoo Mountain Centres (Table 5.2). It ranges from mountain summits and slopes of the Kamiesberg to Calvinia in the Northern Cape. In the Western Cape it is distributed in a belt between 33° and 34° S latitude and from 19° to 21° E longitude. This species is found on the Roggeveld, Witteberg and the Klein Swartberg mountain ranges of the Western Cape and occurs at altitudes of 1 000–1 200 m.

*Passerina falcifolia* is associated with forest and Mountain Fynbos (Rebelo 1998) in the southern Cape and the southern parts of the Eastern Cape. It is a near-endemic to the CFR and occurs in the Karoo Mountain, Southwestern and Southeastern Centres, as well as the Zuurberg, Blaauwkrantz and Alexandria Forests of the Eastern Cape. It most commonly grows in a belt between the coast and the 33° S latitude and 22° to 26° E longitude. *P. falcifolia* is found on mountain plateaus and southeast-facing slopes on Table Mountain Sandstone in shallow, sandy loam soil at altitudes from sea level up to 1 100 m.

Restricted mostly to mountainous areas, *Passerina nivicola* is possibly still under-collected. It is a near-endemic to the CFR and occurs in the Northwestern and Southwestern Centres as well as the Northern Cape Province. The most northerly record is from Sneeukrans in the Roggeveld Escarpment, an area covered by the Escarpment Mountain Renosterveld (Rebelo 1998). The species was more extensively collected in the Ceres District and also further south in the Worcester District, occurring in the Mountain Fynbos or Central Mountain Renosterveld (Rebelo 1998).

*Passerina rubra* is near-endemic to the CFR, occurring in the Langeberg, Karoo Mountain and Southeastern Centres as well as southern parts of the Eastern Cape. It most commonly occurs in a belt between the coast and the 33° S latitude and from 20° to 26° E longitude. *P. rubra* is distributed from the Bontebok National Park in the Swellendam District eastwards to Gowie's Kloof near Grahamstown. It is common in the Steytlerville, Humansdorp, Port Elizabeth and Grahamstown areas of the Eastern Cape and less frequent in the Western Cape. *P. rubra* seems to be well adapted to the calcareous soils in the area between Cradock and Port Elizabeth, renowned for the ancient dunes and flats and abounding in limestone.

### *5.2.3 Species endemic to the Northern, Western and Eastern Cape Provinces and KwaZulu-Natal*

*Passerina obtusifolia* is endemic to the Northern, Western and Eastern Cape. It is centred in a belt between 33° and 34° S latitude and from 19° to 27° E longitude, including all the Centres within the CFR. This species is a Cape ubiquist, distributed from Worcester in the Western Cape to Grahamstown in the Eastern Cape and on some of the mountain ranges in and around the Little Karoo. It is well adapted to drier Karoo habitats and is often found on the north-facing aspect of mountains in the southern Cape. It frequents the boundary of Fynbos and karroid vegetation and is common in the Little Karoo. *P. obtusifolia* grows at altitudes of (300–)670–1 400(–1 700) m.

*Passerina rigida* is distributed from Witsand River Mouth on the western coast of the Cape Peninsula, along the coastline to Lake Sibayi on the northeastern coast of KwaZulu-Natal. It is endemic to the coastlines of the Western Cape, the Eastern Cape and KwaZulu-Natal. This species occurs on littoral sand dunes and hammock dunes just above the level of spring tide. It is also found in marshy places and on sandy banks of river mouths and lagoons.

*Passerina corymbosa* (= *P. vulgaris* in previous chapters) is endemic to the Western and Eastern Cape, where it is found in all the phytogeographic Centres within the CFR. Although this species is distributed from Clanwilliam to Cape Town and eastwards to East London, it most commonly occurs in a belt between the coast and the 33° S latitude and from 18° to 29° E longitude. The specimens collected in KwaZulu-Natal are regarded as outliers, representing remnants of a former wider distribution. It is a species with a wide habitat spectrum, commonly occurring as a pioneer next to roadsides along the whole range of its distribution. *P. corymbosa* occurs at a range of altitudes, from sea level up to 1 300 m.

### *5.2.4 Species endemic or near-endemic to the Great Escarpment of southern Africa*

*Passerina drakensbergensis* is endemic to the Bergville District in the northern KwaZulu-Natal Drakensberg, which falls within the Drakensberg Alpine Centre. It has been collected from Royal Natal National Park to Giant's Castle Game Reserve at altitudes between 1 500 and 1 980 m. It is frequent at Cathedral Peak above Ndedema Gorge, where it is found in a marginal belt between forest and grassland; it also grows along streams and riverbanks and on mountain slopes.

*Passerina montana* is a near-endemic to the Great Escarpment of southern Africa, with distant satellite populations in high-mountain areas of Angola, Namibia and the Limpopo Province of South Africa. It is distributed from Nyanga in Zimbabwe, along the escarpment to Manica and Sofala in Mozambique, the Limpopo Province, Mpumalanga, Swaziland, KwaZulu-Natal, Free State, Lesotho and the Eastern Cape. Outliers in Angola have been recorded on the escarpment of the Huila Plateau near Lubango and the Cheila Mountains. Several specimens of this species have been collected at Moltkeblick on the Auas Mountains in Namibia. In the Limpopo Province *P. montana* is found in the Soutpansberg Area and on the Blouberg as well as on the summit of Krantzberg in the Waterberg Mountains. A single specimen (*Goossens 375*) was collected in the Pretoria District, but the species is probably extinct in this area, because of human impact. *P. montana* grows at altitudes of (900–)1 200–3 000 m.

Based on pollen evidence, Scott *et al.* (1997) regard the dryer forest types of East Africa and Australia as the best apparent analogies for the palaeovegetation of southern Africa during the terminal Cretaceous to the early Tertiary. During the Neogene, plant communities in southern Africa evolved into equivalents of modern biomes of the subcontinent. Currently grassland is widespread on the interior plateau and includes fynbos-like vegetation in moist higher-altitude areas (O'Connor & Bredenkamp 1997). During the Quaternary, highveld grassland expanded at the expense of woody vegetation, coupled by a southward spread of relatively dry mountain fynbos elements. Evidence of vegetation during the Holocene in the contemporary Grassland Biome has been found as far north as the Nyanga Mountains of Zimbabwe (Scott *et al*. 1997). The present author is of the opinion that *P. montana* probably originated from an ancestor in the CFR and adapted to the environmental conditions of the high-mountain grassland, which had a wider northerly distribution during the Quaternary. Because of environmental changes from the Quaternary to the present, the boundaries of the Grassland and Savanna Biomes changed, resulting in relicts of grassland and fynbos elements in high-altitude areas such as Nyanga, the Huila Plateau and the Auas Mountains.

*Passerina montana* on the Huila Plateau and the Auas Moutains most probably originated from a wider northern grassland vegetation, of which relicts remained in the high-mountain areas. In descriptions of the Afromontane Region, White (1981, 1983) and Cowling & Hilton-Taylor (1997) mention the significant outliers of this phytochorion occurring on the high mountains of West Africa and Angola.

Rennie (1936) argued that the occurrence of certain species, including species of *Passerina*, on the Auas Mountains in Namibia could be interpreted as relicts of the CFR, suggesting that northward migration of at least certain elements of that flora took place through present-day Namibia. Unfortunately the *Passerina* specimens available to him were sterile, resulting in their incorrect identification as *P. truncata* (=*P. glomerata*). As the most northerly distribution of *P. truncata* was Steinkopf in Namaqualand, he concluded that *P. truncata* was distributed through Namibia up to the Auas Moutains. However, the specimens from both Auas and Huila are unmistakeably *P. montana*, which is distributed mainly along the eastern Great Escarpment. The present distribution of *P. montana* renders Rennie's interpretation rather improbable.

*Passerina montivaga* has a wide distribution, from Mossel Bay and Oudtshoorn in the Western Cape northwards mainly along the Great Escarpment to KwaZulu-Natal, Swaziland, Mpumalanga, Limpopo Province, Mozambique and Zimbabwe. The most southwesterly distribution of this species is in the southern Cape, which is a region transitional between winter and summer-rainfall. However, over most of its range the species receives summer-rainfall. Because of its wide distribution, especially along the Great Escarpment, *P. montivaga* is adapted to a variety of habitats. It is often found along forest margins in the ecotonal zone between Afromontane Forest and grassland.

### 5.3 Conclusions

Within the CFR, Levyns (1938) considered the Caledon District as the centre of species richness, with a reduction in numbers to the north and east. Oliver *et al.* (1983) regarded the quarter degree 3418BB as the richest area and Beyers (2001) found that the highest number of *Lachnaea* species occurred in the quarter degree 3319AD (Worcester). In *Passerina* the highest numbers of species per grid are concentrated in a belt including the 33° and 34° S latitude and from 18° to 27° E longitude. The highest number of species per grid (nine) occurs in each of the grids 3321 (Ladismith), 3322 (Oudtshoorn) and 3419 (Caledon). The highest diversity of species (six) occurs in the False Bay area, from Seekoeivlei, including the Cape Flats, to De Mond at the Palmiet River (3418B). Hence the Western Cape is here regarded as the centre of diversity for *Passerina*, from where certain species extend west, north and east (Bredenkamp & Van Wyk 2000, 2001a).

*Passerina* species that are near-endemic or endemic to the Great Escarpment probably originated in the CFR and adapted to the environmental conditions of the high-mountain grassland, which had a wider northerly distribution during the Quaternary. The disjunct distribution of *P. montana* is probably due to environmental changes, from the Quaternary to the present. The boundaries of the Grassland and Savanna Biomes changed, resulting in relicts of grassland and fynbos elements on high-altitude areas such as Nyanga, the Huila Plateau and the Auas Moutains.

*Passerina* demonstrates a high degree of regional endemism, with 10 species out of 20 (50%) as well as the four subspecies endemic to the CFR. Of the above-mentioned species, 20% are endemic to one of four of the centres of the CFR: 10% (*P. montana* and *P. montivaga*) are near-endemic to the Great Escarpment and 5% (*P. drakensbergensis*) is endemic to the Bergville District in the northern Drakensberg.

# CHAPTER 6

# PHYLOGENY

## 6.1 Introduction

Cladistic analyses of the tribe Passerineae (Endl.) Bredenk. & A.E.van Wyk (1996, 2001a, 2001b) have not been done before. This analysis is an attempt to group species that share derived characters in *Passerina* in a way that reflects their possible phylogeny. Characters were obtained from research done on *Passerina* as part of a monograph of the genus. *Passerina corymbosa* (= *P. vulgaris*) in previous chapters.

A review of the application of the cladistic methodology in botany was given by Linder (1988). Examples of its application as followed in the present study are Van Wyk & Schutte (1988) and Van Wyk (1991). The cladistic analysis of *Lachnaea* by Beyers (2000, 2001), based on morphological characters, is one of the most recent of its kind for the Thymelaeaceae.

## 6.2 Choice of outgroup

In the cladistic analysis of *Lachnaea*, Beyers (2000, 2001) chose *Struthiola leptantha* Bolus and five *Gnidia* species as outgroup, a choice suggested by the cladistic analysis on the Thymelaeaceae based on sequence data from the *rbc*L gene (Van der Bank pers. comm.). Due to the availability of anatomical information for *Struthiola leptantha* and *S. myrsinites* (Van der Merwe *et al.* 1994), both these species as well as *Lachnaea axillaris* Meisn., *L. eriocephala* L. and *L. filamentosa* Meisn. (Beyers 1992, 2000) were initially chosen as the outgroup for the present analyses. For practical reasons, not all details of all the cladistic analyses are given, but are available from the author on request. As the initial cladograms were not a satisfactory reflection of the phylogeny within the genus, further analyses were done using only *S. leptantha* as the outgroup.

### 6.3 Choice of characters and data matrices

Anatomical characters of *Struthiola leptantha* were obtained from Van der Merwe *et al*. (1994) and morphological characters from herbarium material in the collection at PRE. Characters of possible phylogenetic significance in *Passerina* were indicated by the following studies: palynology, leaf epidermal and leaf and floral structure (Bredenkamp & Van Wyk 1996, 2000, 2001a, 2001b). Initially 48 characters were used in the character set, but after elimination of the *Lachnaea* species as well as subspecies of *Passerina* from the outgroup, the character set changed. Throughout the analysis the character set was modified, substituting characters with low consistency (CI) and retention (RI) indices with more suitable characters, or turning them off during the analysis. The data matrix was also refined throughout the analysis, removing autapomorphies and improving affected character states. Ultimately 51 characters were used in the character list (Tables 6.1, 6.2).

TABLE 6.1.—Character matrix for the cladistic analysis of the genus *Passerina*, using HENNIG 86 and PAUP 4.0 for Macintosh and with *Struthiola leptantha* representing the outgroup

| **Taxon** | **Character states** | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0 | 1–5 | 6–10 | 11–15 | 16–20 | 21–25 | 26–30 | 31–35 | 36–40 | 41–45 | 46–50 | 51 |
| *S. leptantha* | 0 | 00000 | 00000 | 00000 | –000 | 00-00 | 0— | -0000 | -0020 | 00000 | 00000 | 0 |
| *burchellii* | 0 | 11201 | 11010 | 11101 | 00020 | 11111 | 10221 | 10211 | 02121 | 21111 | 11121 | 1 |
| *comosa* | 0 | 10001 | 11111 | 11101 | 01030 | 11110 | 11101 | 10201 | 02010 | 11111 | 10110 | 2 |
| *drakensbergensis* | 0 | 01001 | 11210 | 11101 | 00020 | 11110 | 10201 | 10201 | 01111 | 11111 | 10110 | 3 |
| *ericoides* | 0 | 10101 | 11110 | 11101 | 00030 | 11011 | 10211 | 11221 | 11101 | 01111 | 10120 | 3 |
| *esterhuyseniae* | 0 | 20001 | 11110 | 11101 | 01020 | 11001 | 10110 | 10111 | 11220 | 21111 | 11100 | 3 |
| *falcifolia* | 0 | 00011 | 11310 | 11211 | 10120 | 11210 | 10201 | 00201 | 01101 | 01111 | 10100 | 5 |
| *filiformis* | 0 | 00001 | 11110 | 11101 | 00020 | 11210 | 10010 | 00201 | 01020 | 21111 | 10100 | 3 |
| *galpinii* | 0 | 00001 | 11110 | 11101 | 00020 | 11011 | 10000 | 00201 | 11002 | 01111 | 10110 | 3 |
| *montana* | 0 | 20001 | 11110 | 11311 | 01121 | 12-11 | 10211 | 10201 | 02101 | 01111 | 10121 | 6 |
| *montivaga* | 0 | 01010 | 11310 | 11211 | 10120 | 11210 | 10031 | 00101 | 02020 | 21111 | 10100 | 5 |
| *nivicola* | 0 | 02001 | 01110 | 11000 | –000 | 11001 | 10010 | 00101 | 01000 | 01111 | 10100 | 0 |
| *obtusifolia* | 0 | 00001 | 11110 | 11101 | 02020 | 11010 | 10131 | 10201 | 12101 | 01111 | 10100 | 4 |
| *paleacea* | 0 | 20001 | 11110 | 11311 | 01131 | 12-01 | 10200 | 00121 | 10000 | 01111 | 11121 | 6 |
| *paludosa* | 0 | 01001 | 11010 | 11101 | 00010 | 11110 | 10031 | 00201 | 01022 | 21111 | 10120 | 2 |
| *pendula* | 0 | 01201 | 11210 | 11101 | 00020 | 11111 | 10121 | 10121 | 02101 | 01111 | 10121 | 1 |
| *quadrifaria* | 0 | 00001 | 11211 | 11101 | 00020 | 12-10 | 11101 | 10201 | 02021 | 11111 | 10120 | 3 |
| *rigida* | 0 | 20001 | 11110 | 11311 | 00131 | 11001 | 10201 | 11111 | 12101 | 01111 | 11121 | 6 |
| *rubra* | 0 | 00101 | 11210 | 11101 | 00020 | 11210 | 10201 | 00201 | 02001 | 01111 | 10100 | 3 |
| *truncata* | 0 | 10101 | 11110 | 11101 | 02030 | 12-11 | 10211 | 10211 | 12101 | 01111 | 10121 | 4 |
| *corymbosa* | 0 | 00011 | 11310 | 11311 | 10121 | 11210 | 10231 | 00201 | 02101 | 01111 | 10100 | 6 |

-, not aplicable

TABLE 6.2.—Character list and character states for the cladistic analysis of the genus *Passerina*

1. Leaf length: long 3.1–8.0 mm (0)—medium length 2.5–3.0 mm long (1)—short 1.5–2.4 mm (2)
2. Leaf margin: eciliate (0)—ciliate (1)—tufted (2)
3. Leaf shape: linear to narrowly lanceolate (0)—oblong (1)—rhombic (2)
4. Vascular bundle abaxially: not enclosed in V-shaped palisade parenchyma (0)—enclosed in V-shaped palisade parenchyma (1)
5. Abaxial leaf surface: plane (0)—convex (1)
6. Leaves: isobilateral (0)—inverse-dorsiventral (1)
7. Leaves: amphistomatic (0)—epistomatic (1)
8. Leaf outline in t/s: narrowly transversely elliptic (0)—transversely elliptic (1)—canaliculate (2)—carinate (3)
9. Indumentum of adaxial epidermis: glabrous (0)—villous (1)
10. Indumentum of abaxial epidermis: trichomes absent (0)—present (1)
11. Thickness of cuticle adaxially: ± same as abaxially (0)—very thin 2–5 µm (1)
12. Adaxial epidermal cells: ± same as abaxially (0)—much smaller and irregularly shaped (1)
13. Leaf structural type: structural type A (0)—type B (1)—type C (2)—type D (3)
14. Extraxylary sclerenchyma fibres: completely enclosed by vascular bundle sheath (0)—abaxially not enclosed, often extending to abaxial epidermis (1)
15. Mesophyll: homogenous, palisade-like (0)—palisade parenchyma adjacent to abaxial epidermis (1)
16. Shape of palisade parenchyma: horseshoe-shaped or U-shaped (0)—V-shaped (1)
17. Spongy parenchyma: aerenchymatic (0)—mesomorphic (1)—xeromorphic (2)
18. Bundle sheath: completely enveloping main vascular bundle (0)—forming an adaxial cap (1)
19. Mesophyll: homogenous (0)—number of layers of palisade parenchyma one (1)—two (2)—three (3)
20. Extraxylary fibres: adhering to vascular bundles only (0)—extending to abaxial epidermis and paradermally up to leaf margins forming a sclerenchymatous hypodermal sheath (1)
21. Inflorescence class: monotelic (0)—polytelic (1)

22. Type of inflorescence: solitary flower (0)—reduced spike or multiflowered spike (1)—subcapitulate spike (2)

23. Number of flowers in multiflowered spikes: <12 (0)—12–16 (1)—>16 (2)

24. Colour of hypanthium at pollination: yellow (0)—yellow-pink or greenish pink (1)

25. Length of floral bracts: long, > 4.5 mm (0)—short, 4.5 mm and shorter (1)

26. Bracteoles: present (0)—absent (1)

27. Indumentum of differentiated floral bracts abaxially: glabrous (0)—hairy (1)

28. Indumentum of differentiated floral bracts adaxially: basally to centrally hairy with glabrous wings (0)—comose (1)—villous (2)

29. Plane shape of differentiated floral bracts: ovate (0)—obovate (1)—rhombic (2)—obtrullate (3)

30. Texture of lamina of differentiated floral bracts: chartaceous (0)—coriaceous (1)

31. Wings of differentiated floral bracts: present (0)—absent (1)

32. Fruit: dry (0)—fleshy (1)

33. Texture of hypanthium: herbaceous (0)—membranous (1)—papyraceous and coriaceous (2)

34. Length of hypanthium neck: relatively long, > 0.8 mm (0)—short 0.7–0.8 mm (1)—very short < 0.7 mm (2)

35. Circumscissile articulation in hypanthium above ovary: present (0)—absent (1)

36. Fragmentation of hypanthium after fruiting: at neck base (because of torsification and desiccation) (0)—at circumference of ovary (1)

37. Indumentum of hypanthium outside, trichomes above and below articulation must be homogenous (density could differ): whole of hypanthium glabrous (0)—whole of hypanthium hairy (1)—lower portion of hypanthium glabrous, upper portion hairy (2)

38. Indumentum of adaxial surface of outer sepal lobes: glabrous (0)—hairy (1)—apex hairy (2)

39. Indumentum of abaxial surface of outer sepal lobes: glabrous (0)—hairy (1)—apex hairy (2)

40. Indumentum of adaxial surface of inner sepal lobes: glabrous (0)—hairy (1)—apex hairy (2)

41. Indumentum of abaxial surface of inner sepal lobes: glabrous (0)—hairy (1)—apex hairy (2)

42. Antisepalous stamen whorl: absent (0)—present (1)

43. Stamens: included in hypanthium (0)—exserted (1)

44. Anthers: introrse (0)—extrorse (1)

45. Floral scales: present (0)—absent (1)

46. Perigonal hairs: present (0)—absent (1)

47. Total length of floral envelope: long, 5.0–8.4 mm (0)—short, 4.0–4.9 mm (1)

48. Pollen wall: crotonoid (0)—secondary reticulum (1)

49. Internodes longer, leaves not imbricate (0)—internodes short, leaves overlapping 1–25% (1)—internodes very short, leaves overlapping 26–50% (2)

50. Leaves ascending to spreading horizontally (angle of divergence 16–90°) (0)—leaves appressed (angle of divergence 1–15°) (1)

51. Leaf structural type: A (0)—B1 (1)—B2 (2)—B3–B4 (3)—B5–B6 (4)—C (5)—D (6)

## 6.4 Analysis of the data matrix

### *6.4.1 Analysis A*

The program HENNIG 86 version 1.5 (Farris 1988) and the accompanying manual (Lipscomb 1994) were used to analyse the data. Using the final data set with *Struthiola leptantha* as outgroup, five trees were obtained by the 'mhennig*' command [length 193, CI 0.40 and RI 0.55]. Tree diagnosis was applied using the 'xsteps c' and 'xsteps h' commands, showing the consistency (CI) and retention (RI) indices of the individual characters. In *Passerina*, selected multistate characters were evaluated according to the concept of Fitch parsimony (Lipscomb 1994), claiming that any state is allowed to transform into any other state with only one step in an unordered analysis. Leaf structural types in *Passerina* (anatomical characters concerning the structure of the mesophyll and the main vascular bundle) were regarded as ordered, as these characters are probably irreversible and evolved over a long period of time. Multistate characters such as indumentum type and leaf shape were treated as unordered.

Further settings:

Characters 1, 2, 3, 8, 17, 19, 28, 29, 33, and 37–41 treated as unordered using the 'cc -;' command [mhennig length 170, CI 0.46 and RI 0.58 trees 9].

Characters 5 and 17 with a low RI excluded [hennig length 164, CI 0.46 and RI 0.59].

Character 22 has weight 5 and 32 has weight 10 [hennig length 196, CI 0.47 and RI 0.56].

Character 47 excluded.

The command 'mhennig*' yielded eight trees, from which the best tree was selected. The distribution of characters on the selected tree was examined using the tree editor 'DOS EQUIS' and the character transformation series was interpreted and plotted on the cladogram (Figure 6.1). A Nelson consensus tree was generated (Figure 6.2).

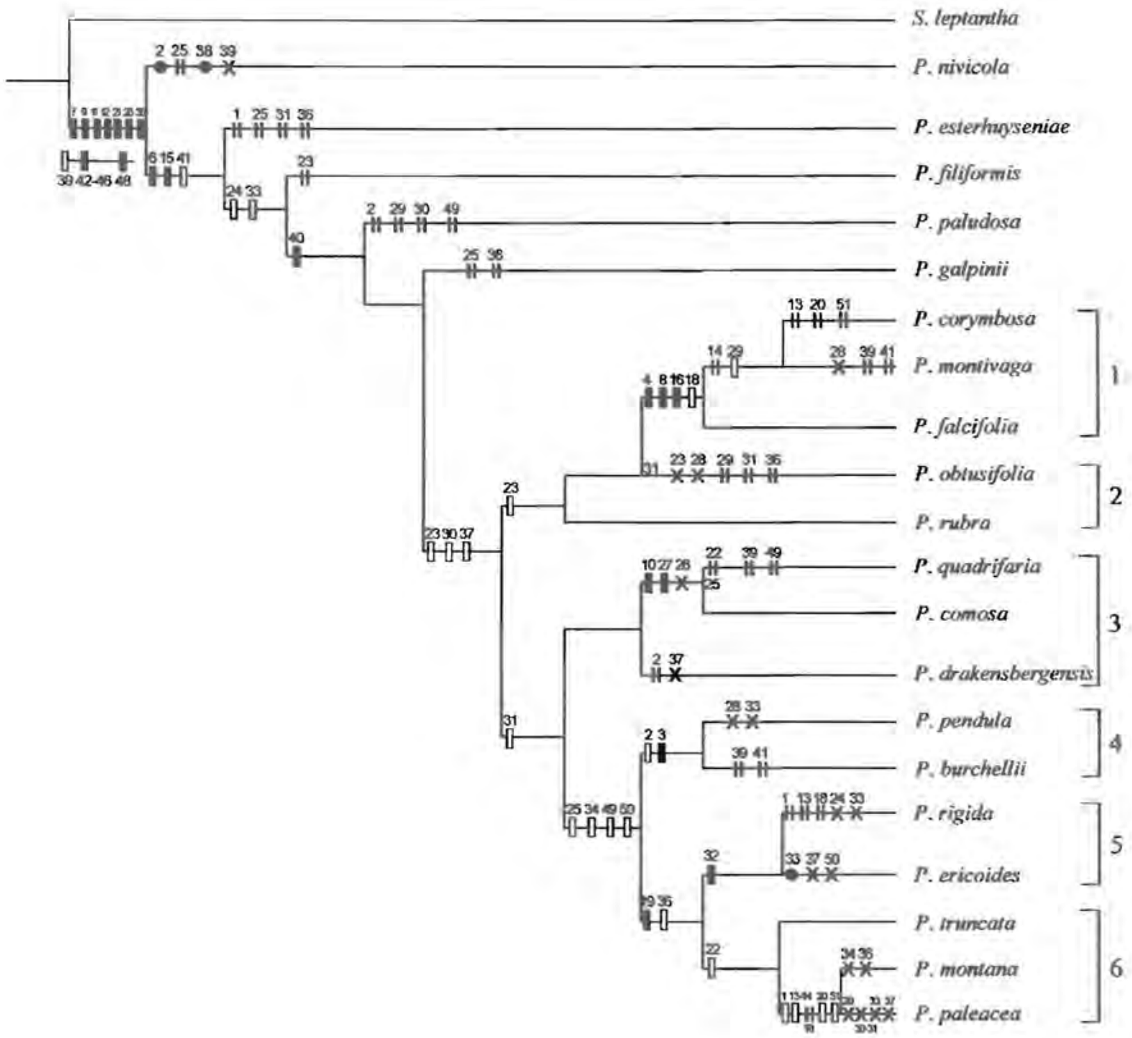


Figure 6.1.—Estimate of possible phylogenetic relationships in the genus *Passerina* as obtained in analysis A. For details see text. Symbols used:▮, synapomorphy showing no homoplasy;▯, synapomorphies showing reversal higher up in the cladogram; ✕, reversals; ‖, convergencies; ●, autapomorphies not included in the analysis.

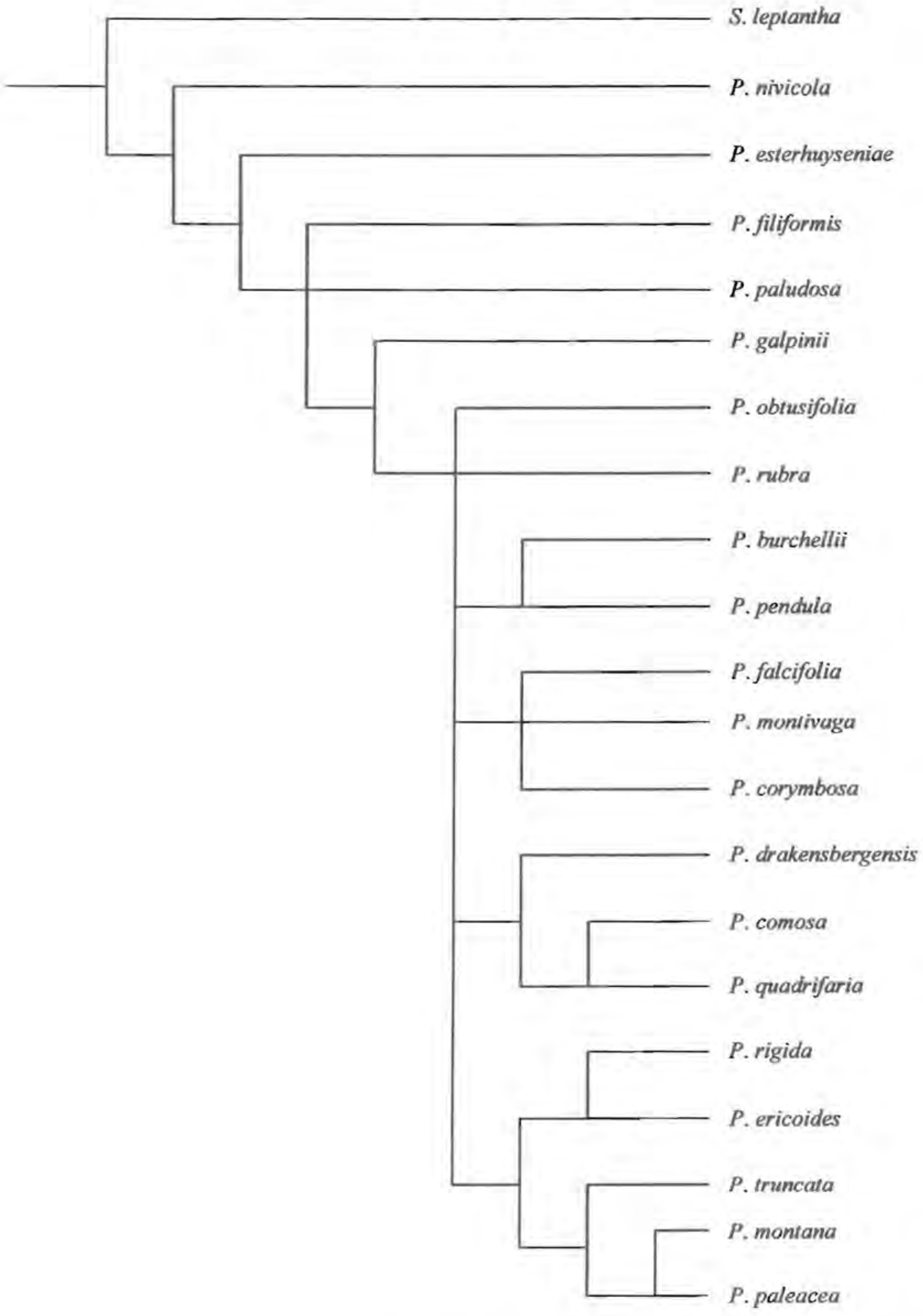


FIGURE 6.2.—Nelson consensus tree obtained in analysis A, after applying selective character weighting and using the program HENNIG 86.

### *6.4.2 Analysis B*

For the determination of bootstrap values, which could not be obtained from HENNIG 86, data were also analysed using the software package PAUP 4.0 for Macintosh (Swofford 1991). Running the same data set as for the HENNIG 86 analysis, the Heuristic search was done, using the following settings:
Optimality criterion = maximum parsimony.
Characters 5, 17 and 47 excluded.
Of the remaining 48 included characters: 35 were of the type 'ord' (Wagner), 13 characters were of the type 'unord' (characters 1, 2, 3, 8, 17, 19, 28, 29, 33, and 37–41).
46 characters had weight 1.
Character 22 had weight 5 and 32 had weight 10.
Starting tree(s) obtained via stepwise addition.
Addition sequence: random.
Number of replicates = 100.
Branch swapping algorithm: tree-bisection-reconnection (TBR).

A cladogram indicating the possible phylogenetic relationships of the species in *Passerina* (Figure 6.3), and a consensus tree indicating the bootstrap values (Figure 6.4) were generated.

### *6.4.3 Analysis C*

Data were analysed using the UPGMA method of the PAUP software package. The same data set as for analyses A and B as well as the following settings were used:
Ties (if encountered) will be broken randomly; initial seed = 274891198.
Distance measure = mean character difference.
3 characters were excluded.
Tree was rooted.

A cladogram was generated indicating the possible phylogenetic relationships of the species in *Passerina* (Figure 6.5) and bootstrap values indicated (Figure 6.6).

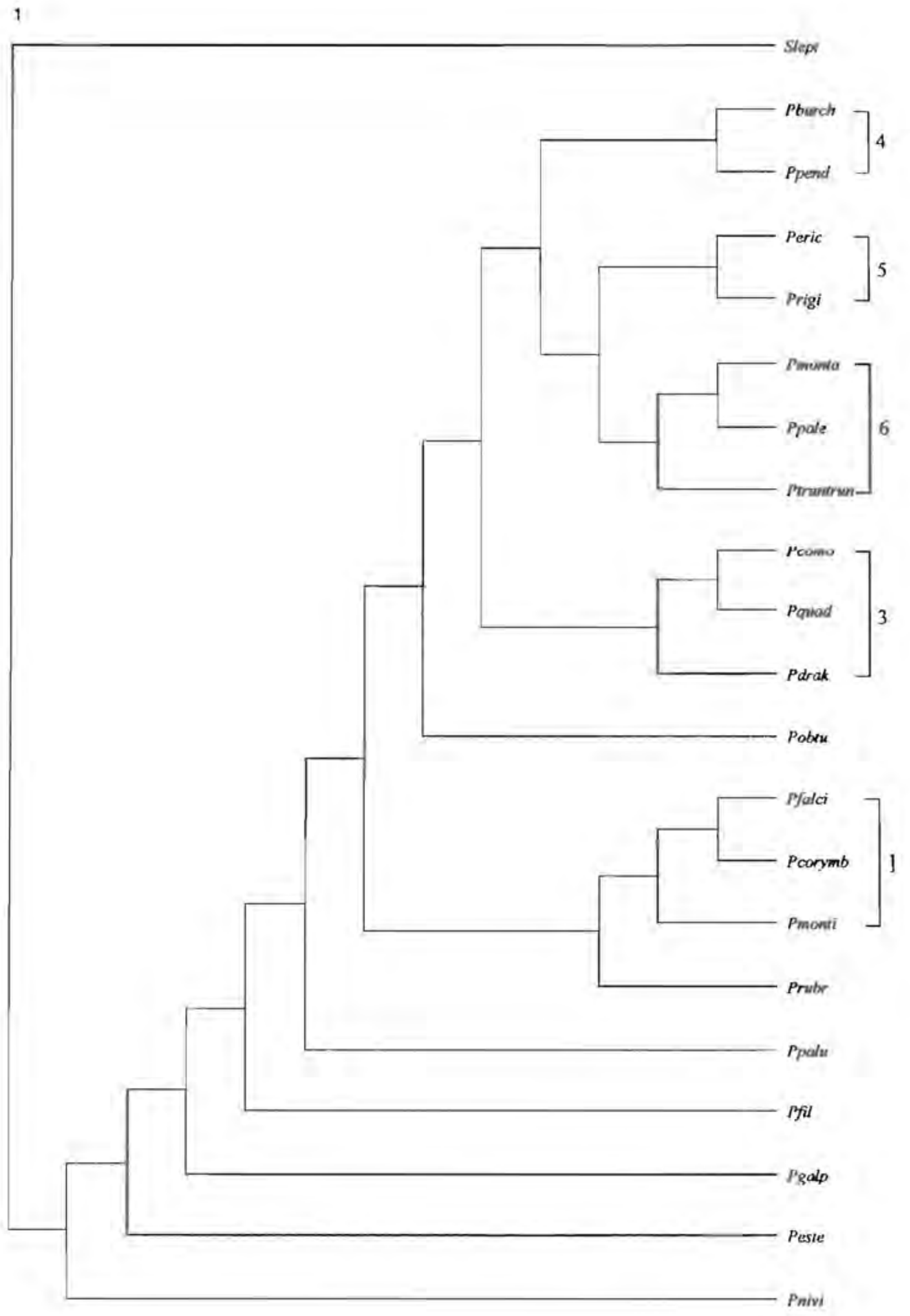


FIGURE 6.3.—Estimate of phylogenetic relationships in the genus *Passerina* as obtained in analysis B, after applying selective character weighting and using the Heuristic search of the PAUP 4.0 for Macintosh software package.

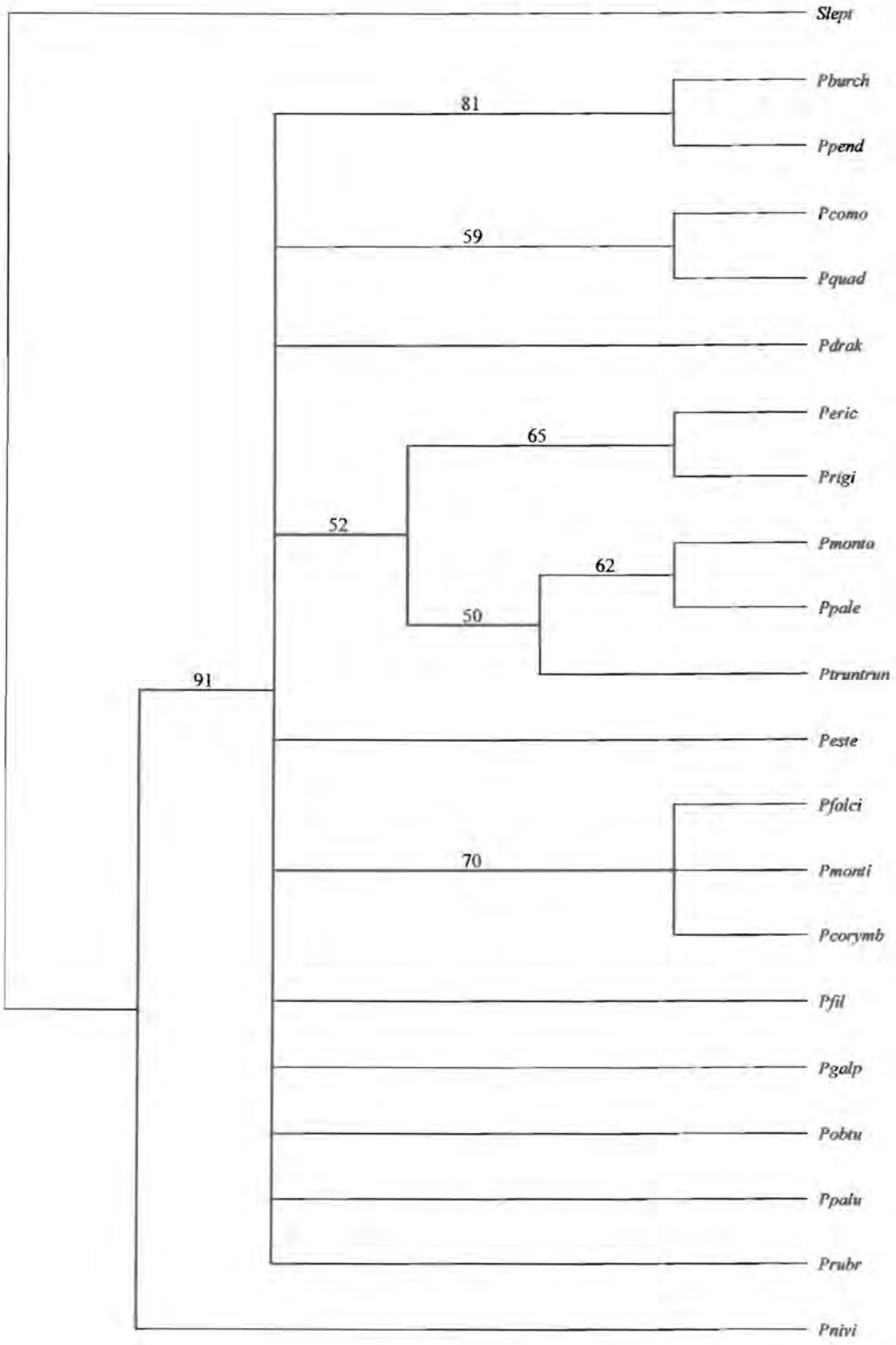


FIGURE 6.4.—Bootstrap values generated in analysis B, after applying selective character weighting and using the Heuristic search of the PAUP 4.0 for Macintosh software package.

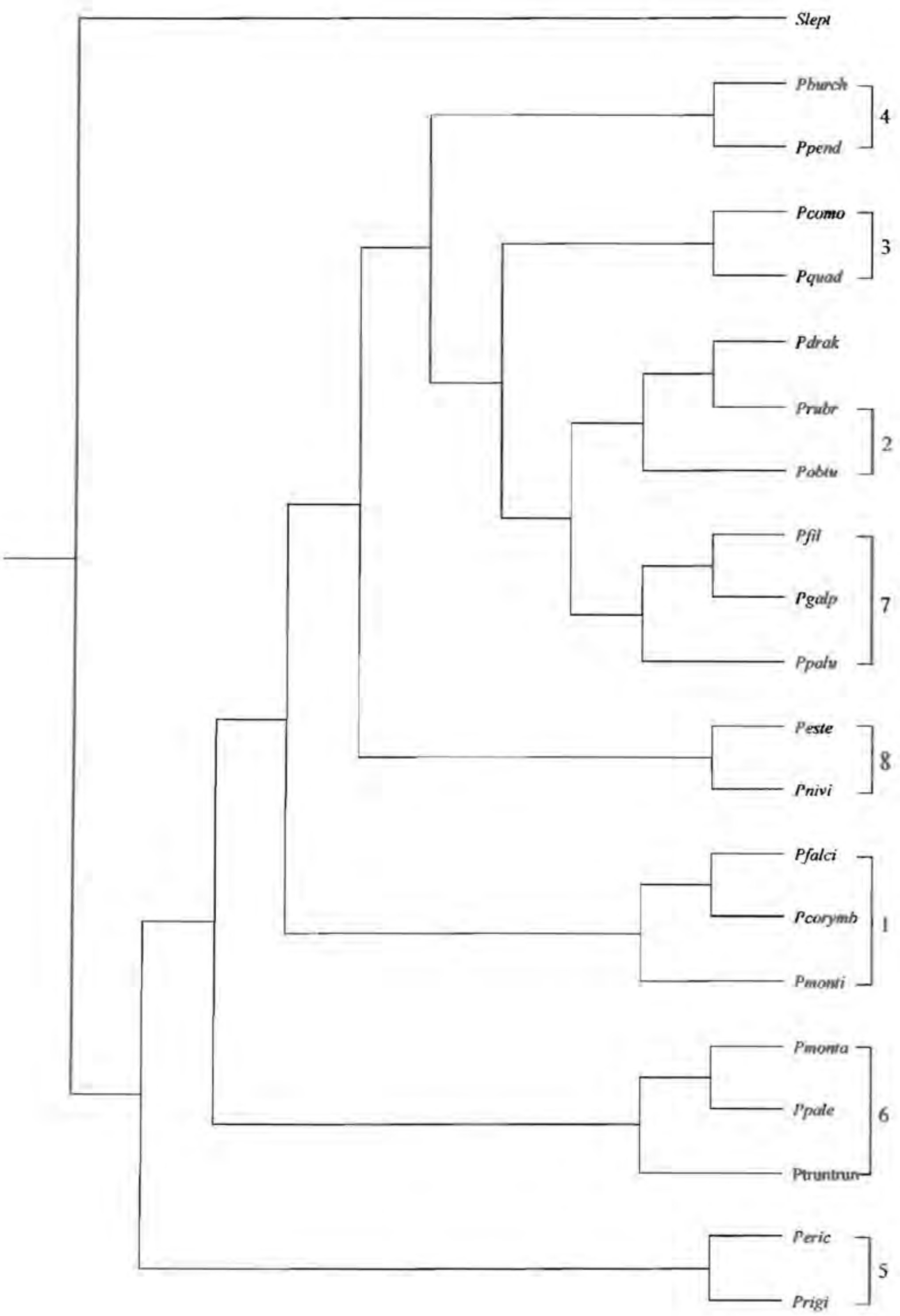


FIGURE 6.5.—Estimate of phylogenetic relationships in the genus *Passerina* as obtained in analysis C, after applying selective character weighting and using the UPGMA search of the PAUP 4.0 for Macintosh software package.

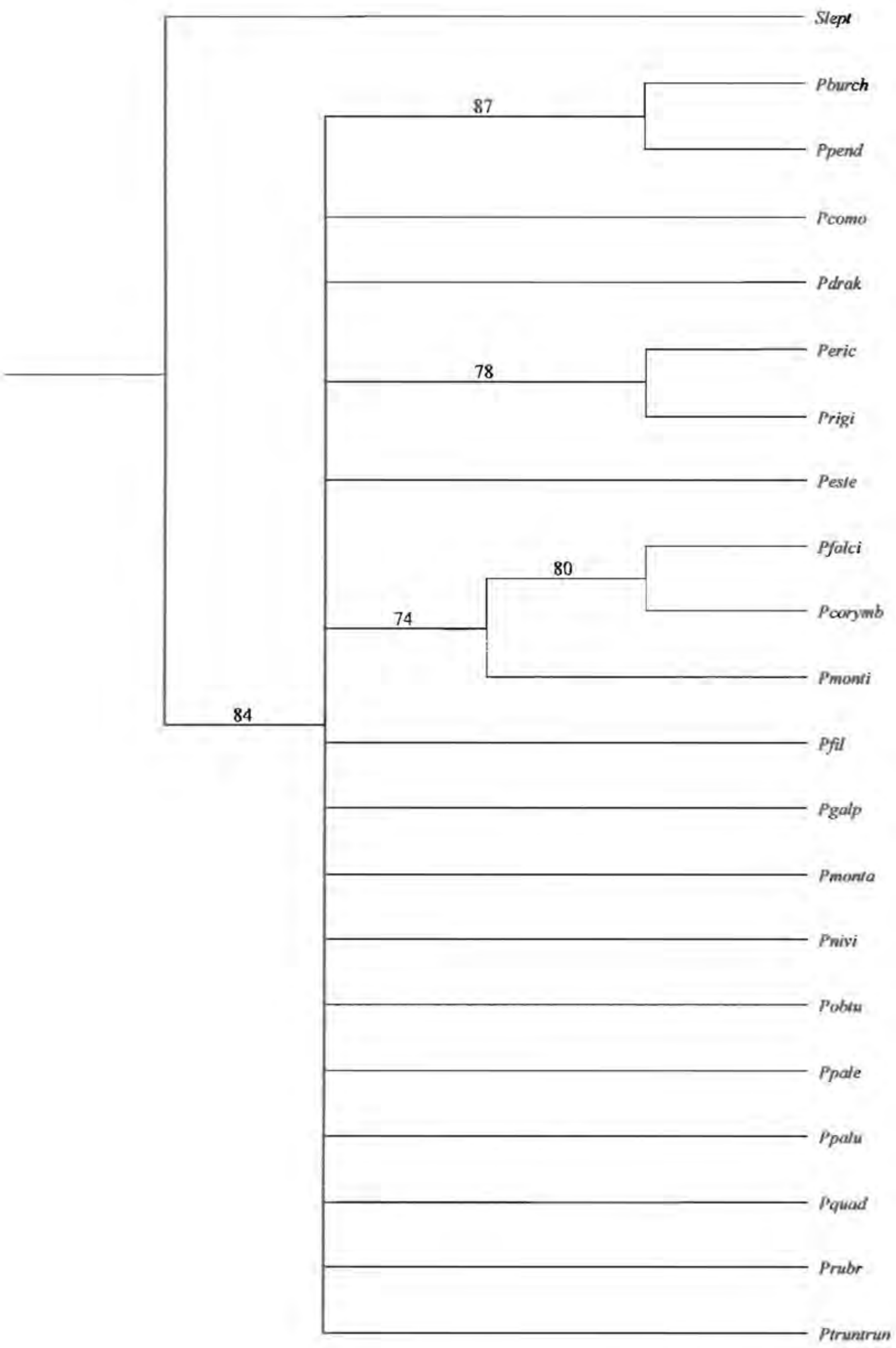
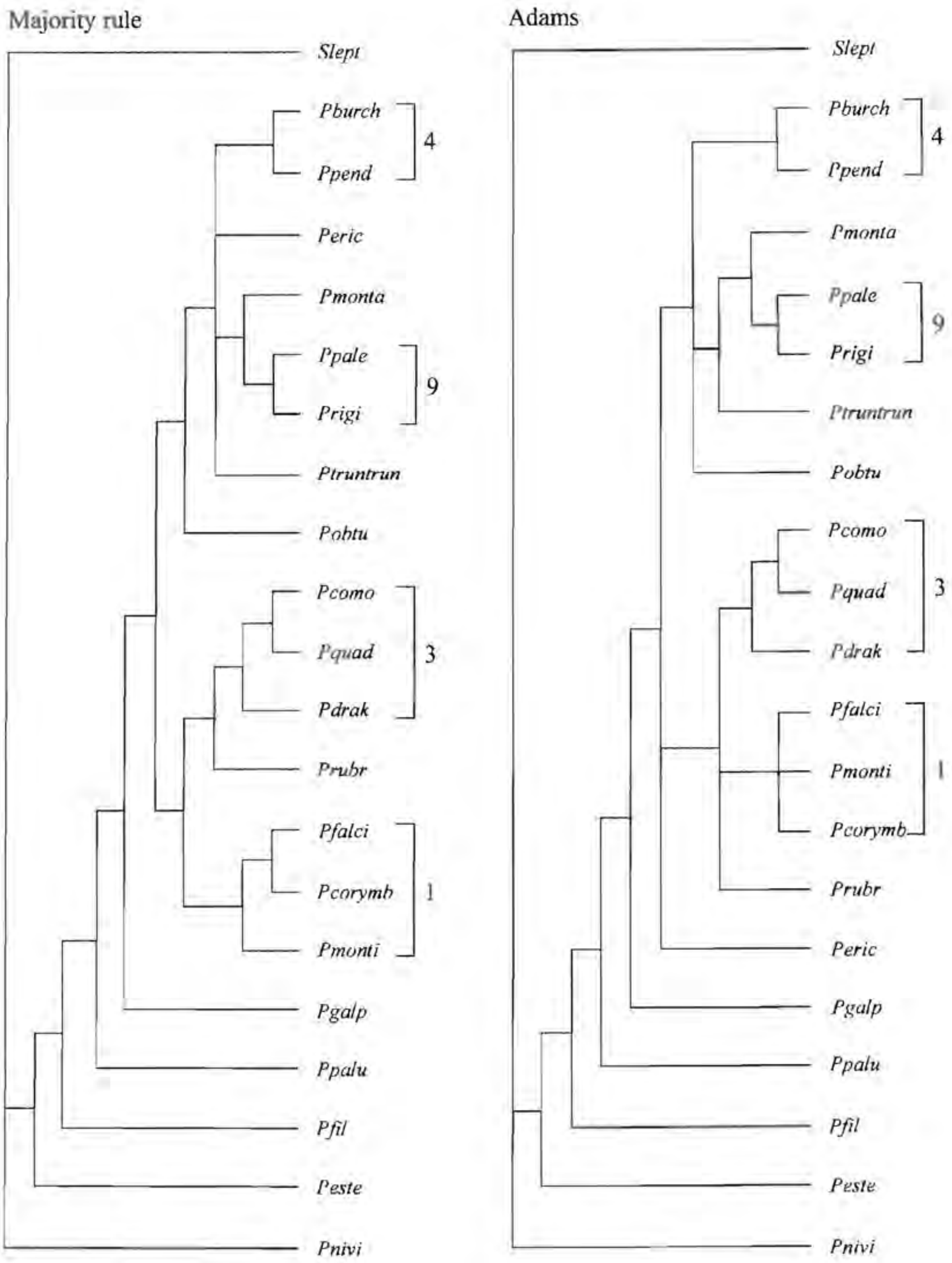


FIGURE 6.6.—Bootstrap values generated in analysis C, after applying selective character weighting and using the UPGMA search of the PAUP 4.0 for Macintosh software package.

### *6.4.4 Analysis D*

Running the same data set as for the HENNIG 86 analysis, but omitting character weighting, data were further analysed using the software package PAUP 4.0 for Macintosh (Swofford 1991). The following settings were used:
Number of replicates = 1000.
Stepwise increase.
Addition sequence: random.
Branch swapping algorithm: tree-bisection-reconnection (TBR) + mulpars + sd.
52 characters used.
52 characters with weight 1.
Compute consensus = strict.

A cladogram indicating the possible phylogenetic relationships of the species in *Passerina* (Figure 6.7) and a consensus tree indicating the bootstrap values (Figure 6.8) were generated.


Majority rule

Adams

FIGURE 6.7.—Estimate of phylogenetic relationships in the genus *Passerina* as obtained in analysis D, without character weighting and using the Majority Rule and Adams options of the PAUP 4.0 for Macintosh software package.

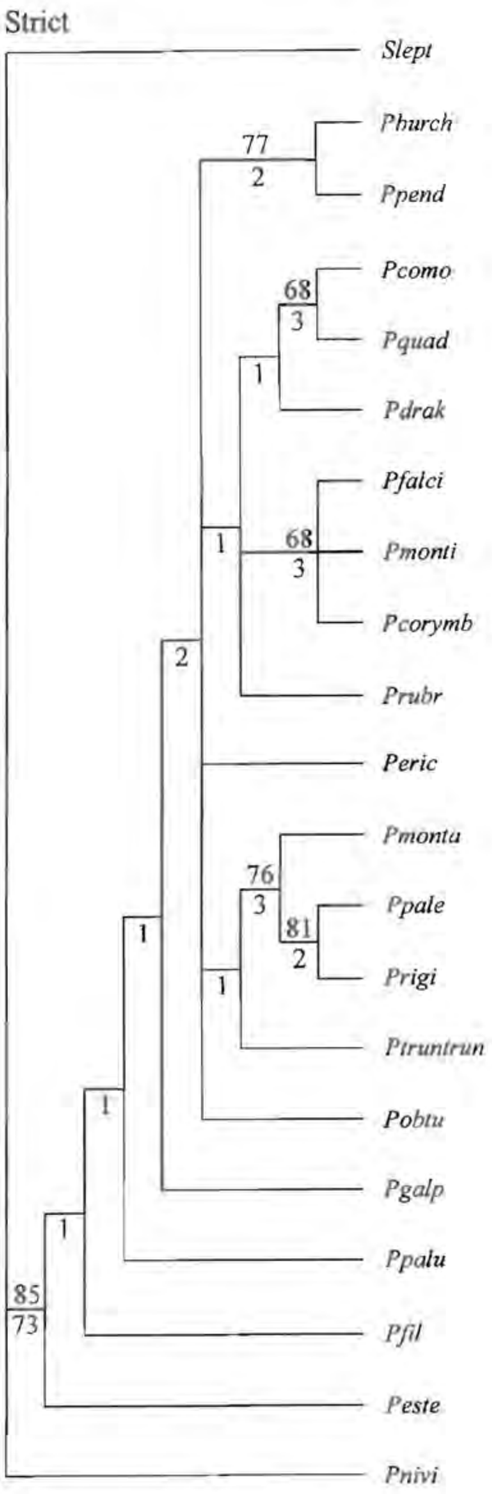


FIGURE 6.8.—Bootstrap values generated in analysis D, without character weighting and computing a strict consensus tree, using the PAUP 4.0 for Macintosh software package.

## 6.5 Results

### *6.5.1 Analysis A*

The command 'mhennig*' produced eight equally parsimonious trees, 192 steps long, CI 0.48 and RI 0.57, from which the best tree was selected. The cladogram in Figure 6.1 indicates the phylogenetic relationships of all the species in *Passerina* obtained from the analysis, illustrating the synapomorphies, reversals, convergency and autapomorphies not included in the analysis. Figure 6.2 shows the Nelson consensus tree.

The cladogram (Figure 6.1) shows that *Passerina* is a strongly supported monophyletic group, delimited as a genus by a variety of characters. Synapomorphic leaf anatomical characters are epistomatic leaves [7 (1)], specialized epidermal characters, for example a villous adaxial epidermis [9 (1)], a very thin adaxial cuticle [11 (1)] and smaller and irregularly shaped adaxial epidermal cells [12 (1)]. The genus is further characterized by polytelic synflorescences [21 (1)] and the absence of bracteoles [26 (1)]. The absence of a circumscissile articulation in the hypanthium above the ovary [35 (1)] is a morphological feature synapomorphic for all the clades in *Passerina*. Characters associated with the adaptation of *Passerina* to wind pollination are synapomorphic to all clades in the genus, e.g. exserted stamens [43 (1)], extrorse anthers [44 (1)], the absence of floral scales in the mouth of the floral tube [45 (1)], the absence of perigonal hairs [46 (1)] and the secondary reticulum of the pollen wall [48 (1)].

*Passerina nivicola* is paraphyletic to the outgroup *Struthiola leptantha* based on the plesiomorphic characters, isobilateral leaves [6 (0)] and a homogenous mesophyl [15 (0)]. Autapomorphies characteristic of *P. nivicola* are tufted leaves [2 (2)] and the hairy apex of the outer sepal lobes [38 (2)]. The synapomorpic characters, inverse-dorsiventral leaves [6 (1)], palisade parenchyma adjacent to abaxial epidermis [15 (1)] and the hairy apex of the abaxial surface of the inner sepal lobes [41 (2)], are characteristic of the basal paraphyletic clades *P. esterhuyseniae*, *P. filiformis* and *P. paludosa*. Character [41 (2)], the hairy apex of the abaxial surface of the inner sepal lobes, reverses in the clades *P. galpinii* / *P. paleacea* and converges in *P. montivaga* and *P. burchellii*.

Differentiated floral bracts that are adaxially villous [28 (2)] and with a coriaceous texture [30 (1)] support the dichotomous clade *P. corymbosa* / *P. paleacea*. The indumentum of the hypanthium, with the lower portion glabrous and the upper portion hairy [37 (2)], is also synapomorpic for this clade. However, reversals of these characters occur higher up in the cladogram. The final analysis of the clade *P. corymbosa* / *P. paleacea* indicates six end-groups of species pairs / triplets.

The clade *P. corymbosa* / *P. rubra* is strongly supported by multiflowered spikes with more than 16 flowers [23 (2)], this character converging in *P. filiformis*. Characters derived from the leaf structural type of the leaf anatomical study (Bredenkamp & Van Wyk 2001) are synapomorphic for the clade *P. corymbosa* / *P. falcifolia*. The carinate leaf in t/s [8 (3)], the presence of V-shaped palisade parenchyma [16 (1)] and the vascular bundle that is abaxially enclosed in V-shaped palisade parenchyma [4 (1)] support *P. falcifolia* and *P. montivaga*. Extraxylary sclerencyma fibres extending to the abaxial epidermis and obtrullate differentiated floral bracts [29 (3)] are synapomorphic for the *P. montivaga* / *P. corymbosa* clade, while leaf structural type D [13 (3), 51 (6)] converges in *P. corymbosa*.

The plesiomorphic character winged differentiated floral bracts is characteristic of the species *P. nivicola* to *P. rubra*. The absence of wings in differentiated floral bracts [31 (1)] is a synapomorphy of the polychotomous clade *P. quadrifaria* / *P. paleacea*, reversing in *P. paleacea* and converging in *P. esterhuyseniae* and *P. obtusifolia*. The clade *P. quadrifaria* / *P. drakensbergensis* is not strongly supported. The indumentum of the leaves and bracts is synapomorphic for *P. quadrifaria* and *P. comosa*; in both cases trichomes are abaxially present on the leaves [10 (1)] and bracts [27 (1)], and bracts are adaxially comose [28 (1)]. Long, differentiated floral bracts [25 (0)] and a long hypanthium neck [34 (0)] are plesiomorphic characters supporting the clades *P. nivicola* / *P. drakensbergensis*; short floral bracts [25 (1)] and a short hypanthium neck [34 (1, 2)] are characteristic of the dichotomous clade *P. pendula* / *P. paleacea*. Other synapomorphies supporting the latter clade are very short internodes, with leaves overlapping 26–50% [49 (2)] and appressed leaves, angle of divergence 1–15° [50 (1)].

Rhombic leaves [3 (2)] with ciliate margins [2 (1)] are synapomorphic of *P. pendula* and *P. burchellii*. The leaf anatomical character, three layers of palisade parenchyma [19 (3)] is synapomorphic for the clade *P. rigida* / *P. paleacea*. Fragmentation of the hypanthium (after fruiting) at the circumference of the ovary [36 (1)] is characteristic of the latter clade, with a reversal in *P. montana*, in which the hypanthium fragments at the neck base. Fleshy fruits [32 (1)] are synapomorphic for *P. rigida* and *P. ericoides*, with coriaceous fruits [33 (2)] autapomorphic for *P. ericoides*. The clade *P. truncata* / *P. paleacea* is characterized by the synapomorphic character, subcapitulate spikes [22 (2)], converging in *P. quadrifaria*. The synapomorphic character, short leaves [1 (2)] and the following leaf structural type characters: bundle sheath forming an adaxial cap [18 (1)]; extraxylary sclerenchyma fibres abaxially not enclosed by the vascular bundle sheath, often extending to the abaxial epidermis [14 (1)]; extraxylary fibres extending to abaxial epidermis and paradermally up to the leaf margins, forming a sclerenchymatous hypodermal sheath [20 (1)] and leaf structural type D [13 (3), 51 (6)], characterise the *P. montana* / *P. paleacea* clade, converging in *P. corymbosa*.

The Nelson consensus tree (Figure 6.2) shows that *Passerina* is a strongly supported monophyletic group, with *Struthiola leptantha* as the outgroup. The consensus tree differs from the cladogram in the following apects:
*P. filiformis* and *P. paludosa* are sister species.
The paraphyletic species *P. obtusifolia*, *P. rubra* and the subclade *P. burchellii* / *P. pendula* are basal to all the other clades in the cladogram.

### *6.5.2 Analysis B*

Using the software package PAUP 4.0 for Macintosh (Swofford 1991), the completed Heuristic search showed the following:
Total number of rearangements tried = 1426832.
13 characters were parsimony-uninformative.

Number of (included) parsimony-informative characters: 35.
Score of best tree(s) found = 191.
Number of trees retained = 66.
Tree length 191, CI 0.482, RI 0.573 (this value is almost identical to the values obtained by the HENNIG 86 analysis: length 192, CI 0.48 and RI 0.57).

The cladogram generated by the Heuristic search (Figure 6.3) is almost similar to the one generated by HENNIG 86 (Figure 6.1), but differs in the following aspects: The paraphyletic *P. galpinii* is placed close to the basal species *P. esterhuyseniae* and *P. nivicola*.
The clade *P. corymbosa* / *P. paleacea* is polychotomous in analysis A (Figure 6.1), but in the Heuristic analysis it is divided into three paraphyletic clades *P. rubra* / *P. falcifolia*, *P. obtusifolia* and *P. drakensbergensis* / *P. comosa*, as well as a dichotomous clade *P. truncata* / *P. burchellii*.
In Analysis A, the clade *P. corymbosa* / *P. paleacea* indicates six end-groups of species pairs / triplets. The same species pairs/triplets can be identified in the Heuristic analysis except that *P. obtusifolia* is paraphyletic to the clade *P. drakensbergensis* / *P. burchellii*.
The species order often differs in the various clades.

Bootstrap values are indicated in Figure 6.4. The clade *P. rubra* / *P. burchellii* is supported by a value of 91% indicating the monophyletic nature of the genus. The clades *P. corymbosa* / *P. falcifolia* (70%) and *P. pendula* / *P. burchellii* (81%) are strongly supported. Although the clade *P. truncata* / *P. ericoides* (52%) is not strongly supported, the *P. rigida* / *P. ericoides* (65%) and the *P. paleacea* / *P. montana* clades (62%) are supported by reasonably high bootstrap values. The *P. quadrifaria* / *P. comosa* clade (59%) does not have strong bootstrap support.

### *6.5.3 Analysis C*

Using the software package PAUP 4.0 for Macintosh (Swofford 1991) and the UPGMA search, a cladogram indicating the possible phylogenetic relationships of the species in *Passerina* (Figure 6.5) was generated. Bootstrap values are shown in Figure 6.6.

The cladogram generated by the UPGMA search differs substantially from the one generated by HENNIG 86 in the following aspects:

*P. ericoides* / *P. rigida* is identified as the basal clade, closest to *Struthiola leptantha*.

The *P. nivicola* / *P. esterhuyseniae* clade is placed in an intermediate position, not basally as in Analysis A.

The *P. truncata* / *P. montana* clade has a basic position.

All the species are divided into six paraphyletic clades, namely *P. rigida* / *P. ericoides*, *P. truncata* / *P. montana*, *P. montivaga* / *P. falcifolia*, *P. nivicola* / *P. esterhuyseniae*, *P. quadrifaria* / *P. comosa* and *P. pendula* / *P. burchellii*, as well as one dichotomous clade *P. paludosa* / *P. drakensbergensis*.

The UPGMA analysis identifies eight end-groups of species pairs/triplets of which the first six agree with those of Analysis A.

In the UPGMA analysis, clades that are statistically supported have relatively high bootstrap values (Figure 6.6). The genus is monophyletic and supported by a bootstrap value of 84%. There is 74% support for the clade *P. montivaga* / *P. falcifolia* and 80% for *P. corymbosa* / *P. falcifolia*. The clades *P. rigida* / *P. ericoides* (78%) and *P. pendula* / *P. burchellii* (87%) are both strongly supported.

### *6.5.4 Analysis D*

Running the same data set as for the Analysis A, but omitting character weighting, data were further analysed using the software package PAUP 4.0 for Macintosh (Swofford 1991). The following results were obtained:

1 character constant.

13 characters parsimony-uninformative.

Number of (included) parsimony-informative characters 38.

Number of trees retained = 3.

Compute consensus = strict.

2000 with constraint.

Tree length 172, CI 0.4942, RI 0.5492 (this value is almost identical to the values obtained by the HENNIG 86 analysis: length 192, CI 0.48 and RI 0.57).

The cladogram generated (Figure 6.7) is almost similar to the one in analysis A, but differs in the following aspects:

Endgroup 1 is characterized by *P. montivaga* which is paraphyletic to the *P. corymbosa* / *P. falcifolia* clade.

*P. rubra* is paraphyletic to the triplet endgroup 3 and *P. obtusifolia* is paraphyletic to the *P. truncata* / *P. burchellii* clade.

The *P. pendula* / *P. burchellii* clade is arranged in the most terminal position of the cladogram, furthest away from the outgroup.

As character weighting was omitted, *P. ericoides* and *P. rigida* are not grouped together, but *P. ericoides* is arranged in an intermediate position in the *P. truncata* / *P. burchellii* clade, while *P. paleacea* and *P. rigida* are sister species (endgroup 9).

Bootstrap values are indicated in Figure 6.8. The clade *P. esterhuyseniae* / *P. burchellii* is supported by a value of 85% indicating the monophyletic nature of the genus. The clades *P. rigida* / *P. montana* (76%) and *P. paleacea* / *P. rigida* (81%) are strongly supported. Both the clades *P. corymbosa* / *P. falcifolia* and *P. quadrifaria* / *P. comosa* are supported by bootstrap values of 68% and the *P. pendula* / *P. burchellii* clade has a bootstrap value of 77%.

## 6.6 Discussion

### *6.6.1 Historical background*

In his treatment of *Passerina*, Meisner (1840) divided the genus into section I. *Pentamerae* and section II. *Tetramerae*. *P. polycephala* E.Mey., *P. anthylloides* L.f. and *P. calocephala* Meisn., with pentamerous flowers (section I), were eventually all placed into the genus *Gnidia* (Meisner 1857; Gilg 1894). Meisner (1857) did not divide *Passerina* into infrageneric taxa, a pattern followed by all subsequent treatments and no further mention was made of the relevant sections. The present study also does not indicate the necessity for sections in *Passerina*.

Meisner (1857) described *Chymococca empetroides* on the basis of fleshy berries. In his study of *Passerina*, Thoday (1924) placed *C. empetroides* in synonymy under *Passerina ericoides*, as the material of the two species was identical. The genus

*Chymococca* could not be upheld by fleshy fruits, as this character was not unique to *P. ericoides*, but was also found in *P. rigida*.

### *6.6.2 Cladogram analyses (Analyses A–D, Figures 6.1–6.8)*

#### Monophyletic origin of *Passerina*

The cladistic analyses support *Passerina* as a monophyletic group (Figures 6.1–6.8). The leaf anatomical study (Bredenkamp & Van Wyk 2001a) indicated that inverse-dorsiventral leaves are highly significant in the distinction of the genus. Other characters associated with inverse-dorsiventral leaves are epistomatic leaves [7 (1)], a villous adaxial epidermis [9 (1)], a very thin adaxial cuticle [11 (1)] and smaller and irregularly shaped adaxial epidermal cells [12(1)]. The genus is further characterized by the following set of floral morphological characters (Bredenkamp & Van Wyk 2001b): polytelic synflorescences [21 (1)], the absence of bracteoles [26 (1)] and the absence of a circumscissile articulation in the hypanthium above the ovary [35 (1)]. The most important character set distinguishing *Passerina* from all other southern African genera in the Thymelaeaceae are those associated with the syndrome of wind pollination, namely exserted stamens [43 (1)], extrorse anthers [44 (1)], the absence of floral scales in the mouth of the floral tube [45 (1)] and the secondary reticulum of the pollen wall [48 (1)]. All the above-mentioned characters played a significant role in the placement of the genus in a tribe of its own, namely Passerineae (Bredenkamp & Van Wyk 1996, 2001a, 2001b).

#### Hypothetical ancestor

The cladograms of analyses A and B (Figures 6.1, 6.3) are characterized by five basal, paraphyletic species, with *Passerina nivicola* as the most basal species, paraphyletic to the outgroup *Struthiola leptantha*. In analysis C (Figure 6.5), *P. nivicola* and *P. esterhuyseniae* are grouped in a clade occupying an intermediate position in the cladogram. We prefer the basal position for *P. nivicola* because of the numerous plesiomorphic characters such as isobilateral leaves [6 (0)], a homogenous mesophyl [15 (0)] and leaf structural type A [13 (0), 51 (0)]. The plesiomorphic characters yellow [24 (0)] and membranous flowers [33 (1)] are present in both *P. nivicola* and *P. esterhuyseniae*, confirming their basal arrangement.

The Western Cape is regarded as the centre of diversity of *Passerina*, as the highest number of species per grid, has been recorded in this area (Bredenkamp & Van Wyk 2000). Of the five above-mentioned basal species, *P. filiformis* and *P. paludosa* occur in the Cape Peninsula. *P. filiformis* is characterized by various plesiomorphic characters such as leaf structural type B [13 (1)]; multiflowered spikes [22 (1)]; long [25 (0)], obovate [29 (1)], chartaceous [30 (0)] and winged [31 (0)] floral bracts; relatively long hypanthium neck [34 (0)] and long internodes [49 (0)] with spreading leaves [50 (0)]. The most important apomorphic character converging in *P. filiformis* is its multiflowered state [23 (2)]; this character is synapomorphic for the clade *P. corymbosa* / *P. rubra*. Most of the plesiomorphic characters in *P. filiformis* are also present in *P. paludosa*, but convergent apomorphic characters are probably caused by the adaptation of this species to the marshy environment of the Cape Peninsula and Cape Flats. Although *P. filiformis* and *P. paludosa* are paraphyletic species in analysis A (Figure 6.1) and analysis B (Figure 6.3), the Nelson consensus tree (analysis A Figure 6.2) indicates that these two species are basal to all the other species in the genus. Based on distribution and array of plesiomorphic characters, they are considered to be morphologically close to the hypothetical ancestor of the species in *Passerina*. *P. nivicola* and *P. esterhuyseniae* are both high-mountain species retaining primitive characters from the hypothetical ancestor, but which have already adapted to conditions prevailing on mountain tops. *P. galpinii* seems best placed amongst the five basal species, based on the plesiomorphic, chartaceous [30 (0)], bullately winged bracts [31 (0)]. The apomorphic, short floral bracts [25 (1)] are probably due to the adaptation of the species to dryer conditions prevalent to the calcareous limestone of the Agulhas Plain Centre, where it occurs.

### The dichotomous *Passerina corymbosa* / *P. paleacea* clade

The dichotomous clade *P. corymbosa* / *P. paleacea* (analysis A, Figure 6.1) is supported by differentiated floral bracts that are coriaceous [30 (1)] and adaxially villous [28 (2)], as well as by the hypanthium that is glabrous in the lower portion and hairy in the upper portion [37 (2)]. The evolvement of these characters are of phylogenetic importance. In most *Passerina* species the achene is always enclosed within the tomentum of the accompanying, enlarged bract, phylogenetically favouring coriaceous bracts that are adaxially villous. In species with fleshy fruits, the young fruits are protected by the villous bracts, but as the mature fruit enlarges beyond the bract, it is protected by the pericarp (Bredenkamp & Van Wyk 2001b). The hypanthium is glabrous in the lower portion, probably because the ovary is enclosed and protected by the villous adaxial surface of the accompanying bract. The upper portion of the hypanthium is hairy, possibly because it is exserted and exposed to the environment.

### The *Passerina corymbosa* / *P. rubra* clade

In analysis A (Figure 6.1) multiflowered spikes with more than 16 flowers [23 (2)] are synapomorphic for this clade; it reverses in *P. obtusifolia* and converges in *P. filiformis*, a hypothetical morphological ancestor. In *Passerina* inflorescence type is a multistate character. The outgroup has single flowers and the multiflowered state is apomorphic. A *Passerina* is wind-pollinated and requires a multitude of pollen grains to be dispersed at once. Although the *P. obtusifolia* / *P. rubra* clade is paraphyletic to the *P. corymbosa* / *P. falcifolia* clade, it can be considered as basal to the latter clade, taking the following facts into account. *P. obtusifolia* is endemic to the Northern, Western and Eastern Cape Provinces. This species is widespread in the Cape Floristic Region (CFR) and is most common in the Karoo Mountain, Langeberg and Southeast Centres of Endemism (Goldblatt & Manning 2000). Intermediates between *P. obtusifolia* and other allopatric species such as *P. truncata*, *P. corymbosa* and *P. rubra* have been recorded in marginal areas where these species overlap. As *P. obtusifolia* is adapted to present Karoo conditions, it has strong xeromorphic characters [51 (4)]. It is therefore suggested that a prototype of this species could possibly be regarded as the ancestor of the other species in the clade. *P. rubra,* a sister species of *P. obtusifolia*, was possibly derived from *P. obtusifolia* and is currently endemic to the Langeberg, Karoo Mountain and Southeastern Centres (Goldblatt & Manning 2000) of the CFR, as well as to southern parts of the Eastern Cape as far as Grahamstown. In the genus, *P. rubra* is characterized by the most prolific multiflowered spikes of up to 30 flowers [16 (2)] and each flower is accompanied by a large, winged [31 (0)] bract, confirming the strong relationship of this species with the others in the *P. corymbosa* / *P. rubra* clade.

Leaf anatomical characters such as the carinate leaf in t/s [8 (3)], the presence of V-shaped palisade parenchyma [16 (1)] and the vascular bundle that is abaxially enclosed in V-shaped palisade parenchyma [4 (1)] are synapomorphic for the

*P. corymbosa* / *P. falcifolia* clade. Extraxylary sclerenchyma fibres not enclosed by the vascular bundle sheath but extending to the abaxial epidermis [14 (1)] and obtrullate bracts [29 (3)] are synapomorphic for *P. corymbosa* and *P. montivaga*. *P. corymbosa* is characterized by the convergent characters, extraxylary sclerenchyma fibres forming a sclerenchymatous hypodermal sheath [20 (1)] and by leaf structural type D [13 (3), 51 (6)]. All the above-mentioned anatomical characters have been derived from leaf structural types, suggesting a xeromorphic gradient from type A to type D (Bredenkamp & Van Wyk 2001a). *P. montivaga* and *P. falcifolia* are both represented by leaf structural type C and because of the development of the sclerenchymatous hypodermal sheath, *P. corymbosa* is represented by type D. Bredenkamp & Van Wyk (2001a) hypothesized about the phylogenetic value of the leaf structural types, but are currently convinced that the xeromorphic gradient from type A to type D can also be interpreted as a phylogenetic gradient.

Although analysis B (Figure 6.3) corresponds closely with analysis A (Figure 6.1), *P. obtusifolia* is excluded from the *P. falcifolia* / *P. rubra* clade. In analysis C, *P. obtusifolia* and *P. rubra* form a separate clade with *P. drakensbergensis*. In both analyses B and C, *P. montivaga* is a sister taxon of the dichotomous clade *P. falcifolia* / *P. corymbosa*. As the various positions of the species do not explain the phylogeny of the genus, the author prefers the phylogenetic arrangement of analysis A.

### The polychotomous *Passerina quadrifaria* / *P. paleacea* clade

In *Passerina* (analysis A, Figure 6.1), differentiated floral bracts are of both taxonomic and phylogenetic importance. The species from *P. nivicola* to *P. rubra* are characterized by winged, differentiated floral bracts. This plesiomorphic character is often manifested by large, ovate or obovate, differentiated floral bracts that are reddish tinged [31 (0)]. The absence of wings in differentiated floral bracts [31 (1)] is a synapomorphy of the polychotomous clade *P. quadrifaria* / *P. paleacea*, reversing in *P. paleacea* and converging in *P. esterhuyseniae* and *P. obtusifolia*. Phylogenetically advanced differentiated floral bracts are smaller, without wings and more coriaceous.

In analysis A, the clade *P. quadrifaria* / *P. drakensbergensis* is not supported by specific characters. *P. quadrifaria*, a recently described species, has incorrectly been identified as *P. comosa* for many years. In the present analysis *P. quadrifaria* and *P. comosa* are sister species, supporting the separate status of *P. quadrifaria*. Both species are characterized by trichomes on the abaxial surfaces of leaves [10 (1)] and bracts [27 (1)] and by bracts that are adaxially comose [28 (1)]. The two species are geographically isolated, with *P. comosa* considered as a 'north-western endemic' of the Cape flora (Weimarck 1941), while *P. quadrifaria* is distributed along the mountain ranges of the southern Cape and western parts of the Eastern Cape Province. *P. drakensbergensis* is paraphyletic to the *P. quadrifaria* / *P. comosa* clade and occurs at altitudes between 1 500 and 1 980 m on the northern KwaZulu-Natal Drakensberg. Except that these three species are all adapted to mountainous habitats, there are no morphological characters supporting the relationship between *P. drakensbergensis* and the other two species.

In analysis B (Figure 6.3), the clade *P. drakensbergensis* / *P. comosa* is paraphyletic to the *P. truncata* / *P. burchellii* clade. The clade *P. quadrifaria* / *P. comosa* is supported by a bootstrap value of 59% (Figure 6.4). In analysis C, the clade *P. quadrifaria* / *P. comosa* is paraphyletic to the *P. paludosa* / *P. drakensbergensis* clade, but without any bootstrap support.

In analysis A (Figure 6.1), the dichotomous clade *P. pendula* / *P. paleacea* portrays a xeromorphic gradient from *P. pendula* to *P. paleacea*. The synapomorphies involved are short floral bracts [25 (1)], a short hypanthium neck [34 (1, 2)], very short internodes [49 (2)] and appressed leaves [50 (1)]. All these characters indicate adaptive strategies to combat dry conditions. The xeromorphic gradient of this clade also has phylogenetic implications, as the clade *P. truncata* / *P. paleacea* can be regarded as the most advanced.

In analysis B (Figures 6.3 and 6.4) the above-mentioned clades correspond to those of analysis A (Figure 6.1), except for the reversed sequence of the clades and the order of certain taxa. In analysis B, the *P. pendula* / *P. burchellii* clade (bootstrap 81%) occupies the most advanced position, which contradicts the phylogeny described in analysis A. In analysis C (Figures 6.5 and 6.6) the clades *P. rigida* /

*P. ericoides* (bootstrap 78%) and *P. truncata* / *P. montana* (no bootstrap support) occupy a basal position, whereas the *P. pendula* / *P. burchellii* clade (bootstrap 87%) is terminal. Taking the phylogenetic arrangement of the mentioned clades in analysis A (Figure 6.1) into consideration, the arrangement of the clades in analysis C is phylogenetically difficult to explain.

*P. pendula* is endemic to the Southeastern Centre of the CFR and distributed from the Kouga Mountains in the Western Cape to the Great Winterhoek Mountain Range in the Eastern Cape. *P. burchellii* is an allopatric species endemic to the Southwestern and Langeberg Phytogeographic Centres (Goldblatt & Manning 2000) of the CFR and common on mountain summits of the Villiersdorp and Genadendal Districts. Both species are adapted to high-mountain conditions, often prone to mist and the synapomorphies supporting the clade are rhombic leaves [3 (2)], with ciliate margins [2 (1)].

An increase in xeromorphism is shown for the clade *P. rigida* / *P. paleacea* based on the leaf anatomical character, three layers of palisade parenchyma [19 (3)]. In all species of this clade the hypanthium fragments over the circumference of the ovary once the fruit has matured [36 (1)], thus protecting the young fruit against possible desiccation. *P. montana* is characterized by a long hypanthium neck [34 (0)] and fragmentation of the hypanthium at the neck base [36 (0)]. The reversal of these characters is regarded as a possible adaptation to summer-rainfall conditions, favouring the distribution of fruits by birds, which are possibly attracted to the crimson coloured, beak-like, fragmented hypanthium neck (Bredenkamp & Van Wyk 2001b).

In *Passerina*, dried fruits are regarded as plesiomorphic and fleshy fruits as apomorphic. Cronquist (1968) stated that fleshy fruits have evolved from dry fruits many times and that dry indehiscent fruits may evolve into fleshy ones. The *Passerina rigida* / *P. ericoides* clade (analysis A) is based on the synapomorphy fleshy fruits [32 (1)], and coriaceous fruits [33 (2)] are autapomorphic for *P. ericoides*. In the Thymelaeaceae, berries are found in the section Euwikstroemia, in species of *Daphnopsis* Mart. et Zucc., *Ovidia* Meisn., *Dirca* L., *Dapne* L., *Pimelea* (Banks & Sol.) Gaertn. and in *Passerina ericoides* L.

(=*P. empetroides* Meisn.), while the fruit of *Peddiea* Harv. is regarded as a drupe (Domke 1934). Thus, in southern African Thymelaeaceae, *P. ericoides* and *P. rigida* are the only two members with berries. Both species occur along the coast in the Western Cape and the range of *P. rigida* extends to St Lucia. In *Passerina*, fleshy fruits are a secondary adaptation to bird dispersal and possibly also to maritime climate (Bredenkamp & Van Wyk 2001b). *P. ericoides* has red berries and *P. rigida* has yellow berries, possibly indicating that these characters developed independently because of different selective pressures. If the fleshy fruits in *Passerina* are considered secondary (apomorphic), then the basal arrangement of the *P. rigida* / *P. ericoides* clade in analysis C (Figure 6.5) is difficult to explain.

In analyses A–C (Figures 6.1–6.6), the character fleshy fruits [32] was weighted ten times. In analysis A (Figure 6.1), characters 1 and 13 are synapomorphic for the *P. montana* / *P. paleacea* clade and convergent in *P. rigida*. Character 18 converges in *P. rigida* and *P. paleacea* and characters 24 and 33 are reversals in both species, emphasizing the morphological similarity between these two species. This phenomenon could probably be explained by the adaptation of these species to maritime conditions. *P. rigida* is a robust plant, often growing on the primary coastal dunes, and it is widely distributed from the Western Cape, along the coast to northern KwaZulu-Natal. *P. paleacea* occurs on secondary dunes and is distributed mainly along the southern coast of the Western Cape.

In analyses A–C (Figures 6.1–6.6), the character inflorescence type [22] was weighted five times. Inflorescence type is considered a multistate character in *Passerina*. *Struthiola leptantha* (outgroup) has single flowers, considered to be the plesiomorphic state. Multiflowered spikes have been described as an adaptation to wind pollination. Subcapitulate spikes are considered to be a secondary adaptation, possibly to drier conditions, involving the reduction of the inflorescence axis and the number of flowers, towards a more economical production of wind-dispersed pollen. The clade *P. truncata* / *P. paleacea* is characterized by the synapomorphic character subcapitulate spikes [22 (2)], converging in *P. quadrifaria*. All the species involved are subject to dryer conditions or physiological drought, which could possibly account for the evolvement of subcapitulate spikes. *P. truncata* is distributed from Steinkopf in the Northern Cape, to Malmesbury, and eastwards to Matjiesfontein in the Western Cape. *P. montana* is adapted to a wide range of habitats in the predominantly summer-rainfall area pertaining to the Great Escarpment of southern Africa. *P. quadrifaria* is distributed along the mountain ranges of the southern Cape and western parts of the Eastern Cape Province and *P. paleacea* is adapted to the maritime conditions of the Western Cape.

In analysis D (Figures 6.7–6.8), no character weighting was applied. The Majority Rule analysis (Figure 6.7) places *P. ericoides* centrally between the *P. truncata* / *P. montana* and *P. pendula* / *P. burchellii* clades. In the *P. truncata* / *P. montana* clade, *P. rigida* and *P. paleacea* are sister species probably on the basis of their natural morphological likeness. However, *P. rigida* is characterized by multiflowered spikes [22 (1)] and fleshy fruit [32 (1)], while subcapitulate spikes [22 (2)] and dry fruit [32 (0)] are typical of *P. paleacea*. Except for *P. rigida*, all the members of the *P. truncata* / *P. montana* clade have subcapitulate spikes, thus complicating the arrangement of this species. In the Adams analysis (Figure 6.7), *P. ericoides* is paraphyletic to the *P. rubra* / *P. comosa* and *P. obtusifolia* / *P. burchellii* clades, while the arrangement of all the other clades remains identical. In this case the identity of *P. ericoides* is reduced to a basal species and the prominence of fleshy fruits, as a taxonomically important character, is not justified. The computed bootstrap values of the strict consensus tree (Figure 6.8) are relatively high. Bootstrap support is as follows: *P. esterhuyseniae* / *P. burchellii* 85%, *P. rigida* / *P. montana* 76%, *P. rigida* / *P. paleacea* 81%, *P. corymbosa* / *P. falcifolia* 68%, *P. quadrifaria* / *P. comosa* 68% and *P. pendula* / *P. burchellii* 77%.

In analysis A (Figure 6.1), the *P. montana* / *P. paleacea* clade is supported by a number of characters. The synapomorphic character short leaves [1 (2)] is considered an adaptation to drier conditions and an increase in xeromorphism. The remaining synapomorphic characters are all concerned with leaf structural type. Bredenkamp & Van Wyk (2001a) have shown a xeromorphic gradient for the leaf structural types in *Passerina*, with leaf structural type D [13 (3), 51 (6)] representing the most xeromorphic form. Characters associated with leaf structural type D are: the bundle sheath forming an adaxial cap [18 (1)]; extraxylary sclerenchyma fibres abaxially not enclosed by the vascular bundle sheath, often extending to the abaxial epidermis [14

(1)]; extraxylary fribres extending to the abaxial epidermis and paradermally up to the leaf margins, forming a sclerenchymatous hypodermal sheath [20 (1)]. The present cladistic analysis clearly indicates that leaf structural type A is plesiomorphic, with *P. nivicola* arranged basally, adjacent to the outgroup. Species with leaf structural types B and C occupy intermediate positions and the species occupying the most terminal position (furthest from the outgroup) are supported by leaf structural type D. Thus the phylogenetic value of leaf structural types (Bredenkamp & Van Wyk 2001a) is clearly indicated by the present cladistic analysis.

The Nelson consensus tree (analysis A, Figure 6.2) shows that *Passerina* is a strongly supported monophyletic group, with *Struthiola leptantha* as the outgroup. The consensus tree indicates that *P. filiformis* and *P. paludosa* could be sister species. The present author agrees with this suggestion, as both *P. filiformis* and *P. paludosa* occur in the Cape Peninsula and they share various plesiomorphic characters. Apomorphic characters in *P. paludosa* are probably due to the marshy environment of the Cape Peninsula and Cape Flats to which these plants have adapted. The Nelson consensus tree also indicates that *P. filiformis* and *P. paludosa* are basal to all the other species in the genus, although these two species are paraphyletic in all the other analyses. Based on distribution and array of plesiomorphic characters, the author is of the opinion that they are morphologically close to the hypothetical ancestor of the species of *Passerina*. In the Nelson consensus tree, the paraphyletic species *P. obtusifolia* and *P. rubra* and the subclade *P. burchellii* / *P. pendula* are basal to all the other clades in the cladogram.

It would be informative to test the hypotheses of phylogeny proposed in the present study with further evidence from molecular data, studies of which are currently in progress (M. van der Bank pers. comm.).

## 6.7 Conclusion

In the present cladistic study, the results generated by the HENNIG 86 analysis were strongly supported by those of the PAUP analysis, to the extent that the cladogram length and the CI and RI values were almost identical. The necessity of using different analyses and procedures was highlighted, especially in the case of

*P. ericoides* (with red berries) and *P. rigida* (with yellow berries), for which it is concluded that fleshy berries probably developed independently because of the selective pressure of bird dispersal and maritime conditions.

Based on leaf and floral morphological and anatomical characters (Bredenkamp & Van Wyk 2001a, 2001b), the cladistic study supports *Passerina* as a monophyletic group (bootstrap values of different analyses ranging from 84–91%). Although *P. filiformis* and *P. paludosa* are paraphyletic species in certain analyses, there are indications that these two species are basal to other species in the genus. Based on distribution and array of plesiomorphic characters, we regard these species as morphologically close to the hypothetical ancestor of the species of *Passerina*.

The different cladistic analyses (Figures 6.4, 6.6, 6.8) indicated the following clades in *Passerina* with relatively high bootstrap support: *P. corymbosa* / *P. montivaga* / *P. falcifolia* (68–74%); *P. corymbosa* / *P. falcifolia* (80%); *P. quadrifaria* / *P. comosa* (59–68%); *P. pendula* / *P. burchellii* (77–87%); applying selective character weighting (analyses A–C, Figures 6.4, 6.6), *P. truncata* / *P. ericoides* (52%), *P. truncata* / *P. montana* (50%), *P. paleacea* / *P. montana* (62%), *P. ericoides* / *P. rigida* (65–78%); without character weighting (analysis D, Figure 6.8) *P. rigida* / *P. montana* (76%), *P. rigida* / *P. paleacea* (81%).

The taxonomic and phylogenetic values of the character set were evaluated (Table 6.3). The following plesiomorphic characters, indicative of a possible ancestor, were identified: leaf structural types A and B [13 (0), (1)]; single flowers and multiflowered spikes [22 (0), (1)]; long [25 (0)], obovate [29 (1)], chartaceous [30 (0)] and winged [31 (0)] floral bracts; relatively long hypanthium neck [34 (0)] and long internodes [49 (0)] with spreading leaves [50 (0)].

The most important synapomorphies were identified. Of these, certain characters portrayed invaluable phylogenetic information and are of considerable taxonomic importance, e.g. differentiated floral bracts that are coriaceous [30 (1)] and adaxially villous [28 (2)], as well as the hypanthium that is glabrous in the lower portion and hairy in the upper portion [37 (2)], the absence of wings in differentiated floral bracts [31 (1)]; inflorescence types [22 (2)] and number of flowers [23 (2)]; fruit types [32 (1)]; leaf structural types and associated anatomical characters [13 (3), 51 (6)].

Taking all the above-mentioned into account, the cladistic analysis in *Passerina*, based on leaf and floral morphological and anatomical characters, is regarded as a contribution towards a better understanding of the taxonomical and phylogenetic status of characters, as well as towards the delimitation of the species in the genus. *Passerina* is a monophyletic genus that evolved as a result of environmental pressure of the climate in the predominantly winter-rainfall area of the Western Cape. The most important climatic features driving phylogenetic change were windy conditions in spring and drought in summer. *Passerina* adapted to these conditions at a generic level and is the only southern African genus in the Thymelaeaceae adapted to wind pollination. The anatomical feature leaf structural types (Bredenkamp & Van Wyk 2001a) evolved because of increasing dry conditions, with expanding speciation further away from the centre of diversity of the genus in the Western Cape. The present cladistic study confirmed that the indicated xeromorphic gradient, from leaf structural type A to type D, can also be regarded as a phylogenetic gradient. In this study *Passerina* has been identified as the only southern African genus in the Thymelaeaceae with fleshy berries (two out of 20 species) and it was shown that fleshy berries evolved from dry fruits, probably as a result of the selective pressure of bird dispersal and maritime conditions. The merit of recognizing a tribe Passerineae (Bredenkamp & A.E. van Wyk 1996, 2001a, 2001b) has been questioned by some botanists, but in the light of the strong characters exclusive to *Passerina*, the present author is convinced of the necessity of this taxon.

TABLE 6.3.—Character transformation series in *Passerina*, with *Struthiola leptantha* as outgroup and generated by HENNIG 86

| **CHARACTER** | **CHARACTER TRANSFORMATION SERIES** |
|---|---|
| 1 | Short leaves (state 2) are synapomorphic of the *P. montana* / *P. paleacea* clade, converging in *P. esterhuyseniae* and *P. rigida*. |
| 2 | Ciliate leaf margins (state 1) are synapomorphic for *P. pendula* and *P. burchellii*, converging in *P. drakensbergensis*, *P. montivaga* and *P. paludosa*. Tufted leaves (state 2) are autapomorphic for *P. nivicola*. |
| 3 | Rhombic leaves (state 2) are synapomorphic for *P. pendula* and *P. burchellii*. |
| 4 | The vascular bundle abaxially enclosed in V-shaped palisade parenchyma, in t/s (state 1) is synapomorphic for the *P. corymbosa* / *P. falcifolia* clade. |
| 5 | Turned off because of low CI and RI values. |
| 6 | Inverse-dorsiventral leaves (state 1) are synapomorphic for all clades in *Passerina*, except for that of *P. nivicola* which has isobilateral leaves. |
| 7 | Amphistomatic leaves represent the plesiomorphic state in *S. leptantha* Epistomatic leaves (state 1) are synapomorphic for all clades in *Passerina*. |
| 8 | Carinate leaves in t/s (state 3) are synapomorphic for the *P. corymbosa* / *P. falcifolia* clade. |
| 9 | The glabrous adaxial epidermis represents the plesiomorphic state in *S. leptantha* and the villous adaxial epidermis (state 1) is synapomorphic for all clades in *Passerina*. |
| 10 | The presence of trichomes on the abaxial epidermis of the leaves (state 1) is considered to be an adaptation to exceptionally dry summer conditions and this character is synapomorphic for *P. comosa* [a 'north-western endemic' of the Cape flora (Weimarck 1941)] and *P. quadrifaria* (endemic to the Karoo Mountain and far southeastern region). |
| 11 | The very thin adaxial cuticle (state 1) is a specialisation of the inverse-dorsiventral leaf and this character is synapomorphic for all clades in *Passerina*. |

| | |
|---|---|
| 12 | Differentiated, smaller and irregularly shaped adaxial epidermal cells (state 1) are synapomorphic for all clades in *Passerina*. |
| 13 | Leaf structural type C (state 2) is synapomorphic for *P. montivaga* and *P. falcifolia*. Leaf structural type D (state 3) is synapomorphic for *P. montana* and *P. paleacea* and converges in *P. rigida* and *P. corymbosa*. |
| 14 | Extraxylary sclerenchyma fibres abaxially not enclosed by the vascular bundle sheath, often extending to the abaxial epidermis (state 1), are synapomorphic for *P. montana* and *P. paleacea* and the character converges in the clade *P. corymbosa* / *P. montivaga*. |
| 15 | A homogenous mesophyll is regarded as plesiomorphic and is present in *P. nivicola*. Palisade parenchyma adjacent to the abaxial epidermis (state 1) is synapomorphic for all other clades in *Passerina*. |
| 16 | The V-shaped palisade parenchyma (state 1) is a xeromorphic adaptation of the mesophyll preventing the loss of water from the enclosed main vascular bundle. This character is a synapomorphy of the clade *P. corymbosa* / *P. falcifolia*. |
| 17 | Turned off because of low CI and RI values. |
| 18 | A bundle sheath forming an adaxial cap (state 1) is a xeromorphic adaptation of the main vascular bundle to prevent the loss of water. This character is synapomorphic for the *P. corymbosa* / *P. falcifolia* clade and converges in *P. montana*, *P. paleacea* and *P. rigida*. |
| 19 | Homogenous mesophyll is plesiomorphic and present in *P. nivicola*. Increasing layers of palisade parenchyma are a xeromorphic adaptation and three layers (state 3) are synapomorphic for the clade *P. rigida* / *P. paleacea*. |
| 20 | Extraxylary fibres extending to the abaxial epidermis and paradermally up to the leaf margins forming a sclerenchymatous hypodermal sheath (state 1) are synapomorphic for the clade *P. montana* / *P. paleacea* and convergent in *P. corymbosa*. |
| 21 | Monotelic synflorescences are regarded as plesiomorphic. Polytelic synflorescences (state 1) are synapomorphic of all the clades in *Passerina*. |
| 22 | Multiflowered spikes (state 1) are considered to be an adaptation to wind |

| | |
|---|---|
| | pollination. Subcapitulate spikes (state 2) could be interpreted as a reduction of spikes, possibly economising on reproductive material. This character is a synapomorphy of the clade *P. truncata* / *P. paleacea* and converges in *P. quadrifaria*. |
| 23 | Multiflowered spikes with more than 16 flowers (state 2) are synapomorphic for the clade *P. corymbosa* / *P. rubra*, with a reversal in *P. obtusifolia* and converging in *P. filiformis*. |
| 24 | The yellow colour of the hypanthium is plesiomorphic as flowers are yellow in the juvenile stage. The yellow-pink or greenish pink colours of the hypanthium (state 1) are synapomorphic for the clade *P. paludosa* / *P. paleacea*, with reversals in *P. rigida* and *P. paleacea*. |
| 25 | Long bracts (state 0) are regarded as plesiomorphic. Short bracts (state 1) are synapomorphic for the clade *P. pendula* / *P. paleacea*, converging in *P. nivicola*, *P. esterhuyseniae* and *P. galpinii*. Most taxa with short bracts have extended west-, north- and eastwards from the Western Cape, the centre of diversity for *Passerina* (Bredenkamp & Van Wyk 2000, 2001). |
| 26 | The absence of bracteoles (state 1) is synapomorphic for all clades in *Passerina*. |
| 27 | Differentiated floral bracts that are abaxially hairy (state 1) are an adaptation to dry summer conditions and are synapomorphic for *P. comosa* and *P. quadrifaria*. |
| 28 | Differentiated floral bracts that are adaxially villous (state 2) are synapomorphic for the clade *P. corymbosa* / *P. paleacea*, with reversals in *P. montivaga*, *P. obtusifolia*, *P. quadrifaria*, *P. comosa* and *P. pendula*. |
| 29 | Obtrullate floral bracts (state 3) are synapomorphic for *P. corymbosa* and *P. montivaga*, converging in *P. paludosa* and *P. obtusifolia*. |
| 30 | Differentiated floral bracts with a coriaceous texture (state 1) are synapomorphic for the clade *P. corymbosa* / *P. paleacea*, reversing in *P. paleacea* and converging in *P. paludosa*. |
| 31 | The absence of wings in differentiated floral bracts (state 1) is a synapomorphy of the clade *P. quadrifaria* / *P. paleacea*, reversing in *P. paleacea* and converging in *P. esterhuyseniae* and *P. obtusifolia*. |
| 32 | Fleshy fruit (state 1) is a synapomorphy of *P. rigida* and *P. ericoides*. |

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| 33 | The papyraceous texture of the hypanthium (state 2) is synapomorphic for the clades *P. filiformis* / *P. paleacea*, with reversals in *P. pendula*, *P. rigida* and *P. paleacea*. The coriaceous texture of the hypanthium is an autapomorphy of *P. ericoides*. |
| 34 | A short to a very short hypanthium neck (states 1.2) are synapomorphic to the clade *P. pendula* / *P. paleacea*, with a reversal in *P. montana*. |
| 35 | The absence of a circumscissile articulation in the hypanthium above the ovary (state 1) is a synapomorphy of all the clades in *Passerina*. |
| 36 | The fragmentation of the hypanthium over the circumference of the ovary (state 1) is synapomorphic for the clade *P. rigida* / *P. paleacea*, with a reversal in *P. montana* and convergence in *P. esterhuyseniae*, *P. galpinii* and *P. obtusifolia*. |
| 37 | The lower portion of the hypanthium glabrous, the upper portion hairy (state 2) is a synapomorphy of the clade *P. corymbosa* / *P. paleacea*, with reversals in *P. drakensbergensis*, *P. ericoides* and *P. paleacea*. |
| 38 | The hairy adaxial surface of the outer sepal lobes possibly evolved from the glabrous state. The hairy apex of the outer sepal lobes (state 2) is an autapomorphy of *P. nivicola* not included in the analysis. |
| 39 | The hairy apex of the abaxial surface of the outer sepal lobes (state 2) is synapomorphic for *P. esterhuyseniae*, *P. filiformis* and *P. paludosa*, with convergence in *P. montivaga*, *P. quadrifaria* and *P. burchellii*, and a reversal in *P. nivicola*. |
| 40 | Both the glabrous and hairy adaxial surfaces of the inner sepal lobes are regarded as plesiomorphic. The hairy apex (state 2) is a synapomorphy of *P. paludosa* and *P. galpinii*. |
| 41 | Both the glabrous and hairy abaxial surfaces of the inner sepal lobes are regarded as plesiomorphic. The hairy apex (state 2) is a synapomorphy of *P. esterhuyseniae*, *P. filiformis* and *P. paludosa*, with a reversal in the clade *P. galpinii* / *P. paleacea* and convergency in *P. montivaga* and *P. burchellii*. |
| 42 | The presence of an antisepalous stamen whorl (state 1) is advantageous for wind pollination and this character is synapomorphic for all clades in *Passerina* . |

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|---|---|
| 43 | Exserted stamens (state 1) are an adaptation to wind pollination and are synapomorphic of all the clades in *Passerina*. |
| 44 | Extrorse anthers (state 1) are an adaptation to wind pollination and is synapomorphic of all the clades in *Passerina*. |
| 45 | The presence of floral scales in the mouth of the floral tube would possibly attract insects and is regarded as plesiomorphic; in wind-pollinated flowers these structures would have no significance. The absence of floral scales (state 1) is synapomorphic for all the clades in *Passerina*. |
| 46 | The presence of perigonal hairs is regarded as plesiomorphic as these structures would not be advantageous for wind-pollinated flowers. The absence of perigonal hairs (state 1) is synapomorphic for all the clades in *Passerina*. |
| 47 | Turned off because of low CI and RI values. |
| 48 | The crotonoid pollen wall is regarded as plesiomorphic as the secondary reticulum is a specialized feature for wind pollination. The secondary reticulum (state 1) is synapomorphic for all the clades in *Passerina*. |
| 49 | Longer internodes with leaves not imbricate are regarded as plesiomorphic, as the reduction of internodes is an adaptation to drier conditions. Very short internodes (state 2) are synapomorphic for the clade *P. pendula* / *P. paleacea*, with convergence in *P. paludosa* and *P. quadrifaria*. |
| 50 | Ascending or spreading leaves are regarded as plesiomorphic. Appressed leaves (state 1), an adaptation to drier conditions, are synapomorphic for the clade *P. pendula* / *P. paleacea*, with a reversal in *P. ericoides*. |
| 51 | Carinate leaves with an abaxial, paradermal sclerenchyma sheath and the main vascular bundle sunk into the V-shaped palisade parenchyma (state 6) probably evolved from flatter leaves with a homogenous mesophyll. State 6 is synapomorphic for *P. montana* and *P. paleacea* and convergent in *P. corymbosa*. |

# [*]CHAPTER 7

# TAXONOMIC TREATMENT

## CONTENTS

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[*] Species sequence according to the key to species

## 7.1 Circumscription of the genus

**Passerina** *L.* Species plantarum: 559 (1753); L.: 168 (1754); P.J.Bergius: 126 (1767); Mill.: (1768); Burm.f.: 12 (1768); L.: 236 (1771); L.: 225 (1782); L.: 374 (1784); Thunb.: 75 (1794); J.C.Wendl.: 18 (1798); Willd.: 429 (1799); Poir.: 39 (1804): Lam. & DC: 359 (1805); Wikstr. 39: 319 (1818); Thunb.: 374 (1825a); Meisn.: 390 (1840); Steud.: 273 (1841); C.A.Mey.: 45 (1843); Meisn. 14: 561 (1857); Harv.: 325 (1868); Gand.: 418 (1913); C.H.Wright: 9 (1915); Thoday 4:146 (1924a); Marloth: 214 (1925); Domke: 137 (1934); Palmer & Pitman: 1583 (1972); Coates Palgrave: 648 (1977); Bond & Goldblatt: 432 (1984); Hilliard & B.L.Burtt: 182 (1987); Goldblatt & Manning: 683 (2000). Type species: *Passerina filiformis* L.

*Sanamunda* [Clus.: 89 (1601); L.: 146 (1737)] Adans. 2: 258 (1763); Lam. & DC.: 359 (1805); Raf.: 104 (1836). Type species: as above.

*Thymelaea* [Tourn.: 594 (1719); L.: 146 (1737)] Adans. 2: 258 (1763); Juss.: 77 (1789); Lam. & DC.: 359 (1805). Type species: *Daphne laureola* L.

*Passerine* Lam. & DC. 3: 359 (1805) orth. var.

*Balendasia* Raf. 4: 105(1836). Type species: *B. ericoides* (Burm.f.) Raf.

*Steiroctis* Raf. 4: 105 (1836). Type species: not designated (Farr. *et. al.* 1979).

*Trimeiandra* Raf.: 105 (1836). Type species: *T. spicata* Raf. nom. illeg. (*Passerina pentandra* Thunb.) ≡ *Lonchostoma* Wikstr. 39: 350 (1818) nom. cons.

*Chymococca* Meisn. 14: 565 (1857); Harv.: 325 (1868); Benth. & Hook.: 194 (1880); Thoday 4:166 (1924a). Type species: *C. empetroides* Meisn.

*Passerina* L. Sectio *Pentamerae* Meisn.: 390 (1840). Type species: not designated.

*Passerina* L. Sectio *Tetramerae* Meisn.: 395 (1840). Type species: not designated.

Shrubs or small trees. *Stems* greyish brown; bark tough and stringy. *Leaves* decussate, imbricate on young branchlets, sessile, closely appressed to stem or spreading at an angle of 5–20°(–60°), cymbiform (boat-shaped), falcate or cigar-shaped; plane shape linear, oblong, lanceolate or narrowly trullate; base sessile or cuneate; apex truncate and hump-backed, obtuse, rounded, acuminate or acute to almost spine-tipped; margins sometimes ciliate; length × depth (leaf shape usually cymbiform, depth of lamina—distance from adaxial groove to main vein situated abaxially) (1.5–)2.5–4.0(–8.0) × (0.8–)1.2–2.0(–3.0) mm; lamina inversely ericoid, adaxial surface concave, tomentose, abaxial surface convex, glabrous, seldom tomentose. *Inflorescences* comprising polytelic synflorescences [apex of main florescence (main axis) not terminating with a flower—indeterminate, co-florescences (lateral brances) of the same structure]; main florescences as well as co-florescences spicate; spikes reduced, resembling terminal subcapitulate inflorescences, each characterized by two terminal leaves with axillary blind-ending rudimentary flowers, enveloping minute growing point, proliferating growth (inflorescence apex growing out and returning to vegetative growth) less common (Figures 7.1–7.5A), or spikes mostly extended, number of spikes reduced or multiflowered main and co-florescences present, proliferating growth common (Figures 7.6–7.22A). *Bracts* enveloping flowers and fruits, largest after anthesis of flowers, becoming more coriaceous and rounded at fruit set, decussate, imbricate, cymbiform or helmet-shaped; plane shape oblong, lanceolate, ovate and obovate to widely ovate and obovate, rhombic and narrowly obtrullate to obtrullate; base sessile, cuneate; main vein strongly developed, often keeled, extending to form a leaf-like point in many species; apex obtuse, rounded or acute; texture mostly coriaceous; lamina with adaxial surface (inside) concave, abaxial surface (outside) convex, outside usually glabrous, inside, base or midrib tomentose or completely tomentose, coriaceous or chartaceous, rugose or smooth, ± succulent or thin, sometimes ± 3–5-ribbed, reticulately veined or ribbed and reticulately veined on each side of main vein; wings absent or bullate, coriaceous, chartaceous or membranous; margins often ciliate to setose; size variable, bracts without leaf-like point, length × depth (2.5–)3.5–4.5(–5.5) × (0.9–)1.0–1.5(–2.4) mm or bracts with leaf-like point, length × depth (4.0–)5.1–6.3(–7.3) × (1.4–)1.5–2.0(–2.6) mm. *Flowers* actinomorphic, hypogynous. *Floral envelope* constituting hypanthium and sepals, membranous during pollination and yellowish in *P. rigida*, *P. paleacea*, *P. nivicola* and *P. esterhuyseniae*, 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 (fused calyx and androecium, differentiating into sepals and diplostemonous androecium arising from hypanthium rim at separation of sepals) (Figure 7.1); 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 discernable, articulation plane absent, after fruiting fragmentation of neck base caused by dehydration and torsification of tissue, the sepals and androecium being shed in most species. *Sepals* 4, petaloid; imbricate in bud, flexed in flower, often setose with up to 5 long trichomes on outer surface and glabrous to tomentose on inner surface; outer sepals cymbiform or concave; inner sepals oblong, elliptic or obovate. *Corolla* absent. *Disc* absent. *Androecium* dimorphic diplostemonous, arising from hypanthium at separation point of sepals; filaments of antipetalous whorl (0.4–)0.7–1.2(–1.5) mm long, those of antisepalous whorl (1.2–)1.4–2.2(–2.4) mm long; anthers (0.5–)0.7–0.9(–1.1) × (0.2–)0.3–0.4(–0.7) mm, sub-basifixed, 2-thecous and 4-locular, exserted, extrorse. *Ovary* superior, (1.6–)2.0–2.5(–2.7) × (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, the fragmented hypanthium, sepals and androecium being shed; in *P. ericoides* and *P. rigida* a fleshy 1-seeded berry, 5.3 × 4.0 mm; in all other species an achene, pericarp membranous and dry, 2.5 × 1.2 mm. *Seed* broadly fusiform with outgrowths at both micropylar and funicular ends; tegmen black and shiny, often with white spots; size 2.2(–2.9) × 1.2(–1.6) mm; endosperm formation nuclear, but later becoming cellular throughout.

**Nomenclatural notes**

See Table 7.1, for a summary of taxa in the most comprehensive works on *Passerina* from Linnaeus (1753) to the present study.

## Diagnostic characters

Plants of *Passerina* are shrubs or small trees, distinguished by the inversely ericoid leaves, that are inverse-dorsiventral in c/s. The inflorescences are few- to multiflowered, simple or compound spikes, often reduced, artificially resembling terminal subcapitulate inflorescences. Each flower is enveloped by a conspicuous bract, becoming more coriaceous and rounded at fruit set. The flowers are adapted to wind pollination. During pollination the flower colour is yellow-pink, the four petaloid sepals are flexed and the anthers are exserted and extrorse (unique for Thymelaeaceae in southern Africa). All anthers open explosively and the pollen is shed at once. The stigma is mop-like. The fruit is enveloped by a persistent, loosely arranged hypanthium. Because of the absence of an articulation plane, the hypanthium fragments at neck base or, in some species, over widest circumference of fruit, the fragmented hypanthium, sepals and androecium being shed. *P. ericoides* and *P. rigida* are characterized a fleshy 1-seeded berry and all other species by an achene.

## Etymology

*Passerina* refers to the Latin *passer* (= a sparrow) as the seeds resemble a sparrow's beak.

## Common names

The vernacular name 'sparrow-wort' was suggested by Miller (1768) for all *Passerina* species and Wendland (1798) used the name *fadenförmige Vogelkopf*. According to Smith (1966) *gonna* is a collective name once used by the Khoekhoe for various members of Thymelaeaceae, e.g. several species of *Passerina* and *Struthiola*.

## Uses

Many *Passerina* species grow on sand dunes and in sandy areas, with parts of the woody stem subterraneous, forming runners and developing an extended root system.

Most of these plants are pioneers and resprouters, increasing their chances of survival in disturbed areas. These plants are excellent sand binders and are suitable for binding problematic sandy areas, especially after the clearing of invader species. Sim (1919) recommended *Passerina* in his list of trees and shrubs for coastal areas exposed to sea winds. Certain *Passerina* species are small trees and can be used as ornamental garden plants. The bark is exceedingly tough and is used for tying down thatch. According to Watt & Breyer-Brandwijk (1962) it is also plaited into whip thongs and used as twine. Members of the genus are not browsed by stock as the plants are apparently unpalatable (Story 1952).

### Flowering and fruiting

Most *Passerina* species flower profusely in spring, from September to October. During this season the Cape Floristic Region is quite windy and large amounts of pollen is produced, as *Passerina* is wind-pollinated. Pollen is often wafted away in clouds, causing a kind of hay-fever in sensitive persons (Marloth 1925). Fruiting time is mostly from December to January. The fleshy fruits of *P. ericoides* and *P. rigida* are dispersed by birds or rodents inhabiting the distribution ranges of these species along the South African coast. Fruits of *P. truncata* subsp. *truncata*, growing in the Karoo, passively fall to the ground, where they are probably dispersed by ants or rodents. The fruits of *P. montana*, occurring along the Great Escarpment, are probably dispersed by birds as they are arranged at the tips of branchlets, exposed, red, and beak-like, possibly resembling the beaks of nestlings.

### Distribution and ecology

Of the 20 species, 14 are endemic or near-endemic to the Cape Floristic Region. *P. obtusifolia* is widespread in the Northern, Eastern and Western Cape Provinces, while *P. corymbosa* occurs in the Western and Eastern Cape Provinces, with outliers in KwaZulu-Natal. *P. rigida* is distributed from the Western Cape, along the coast to northern KwaZulu-Natal; all these species are endemic to the southern African provinces in which they occur. *P. drakensbergensis* is endemic to the Bergville District in KwaZulu-Natal. *P. montivaga* is found from Mossel Bay and Oudtshoorn to the Eastern Cape and along the escarpment northwards to Zimbabwe and

*P. montana* is distributed from the eastern mountains and Great Escarpment of southern Africa to Zimbabwe and Malawi.

### 7.2 Key to the species

1a Inflorescences comprising terminal subcapitulate spikes; proliferating growth (inflorescence apex growing out and returning to vegetative growth) uncommon (Figures7.1–7.5A):

2a Floral envelope yellow and membranous, up to ± 4 mm long, neck (portion of hypanthium between ovary and sepals) very short, ± 0.3 mm long; bracts widely ovate, wings membranous and obscurely veined ............................ 1. *P. paleacea*

2b Floral envelope yellow-pink and papyraceous, 4.9–6.4 mm long, neck 0.7–1.4 mm long; bracts variously shaped, wings present or absent:

3a Leaves narrowly oblong to oblong; base sessile, dilated; apex truncate, or truncate to rounded, keeled, often appearing humped on the back ...............2. *P. truncata*

3b Leaves linear-lanceolate; base diamond-shaped to rounded; apex rounded to acute:

4a Abaxial surface of young leaves tomentose; bracts ovate to widely ovate; lamina comose on inside, sparsely hairy to tomentose on outside, ± 3-ribbed on each side of main vein, coriaceous and rugose; length × depth (leaf shape usually cymbiform, depth of lamina—distance from adaxial groove to main vein situated abaxially) (4.5–)4.9 × 1.5(–1.8) mm .........................................3. *P. quadrifaria*

4b Abaxial surface of young leaves glabrous; bracts ovate to obovate; lamina villous on inside, glabrous on outside, obscurely ribbed on each side of main vein, thinly coriaceous; length × depth (3.2–)4.0 × 0.9(–1.6) mm ..................... 4. *P. montana*

1b Inflorescences comprising extended spikes, number of spikes often reduced, or many compound, multiflowered spikes present; proliferating growth common (Figures 7.6–7.22A):

5a Inflorescences reduced, often to solitary spikes; dwarf shrubs up to 300 mm high; bracts rhombic, dark green when fresh, dark brown in dried specimens, coriaceous, membranous wings absent .......................................... 5. *P. burchellii*

5b Inflorescences with multiflowered main and co-florescences; low shrubs, shrubs or small trees; bracts variously coloured, textured and winged:

6a Fruit fleshy; floral envelope greenish or yellow, coriaceous or membranous; leaves greyish green:

7a Fruit a red berry; floral envelope greenish and coriaceous, hypanthium strigose; leaves oblong, apex obtuse to subacute; bracts larger, oblong to lanceolate, leaf-like .......................................................................................... 6. *P. ericoides*

7b Fruit a bright yellow berry; floral envelope yellow and membranous, floral envelope glabrous at ovary, tomentose at neck; leaves narrowly lanceolate to ovate, apex acute with main vein visible as a blunt keel; bracts widely ovate, apex acute ......................................................................................... 7. *P. rigida*

6b Fruit dry (an achene); floral envelope yellow, yellow-pink or red, membranous or papyraceous; leaves variously coloured:

8a Floral envelope membranous, yellow or yellow-pink:

9a Floral envelope yellow or yellow-pink; bracts chartaceous, widely obovate, wings membranous, often bullate, tinged red at margins .......................... 8. *P. nivicola*

9b Floral envelope yellow; bracts thinly chartaceous, smooth and helmet-shaped with membranous rims........................................................ 9. *P. esterhuyseniae*

8b Floral envelope papyraceous, yellow-pink or red:

10a Young leaves and bracts abaxially sparsely hairy, becoming tomentose towards apex, older leaves rugose or warty with bases of fallen hairs.......... 10. *P. comosa*

10b Young leaves and bracts abaxially glabrous:

11a Bracts shorter than 4.5 mm:

12a Bracts rhombic in outline, softly coriaceous, with membranous wings, margins brownish ciliate .......................................................................... 11. *P. pendula*

12b Bracts oblate in outline, chartaceous, with bullate membranous wings, margins glabrous........................................................................................ 12 *P. galpinii*

11b Bracts longer than 4.5 mm:

13a Floral envelope ± 5.9 mm long; outer and inner sepals concave and lanceolate; bracts larger than leaves, bracts and leaves lanceolate and glaucous ......................................................................... 13. *P. drakensbergensis*

13b Floral envelope 6.0–8.4 mm long; outer and inner sepals variously shaped; bracts not as above, variously shaped and coloured:

14a Midrib of bract shortly extended into an acute apex, lamina rhombic to obtrullate, distinctly angled, 4- or 5-ribbed; leaves with a distinct midrib, laterally compressed, greyish green, drying greyish brown ..................... 14. *P. corymbosa*

14b Midrib of bract extending beyond lamina into a leaf-like point, lamina variously shaped and ribbed; leaves with a distinct midrib, or midrib less obvious, abaxially convex or laterally compressed, variously coloured:

15a Bracts with leaf-like point obtuse at apex, lamina closely 2-ribbed at margin; hypanthium fragments at circumference of ovary...................... 15. *P. obtusifolia*

15b Bracts with leaf-like point variously shaped, but not obtuse, lamina (faintly ribbed in *P. drakensbergensis*) extending into a membranous margin; hypanthium fragments at neck base:

16a Adaxial (inner) surface of bracts basally to centrally setose or tomentose over entire length of midrib; wings glabrous:

17a Bracts with midrib and leaf-like point stout and strongly developed, apex acute......................................................................................... 16. *P. paludosa*

17b Bracts with midrib forming a straight or filiform, leaf-like point, or midrib shortly extended:

18a Bracts with leaf-like point straight or slightly incurved; wings of bracts ovate, margins hairy in distal half, or obtrullate, narrowing abruptly into midrib .......... 17. *P. montivaga*

18b Bracts with leaf-like point shortly extended or extended into a filiform, slightly falcate point; wings of bracts ovate-acuminate, gradually narrowing to a point or widely obovate, narrowing abruptly into midrib .......... 18. *P. filiformis*

16b Adaxial (inner) surface of bracts completely villous:

19a Bracts with midrib extended, leaf-like point falcate; wings of bracts ± 4-ribbed; hypanthium neck ± 3.0 mm long, tomentose, often arcuate; spikes lax, often arcuate, mottled grey-green, with up to 16 fertile, enlarged bracts .......... 19. *P. falcifolia*

19b Bracts with midrib shortly extended into a short point, apex acute; wings of bracts ± 5-ribbed; hypanthium neck ± 2.0 mm long, glabrous to sparsely pubescent; spikes robust, rigid and extended, glaucous, with up to 30 fertile, enlarged bracts .......... 20. *P. rubra*.

### 7.3 Species treatment

1. **Passerina paleacea** *Wikstr.* Kunglinga Svenska Vetenskapsakademiens Handlingar 39: 323 (1818); Meisn.: 400 (1840); Meisn. 14: 562 (1857); C.H.Wright: 12 (1915); Thoday 4: 164 (1924a); Thoday 10: 388 (1924b). Type: Caput Bonae Spei, Herb. Wikströmii, *Sparrman s.n.* (S!, lecto., here designated; UPS!).

*Lachnaea paleacea* Herb. Banks, ined., fide Wikstr. 39: 324 (1818); Meisn. 14: 562 (1857); C.H.Wright: 12 (1915); Thoday 4:164 (1924a), nom. inval. in synonymy.

*Passerina glomerata* sensu Thunb.: 374 (1825a) pro parte quoad specim. *Herb. Thunberg 9596D, 9579.*

*Lachnaea conglomerata* L. sensu Thunb.: 374 (1825a) pro parte quoad specim. *Herb. Thunberg 9596D*.

*Passerina ericoides* sensu Thunb.: 374 (1825a) pro parte quoad specim. *Herb. Thunberg 9596D*, *9579*, non L.; *P. ericoides* sensu Meisn.: 401 (1840) pro parte, non L.; Meisn. 562 (1857) pro parte quoad specim. *Drège s.n.* (G!, K!, P!, S!).

Shrubs or shrublets 0.1–1.5 m high. *Stems* branching from base to up to growing points, young branchlets ascending, branchlets from previous growth persistent, arcuate, indurate; younger branchlets densely white-tomentose, villous closer to growing points; shredded bark of older branchlets greyish brown, remains of tomentum forming lengthwise strips; leaf scars conspicuous; older stems fissured lengthwise exposing greyish white sclerenchyma fibres; internodes shorter than leaves. *Leaves* imbricate on young branchlets, closely appressed to stem, diverging at an angle of ± 0–5°, cymbiform, often expanding, becoming thickly chartaceous and bract-like towards inflorescences; lamina inversely ericoid, adaxial surface concave, tomentose, abaxial surface laterally compressed and glabrous, plane shape linear to linear lanceolate; base sessile, dilated; apex acute, median vein forming a distinct keel incurved at apex; margins involute; length × depth 1.5–2.5(–4.0) × 0.6–0.8(–1.2) mm. *Inflorescences* subcapitulate, ± ellipsoid. *Bracts* decussate, imbricate, sessile, appressed, widely ovate in outline; lamina adaxially (inside) concave and villous, abaxially (outside) convex and glabrous, thickly chartaceous, smooth on each side of main vein, concolorous, greyish green, senescing to yellowish brown; base cuneate; main vein extending into obtuse apex; wings membranous, borders glabrous, obscurely veined; length × depth (2.5–)2.7 × 1.2(–1.9 mm). *Floral envelope* membranous and yellow during pollination, dehydrated after shedding of pollen, turning red to brownish, ± 4.2 mm long. *Hypanthium* glabrous, neck ± 0.3 mm long, abscission tissue and articulation plane absent. *Sepals* concave, elliptic or subrotund and glabrous. *Androecium* with filaments of antipetalous whorl ± 0.7 mm and antisepalous whorl ± 1.4 mm long; anthers 0.6 × 0.5 mm. *Ovary* 2.4 × 1.4 mm. *Fruit* an achene with pericarp membranous and dry, 2.3 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium fragmenting over widest circumference of fruit, the fragmented hypanthium, sepals and androecium being shed. Figure 7.1A–H.

## Nomenclatural notes

In the latter half of the eighteenth century *Lachnaea conglomerata* L. (1753), *Passerina ericoides* L. (1753) and *P. glomerata* Thunb. (1794) were constantly confused by botanists, causing Wikström (1818: 322) to place *P. glomerata* and *L. conglomerata* in the synonymy of *P. conglomerata* Thunb. In the same publication Wikström delimited and described *P. paleacea*. However, *P. paleacea* is not mentioned in Thunberg's revision of 1825, in which he described *P. glomerata* occurring in 'Hautbay', the currently known locality of both *P. paleacea* and *P. ericoides*. This confusion is reflected on many herbarium specimens, e.g. the specimen *Herb. Thunberg 9579*, bearing the inscriptions *P. ericoides*, *P. glomerata* (struck out) and the word 'paleacea' written in pencil. Although Thoday (1924b) chose the specimen *Herb Thunberg 9597* as the type of *P. paleacea*, this specimen was not chosen as lectotype in the present study, as the Sparrman specimen cited by Wikström (1818: 324) was located at **S**. The specimen *LINN 504.3*, positively identified as *P. paleacea*, bears the inscription 'sp 161', possibly referring to Sparrman. However, there will always be doubt whether it is a duplicate of the Sparrman specimen cited by Wikström.

## Diagnostic characters and relationships

*Passerina paleacea* can easily be confused with *P. rigida*, as both occur on sand dunes along the coast. The branches of *P. rigida* are nodding and abundantly covered by pendulous branchlets, spikes are extended and the fruits are fleshy yellow berries. Plants of *P. paleacea* are less robust, reaching a maximum height of 1.5 m, and are characterized by an abundance of subcapitulate inflorescences and dry fruit. The subcapitulate inflorescences at times led to the confusion of *P. paleacea* with *P. truncata* (=*P. glomerata*), but, these two species are morphologically as well as geographically distinct. *P. paleacea* has a maritime habit and *P. truncata* is distributed from Vanrhynsdorp, along the Cederberg mountains, to Malmesbury, Ceres, Tulbagh and Matjiesfontein up to Seven Weeks Poort. The earlier confusion between *P. paleacea* and *P. ericoides* was probably due to their sympatric occurrence, but these two species are morphologically quite different.

### Etymology

The Latin specific epithet *paleacea* (= chaffy) probably refers to the chaff-like subcapitulate inflorescences.

### Distribution and ecology

*Passerina paleacea* occurs in both the Southwestern and the Agulhas Plain Centres of the Cape Floristic Region (CFR) (Goldblatt & Manning 2000) and is a typical fynbos element. It grows on coastal dunes and other in maritime habitats from Langebaan, round the Cape Peninsula to the Cape Flats, Kogel Bay, Hermanus, Gansbaai, De Hoop, the Potberg coast, Bredasdorp, Arniston, Vermaaklikheid and Puntjie up to Stilbaai. It can be confused with *P. rigida*, a robust plant often growing on the primary dunes and widely distributed from the Western Cape, along the coast to northern KwaZulu-Natal. The vegetation types Dune Fynbos and dune thicket form a mosaic along many parts of the southern Cape coast (Lubke 1998a, 1998b; Lubke & Van Wijk 1998). This same distribution pattern is displayed by *P. paleacea* as it is found in the dune scrub, amongst typical fynbos species, but not in the dune thicket amongst larger shrubs or small trees with mesophytic leaves such as members of *Chrysanthemoides*, *Mimusops*, *Morella*, *Rhus* and *Sideroxylon*. Figure 7.11.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3318 (Cape Town): Langebaan, Schrywershoek, (–AA), *Boucher 2951* (NBG, PRE); Melkbosch Strand, (–CB), *Pillans s.n.* (GRA); Camps Bay, (–CD), *Hutchinson 143* (BOL, K, PRE); *Alexander-Prior s.n.* (PRE); *Schlechter 1363* (C, PRE); Stellenbosch District, Bottelary, (–DC), *Bolus 17197* (BOL). 3418 (Simonstown): Simonstown, (–AB), *Acocks 1001* (S); Witsand, *Andraea 581* (NBG PRE); near Wynberg, *Bolus 2926* (K); Kommetjie, *Bredenkamp 960* (PRE); Glencairn, Table Mountain, *Compton 11594* (NBG, S); Hout Bay, *Compton 9172* (NBG); Ronde Vlei, *Compton 24363* (NBG); between Muizenberg and sewage works, *Esterhuysen 35504* (BOL, C, M, MO); Hout Bay, *Krauss s.n.* (M); Witsand, *Gillett 814* (NBG); Klipfontein, *Gillett 1012* (NBG); Mountains between Fish Hoek and Simonstown, *Hutchinson 149* (BOL, GRA, K, PRE); Simonstown, *Lindeberg s.n.* (S); N of Wildevoëlvlei, *O'Callaghan 708* (NBG); NW of Simon's Bay, *Pillans 3783* (BOL, PRE); Noordhoek, *Thoday 216* (K, NBG, PRE); beyond Simonstown, *Wolley-Dod 2927* (BM, K); Hout Bay, *Wolley-Dod 1575* (PRE, K); Simons Bay, *Wright s.n.* (K, MO, P, TCD); Hout Bay, *Zeyher 38* (MO); Cape Maclear, (–AD), *Bredenkamp 961* (PRE); Cape Point, *Lewis 71* (NBG); near Cape Maclear, *Salter 6220* (BM, K); Krom River, *Taylor 7123* (K MO PRE); Cape of Good Hope, *White 5230* (PRE); Cape Flats, (–BA), *Alexander-Prior s.n.* (PRE); Cape Flats along Athlone Road, *Bolus s.n.* (BOL, PRE); Cape Flats, *Burchell 8389* (K); *Compton 13486* (NBG); Strandfontein, *Esterhuysen 35507* (S); between Eersterivier and Swartklip, *Pillans 9240* (BOL); Swartklip, Cape Flats, *Taylor 8166* (NBG PRE); between Strand and Paarl Roads, (–BB), *Acocks 184* (S); sanddunes the Strand, *Garside 1577* (K); sanddunes Gordon's Bay, *Garside 491* (K); Faure District, S of Kranat, *Jordaan 655* (PRE); Strand, *Parker 3843* (K NBG); Somerset Strand, *Rehm s.n.* (M); *Strey 715* (PRE); Cape Flats near Faure, *Van Rensburg 443* (K, M, NBG, PRE); Kogel Bay, (–BD), *Boucher 468, 469 & 470* (NBG, PRE); Harold Porter NBG, *Bredenkamp 952 & 954* (PRE); Hangklip Caledon, *Compton 13600* (NBG); Pringle Bay, *Greuter 21500* (PRE); Kogel Bay, *Parker 4109* (K, PRE); Rooiels near Hangklip, *Parsons 61* (NBG). 3419 (Caledon): Wildevlei Reserve, Hawston, (–AC), *Hubbard 224* (NBG); Walker Bay, Hermanus, (–AD), *Britton 12* (NBG); Mossel River shore, *Compton 23625* (NBG); Vogelklip, Hermanus, *Williams 440* (K MO); Rooi Els, (–BD) *Compton 15996* (NBG); Hangklip, Caledon, *Compton 22941* (NBG); between Gordon's Bay and Rooiels, *Dela Bat s.n.* (NBG); 2 mi. W of Betty's Bay, *Marsh 541* (K, PRE); Kogelberg, Rooiels, *Rycroft 1331* (NBG); Hangklip, *Stokoe s.n.* (NBG); Harold Porter NBG, *Topper 122* (NBG); Gansbaai, Bredasdorp, (–CB), *Compton 18159* (MO, NBG); Stanford Lagoon, dunes, *Compton 19930* (C, NBG); Gansbaai, *Esterhuysen 1855* (BOL); *Leighton 1855* (PRE); Uilskraal River Mouth, *Parsons 112* (NBG); Baviaansfontein, *Taylor 6996* (PRE, NBG, S); Pearly Beach, (–DA), Boucher 1603 (PRE); S of Elim, *Goldblatt 2599* (MO, PRE, S); Pearly Beach, Afsaal Campsite, *Taylor 10022* (PRE, K); Ratel River, *Van Breda 823* (PRE); Brandfontein, dune fynbos, (–DB), *Cowling 3436* (NBG). 3420 (Bredasdorp): De Hoop Nature Reserve, Koppie Alleen, (–AD), *Bredenkamp 950* (PRE); Potberg Nature Reserve, Dronkvlei, *Burgers 2186* (PRE); De Hoop, *Van der Merwe 1186* (PRE); Potberg Farm, 0.3 km from coast, (–BC), *Burgers 1015* (PRE); Potberg Coast, *Burgers 2268* (NBG PRE); Arniston, (–CA), *Acocks*

*22606 & 22615* (PRE); 1 km from Arniston en route to Bredasdorp, *Bredenkamp 949* (PRE); Die Mond, Bredasdorp, *Compton 22122* (BOL, NBG); Arniston, *Levyns 9725* (BOL); *Taylor 3802* (NBG, PRE); Bredasdorp District, Dronkulie Farm, *Van Breda 1633* (PRE); De Hoop, Buffelsfontein, fynbos, (–CB), *Fellingham 773* (C, PRE). 3421 (Riversdale): Riversdale, (–AB), *Jacot Guillarmod 20776* (GRA); 6.7 mi. SE of Vermaaklikheid P.O., (–AC), *Acocks 22528* (PRE); 4.5 mi. S of Vermaaklikheid, *Acocks 24212* (K, NBG PRE); Duivenhok's River, Puntjie, *Boucher 2219* (NBG, PRE); 6,7 km from Vermaaklikheid P.O., *Bredenkamp 937 & 938* (PRE); Puntjie, *Bredenkamp 940* (PRE); Stilbaai, (–AD), *Muir 4496* (K, PRE); Stilbaai, Blombos Road, *Wurts 1567* (NBG). Grid ref. unknown: *Acocks 5756* (S); Dunes W of Sarepta, *Acocks 583* (S); *s.n.* (K, S); between Grasbergrivier and Waterval, 2 500–3 000 ft, *Drège s.n.* (S); *Ecklon & Zeyher s.n.* (PRE); *Grey 4* (C); *Herb. Banks & Wikstr.* (C); *Herb. Banks & Swartz s.n.* (S); *Herb. Thunberg 9579 & 9596D* (UPS); *Masson s.n.* (BM); Cape Peninsula, *Moss 5760* (BM); *Museum Bot. Hauniense* (C); False Bay, *s.n.* (TCD); Cape Peninsula, Red Hills, *Lam & Meeuse 4272* (S); *Savage Cat. 504.2* (LINN); *Savage Cat. 504.3, Sp. 161* (LINN); Caput Bonae Spei, Herb. Wikströmii, *Sparrman s.n.* (S); Caput Bonae Spei, Herb Gastromii, *Sparrman s.n.* (S).

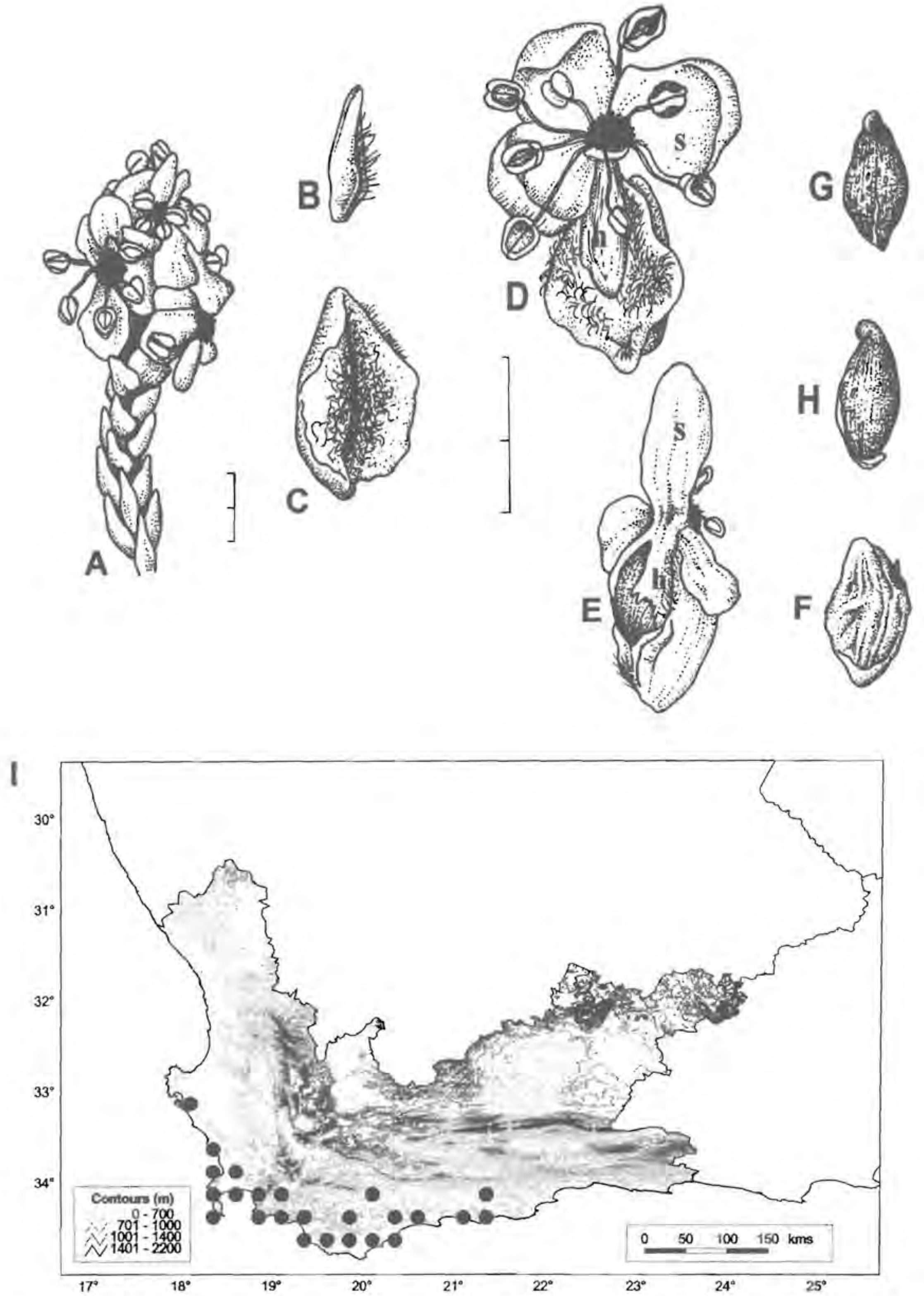

FIGURE 7.1.—*Passerina paleacea* (*Bredenkamp 960*). A, spike reduced, resembling terminal subcapitulate inflorescence; B, leaf; C, bract; D, flower clasped by bract in ventral view; E, hypanthium fragmenting at circumference of ovary; F, achene, enveloped by membranous pericarp; G, achene in lateral view; H, achene in ventral view. h, hypanthium; s, sepal. Scale bars: 2 mm.

I, known distribution of *Passerina paleacea*.

2. **Passerina truncata** (*Meisn.*) *Bredenk. & A.E.van Wyk*, stat. nov. Type: Western Cape, near Tulbagh Waterfall, April 1865, *Zeyher 43* (K!, lecto., here designated; MEL!, MO!, NBG!, S!, W!).

*Passerina rigida* Wikstr. var. *truncata* Meisn. 14: 563 (1857); C.H.Wright: 13 (1915); Thoday 4:153 (1924a). Type as above.

*Passerina rigida* Wikstr. var. *tetragona* Meisn. 14: 563 (1857) pro parte quoad specimen *Drège 2971*; C.H.Wright: 13 (1915); Thoday 4:153 (1924a). Type: Western Cape, circa Ezelsbank, *Drège 2971* (P!, lecto, here designated; K!).

*Passerina glomerata* sphalm. quoad *Lachnaea conglomerata* L. sensu Thunb.: 75 (1794); Willd.: 434 (1799); Wikstr. 39: 323 (1818); Thunb: 374 (1825a); Meisn. 14: 562 (1857); Cafferty & Beyers: 171, 172 (1999). *Lachnaea glomerata* sphalm. quoad *L. conglomerata* L. sensu Thunb.: 75 (1794).

*Passerina ericoides* sensu Thunb.: 374 (1825a) non L.

*P. glomerata* Thunb. sensu Thoday 4:153 (1924a). Type: '*P. glomerata* α (Lin. Herb.)'(Thoday 1924b: 387). *Herb. Thunberg 9577* (UPS!).

Shrubs, shrublets or low stunted shrublets (0.2–)0.4–1.5(–2) m high. *Stems* branching from base to growing points; branchlets ascending, straight or arcuate (subsp. *monticola*), greyish brown, younger branchlets whitish tomentose, older branchlets with whitish scales, remains of indumentum and scales flaking off with cork on older branchlets; cork fissured between leaf scars or tessellate, scaberulent. *Leaves* imbricate on young branchlets, diverging at an angle of 15–45°, 4-ranked, cymbiform; lamina inversely ericoid, adaxial surface concave, tomentose, abaxial surface laterally compressed and glabrous, plane shape narrowly oblong to oblong, length × depth (1.7–)2.0–3.0(–4.0) × (0.6–)0.8–1.0(–1.7) mm; base sessile, dilated; apex truncate, keeled, appearing humped on back or rounded (subsp. *monticola*); margins involute. *Inflorescences* comprising polytelic synflorescences, spikes reduced, artificially resembling terminal subcapitulate inflorescences, each characterized by 2 terminal leaves with axillary blind-ending rudimentary flowers, enveloping minute growing point; proliferating growth less common; subcapitulate inflorescences ± ellipsoid, pale green or straw-coloured. *Bracts* enveloping flowers and fruits, largest after anthesis, becoming more coriaceous and rounded at fruit set, decussate, imbricate, sessile, appressed or ascending, obovate to widely obovate in outline, length × depth (2.5–)2.9–4.0 × 1.4(–2.4 mm); lamina adaxially concave (inside), abaxially convex (outside), villous on inside, glabrous on outside, coriaceous to thickly coriaceous, ribbed (subsp. *monticola*) or ribbed and reticulately veined on each side of main vein, concolorous, pale green or greyish green, senescing to yellowish brown or pale brown (subsp. *monticola*); base cuneate; main vein extending into obtuse to acute apex; margins involute. *Flowers* actinomorphic, hypogynous. *Floral envelope* 4.9–6.4 mm long, comprising a hypanthium (fused calyx and androecium) and sepals, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Pedicel* very short or absent. *Receptacle* very short. *Disc* absent. *Hypanthium* a membranous cylindric tube, glabrous at ovary or apex of ovary tomentose, neck tomentose, 0.7–0.8 mm long, abscission tissue and articulation plane absent. *Sepals* 4, petaloid; imbricate in bud, flexed in flower; outer sepals concave, ovate or cymbiform, adaxially scantilly pubescent or apex tomentose, abaxially glabrous; inner sepals oblong to elliptic or widely obovate, adaxially scantilly pubescent or tomentose, abaxially glabrous. *Corolla* absent. *Androecium* dimorphic, diplostemonous, arising from hypanthium at separation point of sepals; filaments of antipetalous whorl 0.9–1.2 mm and those of antisepalous whorl ± 1.4 mm long; anthers (0.8–)0.9 × 0.4 mm, sub-basifixed, 2-thecous and 4-locular. *Ovary* superior (2.4–)2.5 × 0.9 mm, pseudomonomerous (Heinig 1951) at maturity, unilocular, placentation parietal; ovule 1, pendulous, 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* an achene with pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, the latter fragmenting over widest circumference of fruit, resulting in the fragmented hypanthium, sepals and androecium being shed.

## Nomenclatural notes

The name *Lachnaea conglomerata* L. 1753 was thought by early authors to apply to what is here called *P. truncata*. The only extant material , however, is an illustration by Breyne 1678, which is found to be identifiable as *Phylica stipularis* L.1771 (Cafferty & Beyers 1999). The name *P. glomerata* published by Thunberg 1794 is interpreted as a mistake for *L. conglomerata*, and may be cited as *P. conglomerata* (L.) Thunb. 1794, and must also be typified by the illustration of the *Phylica*. Both *L. conglomerata* and *P.* conglomerata (L.) Thunb. Were proposed for rejection by Cafferty & Beyers (1999) and this proposal has been accepted (Brummitt 2000). These names are therefore referred to the list of 'Excluded species' starting on p. 315.

Because Meisner (1857) had placed both *P. glomerata* and *L. conglomerata* in synonymy under *P. ericoides*, he described two new varieties, namely *P. rigida* var. *tetragona* and *P. rigida* var. *truncata*. Both these varieties included authentic material later cited by Thoday (1924a) in his description of *P. glomerata*. Based on the specimen *Herb. Thunberg 9577* (UPS) as the type, Thoday (1924a) reinstated *P. glomerata* Thunb. and placed Meisner's two varieties in synonymy, disregarding the fact that Thunberg (1794) had made the combination *P. glomerata*, in error. The rejection of *L. conglomerata* (Cafferty & Beyers 1999; Brummitt 2000) and *P. glomerata* implied the choice of a new name for the existing species. As all the specimens included in *P. rigida* var. *truncata* are characterized by '*foliis ramulo adpressis vel semipatulatis truncatis*' and their distribution coincide perfectly with the distribution of the previously known *P. glomerata sensu* Thoday, var. *truncata* is here selected and raised to the species level. Var. *tetragona* included *Drège 2971* (K, P) from Ezelsbank in the Western Cape, and has now been placed in synonymy under *P. truncata*, and *Drège s.n.* from Stormberg in the Eastern Cape has now been identified as *P. montana*.

## Etymology

The Latin specific epithet *truncata* (= ending very abruptly, as if cut straight across), describes the blunt, keeled apex of the leaves, which appear humped on the back.

## Key to subspecies

1a Shrubs or shrublets from various habitats; stems branching from base, straight; branchlets straight; leaves diverging at angle of ± 15°, narrowly oblong to oblong, apex truncate, keeled, appearing humped on back; bracts appressed, thickly coriaceous, ribbed and reticulately veined on each side of main vein, greyish green, senescing to yellowish brown ........................................ 2a. subsp. *truncata*

1b Shrubs or low shrublets from mountain habitats; stems often stunted; branchlets lax, arcuate; leaves diverging at angle of ± 45°, narrowly oblong, apex truncate to rounded and keeled; bracts ascending, coriaceous, ribbed on each side of main vein, pale green, senescing to pale brown............................ 2b. subsp. *monticola*

### 2a. subsp. **truncata**

Shrubs or shrublets 0.4–2.0 m high. *Stems* branching from base to growing points; branchlets ascending, younger branchlets whitish tomentose; cork tesselate. *Leaves* diverging at an angle of ± 15°, plane shape narrowly oblong to oblong, length × depth (1.7–)2.0–3.0(–4.0) × (0.6–)0.8–1.0(–1.7) mm; apex truncate, keeled, appearing humped on the back. *Inflorescences* subcapitulate, ± ellipsoid, pale green or straw coloured. *Bracts* thickly coriaceous, ribbed, reticulately veined on each side of main vein, extending into obtuse apex; greyish green, senescing to yellowish brown; length × depth (2.5–)2.9–4.0 × 1.4(–2.4) mm. *Floral envelope* ± 4.9–6.4 mm long. *Hypanthium*: ovary glabrous, neck tomentose, 0.7–0.8 mm long. *Sepals*: outer sepals cymbiform, adaxially tomentose, abaxially glabrous; inner sepals oblong to elliptic, adaxially tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl 0.9–1.2 mm and those of antisepalous whorl ± 1.4 mm long; anthers 0.8 × 0.4 mm. *Ovary* 2.4 × 0.9 mm. Figure 7.2A–F.

### Diagnostic characters and relationships

Subsp. *truncata* can easily be distinguished from the other subspecies by its decussate, imbricate, four-ranked leaves, spreading at an angle of 15°. The leaves are abaxially laterally compressed and glabrous, narrowly oblong to oblong, with a dilated base and a truncate, keeled apex, appearing humped on the back. Inflorescences are reduced spikes, terminally subcapitulate. The bracts are obovate to widely obovate, greyish green, senescing to yellowish brown. The lamina of the bracts is villous on the inside and glabrous on the outside. It is thickly coriaceous, ribbed and reticulately veined on each side of the main vein, which extends into an obtuse apex. *P. truncata* could be confused with *P. quadrifaria*, which is characterized by shortened leaf-bearing branchlets with closely arranged nodes, very short internodes and leaves spreading at an angle of 45°; the abaxial surface is convex and tomentose in young leaves and the leaf apex is rounded.

### Distribution and ecology

Subsp. *truncata* is confined mainly to the Fynbos (Rebelo 1998) and Succulent Karoo Biomes (Hoffman 1998) of the Northern and Western Cape. It occurs in the Northwestern, Southwestern, Karoo Mountain and Southeastern Centres within the CFR. In the Northern Cape, it is distributed from Steinkopf, through Namaqualand, Nieuwoudtville and Vanrhynsdorp to Wolfberg. This subspecies is common in the Western Cape, where it is distributed from Vanrhynsdorp, the Koue Bokkeveld, Clanwilliam, the Olifants River Valley, Citrusdal, along the Cederberg Mountains to Malmesbury, Ceres, Tulbagh, Matjiesfontein and Seven Weeks Poort. The most southeasterly locality is Baviaanskloof near Patensie; the specimen *Bayliss 546* is an outlier, collected as a voucher for cancer research and is currently housed at PRE. Subsp. *truncata* is adapted to a wide range of habitats. It occurs on low-lying plains as well as on several mountain ranges, where it is common on level ground, rocky slopes and along watercourses. It is one of the dominant taxa between Tulbagh and Clanwilliam, where the size of the shrubs varies from 0.4–1.5(–2) m on flat areas and plains. These plants grow prolifically and during flowering time yellow, yellowish pink and red flowers can often be seen on the same plant, representing various stages of maturation. This subspecies is also common in the arid karoo environment of the Witteberg Mountains near Matjiesfontein, where it grows in rocky areas. In extremely dry areas of Namaqualand, the Ceres-Karoo and on top of the Skurweberg and Cederberg Mountains, subsp. *truncata* becomes a hardy, skeletal, sparsely branched, sclerophyllous shrublet, with yellow, coriaceous leaves, closely arranged on the stem, but with each growing point protected by a pair of conspicuous, coriaceous bracts. Figure 7.2G.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

NORTHERN CAPE.—2917 (Springbok): Namaqualand, Steinkopf, (–BC), *Meyer 74* (NBG); Spektakel Pass, (–CA), *Zietsman & Zietsman 925* (PRE); Spektakelberg, (–DA), *Bolus 9507* (BOL, K); top of Spektakel Pass, *Goldblatt 2802* (C, PRE, M, MO); north side of road, *Le Roux 2310* (PRE); 24 km from Springbok to Kleinsee, *Stirton 10148* (PRE); Farm Naries, between Kleinsee and Springbok, *Van Wyk 6485* (PRE, PRU); Vogelklip, (–DB), *Pearson & Pillans 5928* (K); Steinkopf District, (–DC), *Marloth 6873* (PRE); Little Namaqualand, Springbok District, Komaggas Mountains, *Marloth 6957* (PRE). 3017 (Hondeklipbaai): Namaqualand, Kanariesfontein, (–BA), *Acocks 19397* (K, M, PRE); 12 mi. S of Kamieskroon, (–BB), *Merxmüller & Giess 3832* (M); between Kamieskroon and Garies, *Salter 1568* (K); Kamieskroon, Skilpad, Wild Flower Reserve, *Van Rooyen 2401, 2626* (M); between Garies and Kamieskroon, (–BD ), *Hutchinson 834* (GRA, K, PRE); Bachgrund, 12 mi. S of Kamieskroon, *Merxmüller & Giess 3832* (PRE). 3018 (Kamiesberg): Bovlei, (–AA), *Archer, F. 120* (NBG, PRE); Anegas, upper slopes of Zuurberg, *Pearson, 6256* (BOL, K); between Garies and Leliefontien, (–AC), *Esterhuysen 1327* (BOL); Studer Pass, *Evrard 9001* (MO, PRE, UPS); hills above Twee Rivieren, *Pearson 6765* (K); *Pearson 6773* (BOL); Kamiesberg, *Stokoe 22331* (BOL, PRE); Ezelsfontyn, *Whitehead s.n.* (TCD). Grid ref. unknown: Namaqualand, Bowesdorp, *Stokoe s.n.* (NBG). 3119 (Calvinia): top of Vanrhyn's Pass, (–AC), *Bredenkamp 1011* (PRE); Dwarsrivier, on road to Algeria, *Emdon 197* (PRE); 10 km SW of Nieuwoudtville, *Greuter 21765* (PRE); top of Vanrhyn's Pass, *Levyns 4108* (BOL); Nieuwoudtville, Willemsrivier Farm, *Nortje 17* (NBG); 10 km from Nieuwoudtville to

Vanrhynsdorp, *Strid 37832* (C, NBG); Vanrhyn's Pass, *Taylor 2865* (NBG, S); Nieuwoudtville, *Van Son s.n. TRV 36623* (PRE); Wolfberg Arch, *Kruger 911* (PRE); Calvinia District, Lokenburg, (–CA), *Acocks 17234* (K, PRE); *Story 4303* (K, GRA, PRE); Lokenberg Farm, *Bremer 264* (PRE, S). 3219 (Wuppertal): Wolfberg near Arch, (–AD), *Kruger 911* (NBG); Matjesrivier, Cederberg, *Wagener 259* (NBG);

WESTERN CAPE.—3018 (Kamiesberg): Rietkloof Mountain, (–DC), *Pearson 5709* (BOL). 3118 (Vanrhynsdorp): Nardouw Pass, (–BC), *Bayliss BRI B591* (K, MO, PRE); Vanrhynsdorp, (–DA), *Almborn 475* (MO); *Linscherg s.n.* (S); Bokkeveld Mountains, Meulstein Farm, *Marloth 12943* (PRE); Gifberg Pass, halfway up at stream crossing, (–DB), *Boucher 2872* (K, NBG, PRE); Heerenlogementsberg, above monument, (–DC), *Boucher 3177* (C, K, NBG, PRE); Clanwilliam, Trawal road, *Bredenkamp 1010* (PRE); sandy slopes of Bullshoek, *Goldblatt 2757* (M, NBG, PRE, S); sand flats between Driefontein and Heerenlogement, *Pearson 6782* (K); Heerenlogementsberg, 14 mi. N of Graafwater, *Taylor 3921* (PRE); Nardouw Mountains, Olifants River, *Thompson 2823* (K, MO, NBG, PRE); Piketberg road, *Tyson 1452* (PRE); Trawal, *Van Rooyen, Steyn & De Villiers 618* (NBG); Gifberg, (–DD), *Bayliss 577*, (M, MO, PRE); 39–40 km NE from Clanwilliam, *Bellamy 2* (PRE); Nardouw Kloof, *Stokoe s.n.* (NBG); Gifberg plato, *Zietsman & Zietsman 1151* (PRE). 3218 (Clanwilliam): S of Lambert's Bay, (–AB), *Taylor 4011* (NBG); roadside at Alpha, (–BB), *Acocks 3045* (S); 9 mi. S of Clanwilliam, *Almborn 539* (M); Rheboksvallei, next to road between Calvinia and Clanwilliam, *Bredenkamp 1008, 1009* (PRE); Olifants River Valley, *Compton 4901* (BOL); Pakhuis Kloof, *Compton 6902* (NBG); Pakhuis Pass, *Compton 9537* (NBG); Nardouw road, *Compton 22821* (S); Pakhuis Pass, *Esterhuysen 26859* (K); *Galpin 11209, 11210, 11218* (BM, C, PRE, UPS); Kransvlei Pass, summit, *Gillett 4012* (BOL, K, PRE); 12 mi. from Clanwilliam on Citrusdal road, *Hardey 448, 449* (PRE, BM, K, M); Zeekoe Vlei, *Levyns 1232* (BOL); Elandskloof, *Lewis 4061* (NBG); Cederberg Mountains, *Stokoe 8042* (BOL, GRA, NBG, PRE); Nardouw Mountain Pass, (–BC), *Bayliss 591* (K, MO, PRE); Olifants River Mountain, (–BD), *Compton 4901* (NBG); Witelskloof, *Hugo 679* (K, PRE); Kriedouw, *Levyns 1335* (BOL); W end of Elandskloof, *Lewis s.n.* (NBG); Kriedouw, *Pocock 770* (NBG, PRE); Langfontein, S of Clanwilliam, *Taylor 9293* (PRE); N of Clanwilliam, *Thompson 1278* (NBG); Het Kruis, Eendekuil, (–DA), *Acocks 1002* (S); Het Kruis, *Compton 15020* (NBG); 1 km N of Goedverwacht, *Dahlgren & Peterson 257* (K); De Hoek, *Lewis 62671* (MO); base of Kapteins Kloof, *Pillans 8021* (BOL); Olifants River Valley, (–DB), *Barker 5751* (NBG); *Stephens 7226* (K); near Eendekuil, *Levyns 1377* (BOL); 2 mi. S of Citrusdal, *Maguire 2025* (C, NBG); Zebra Kop, *Pillans 7298* (K); Middelpos, (–DC), *Morley 250* (NBG, PRE); Rietkloof Mountains, *Pearson 5709* (K); Nardouw Kloof, *Stokoe s.n.* (NBG); De Hoek, *Compton 19949* (NBG MO); *Lewis 2730, 4062, SAM67057 & SAM67058* (NBG, PRE); Piketberg road, *Tyson 318* (NBG). 3219 (Wuppertal): Pakhuispas, (–AA), *Bredenkamp 1005* (PRE); Rheboksvallei, *Bredenkamp 1006, 1007* (PRE); Klipfonteinrand, NE of Pakhuis, *Esterhuysen 32195* (MO); Platkloof, Citrusdal, *Hanekom 1249* (K); 2 km N of Pakhuis, *Hugo 545* (K, PRE); Cederberg, *Marloth 11686* (PRE); Eikeboom, en route to Algeria, *Bredenkamp 988* (PRE); between Sneeukop and Sneeuberg hut, at Hoogvertoon, *Bredenkamp 989, 991* (PRE); above road from Cederberg, (–AC), *Acocks 3214* (S); roadside Algeria to Clanwilliam, *Boucher*

*2880* (PRE); Crystal Pool, *Bredenkamp 990* (PRE); at the base of Sneeukop, *Bredenkamp 992* (PRE); Jantjieshoek, *Bredenkamp 993* (PRE); Kromrivier Farm, *Bredenkamp 994* (PRE); 3 km from Algeria en route to Clanwilliam, *Bredenkamp 1004* (PRE); Ezelsbank, *Drège 2971* (K, P); on road to Algeria, few miles from Dwars River, *Emdon 197* (C, K); Olifants River Mountain, *Howes 225* (K, PRE); De Hangen Farm, *Metelerkamp 562, 562a* (BOL); Nieuwoudt Pass, *Stokoe s.n.* (NBG); pass S of Wuppertal, *Taylor 10483* (NBG, PRE); Cederberg, near Spitskop, *Taylor 10618* (NBG, PRE); Middelpos Farm, (–CA), *Bredenkamp 986* (PRE); 10 mi. E of Citrusdal, Elandskloof, *Compton 519* (NBG S); Citrusdal, NE Cederberg Mountains, *Goldblatt 7264* (MO, PRE, S); Platkloof, *Hanekom 1249* (PRE); Citrusdal, *Rauh 3553* (M); Gideon's Kop, (–CB), *Stokoe s.n.* (NBG); Piketberg, Dasklip Pass, Cardouw, (–CC), *Barker 10286* (NBG); Porterville Grootfontein Farm, *Boucher 1983* (NBG); Porterville, Dasklip Pass, (–CC), *Hugo* & *Mauve 4* (K, MO, NBG, PRE); Clanwilliam, Cardouw Road, *Compton 22821, 24331* (NBG, MO); Dasklip Pass, *Thompson 1519* (NBG); Ceres-Karoo, Skurweberge, W of farm Tweefontein (-CD), *Bredenkamp 983* (PRE); 15 km from Citrusdal, Piekenierskloof Pass, *Bredenkamp 985* (PRE); Swartrug, between Koue Bokkeveld and Ceres-Karoo, *Hanekom 943* (NBG, PRE); W base of 'Schurfteberg', *Pillans 9606, 63799* (BOL, MO, PRE); Swartruggens, Groenfontein Farm, S.A. Nature Heritage No. 77, (–DC), *Bredenkamp 977* (PRE); Kagga Kama road, *Bredenkamp 978* (PRE); E slopes of Swartruggens, *Levyns 1808* (BOL); Koue Bokkeveld, near Konkelhaaks River, *Levyns 1941* (BOL); foothills of Cold Bokkeveld, *Stephens 7264* (K). 3318 (Cape Town): Moorreesburg, Bakkersbos, (–BA), *Jordaan 545* (NBG); Oshoekkop N of Moorreesburg, *Van Zyl 3295* (K, MO, PRE); Porterville, Piketberg, (–BB), *Loubser 598* (NBG); Malmesbury, Riebeek Kasteel, (–BD), *Compton 11718* (NBG); *Pillans 10705* (MO); Malmesbury Clanwilliam road, *Alice Godman 527* (BM). 3319 (Worcester): Hills near Saron, *Schlechter 10627* (BM, K, MO, PRE, S); Saron 3 000 ft, (–AA), *Schlechter 10660* (BM, K, PR, PRE, S); Ceres, Gydo, (–AB), *Compton 18781* (NBG); Koue Bokkeveld, Driefontein, *Marloth 10668* (NBG); 'Skurfteberg', Justice Diemont's Property, *Taylor 8664* (K, NBG, PRE, S); Tulbagh, Gouda, (–AC), *Barker 9217* (NBG); road between Wolseley and Tulbagh, Farm 'The Wild Olive', *Bredenkamp 972* (PRE); 8 km from Tulbagh, *Bredenkamp 973* (PRE); Roodesandberg, *Compton 6546* (NBG); New Kloof, *Compton 11701* (NBG); mountains near Tulbagh Kloof, *Davis s.n.* (NBG, PRE, SAM); New Kloof, *Gillette 397* (NBG); above Tulbagh Waterfall, *Hutchinson 416* (BM, GRA, K, PRE); Elands Kloof Bridge, 10 mi. from Citrusdal, *Johnson 519* (NBG); Lewerfontein Farm, *Kotze 45* (NBG); Tulbagh 400 m, *Marloth 4238* (K, PRE); Tulbagh Mountains, *Marloth 13006, 13007* (NBG, PRE); *Pappe s.n.* (K); Voëlvlei Tortoise Reserve, *Solomon 92* (NBG); Tulbagh Waterfall, *Stokoe 1460* (PRE); *Stokoe* & *Davis s.n.* (NBG); Piketberg road, *Tyson 2318* (K); Tulbagh, *Zeyher 43* (K, NBG, MO, S); Ceres, Bonteberg, (–AD), *Compton 3743* (NBG); Conical Peak, *Stokoe s.n.* (NBG); *Stokoe 8041* (BOL); Ceres District, Visgat, *Stokoe s.n.* (NBG); Spes Bona, foot of Zwarteruggens, (–BA), *Marloth 13144* (PRE); Kavadouws Mountains near Orchard, (–BC), *Esterhuysen 10886* (BOL); Buffelskraal West, *Forrester s.n.* & *114* (NBG); Bonteberg, (–BD), *Compton 9970* (MO, NBG); Eikenbosch, *Esterhuysen 3703* (K); Matroosberg, *Phillips 2057* (NBG); Ertjiesland Kloof, (–CA), *Esterhuysen 2273* (BOL); near base of Sneeukop, *Compton 4894* (BOL); Worcester District, *Van Breda 198*

(PRE); Worcester Waterfall, *Ecklon & Zeyher s.n.* (BREM, S); between Eendracht and Triangle, (–DB), *Buchell 387* (PRE). 3320 (Montagu): poort N of Pienaarskloof, (–AA), *Acocks 23678* (PRE); Tweedside, near top of Witteberg Koppie, (–AB), *Levyns 2382* (BOL); Tweedside, *Marloth 10798* (PRE); Pienaarskloof Poort, (–AC), *Taylor 6495* (NBG; PRE); Matjiesfontein, (–BA), *Marloth 11426* (PRE); Matjiesfontein, Whitehall, *Thoday 213* (NBG); White Hill, near Matjiesfontein, quartsite ridges S of railway line, *Thoday 1921* (BOL); Laingsburg, Witteberg, (–BC), *Compton 2800* (BOL, NBG); *3327* (BOL, K); *5890* (BOL, NBG); *12237* (NBG). 3321 (Ladismith): Seven Weeks Poort, (–AD), *Levyns 2415a* (BOL). 3322 (Oudtshoorn): near Rondevlei, Sedgefield, (–DC), *Bayliss 1105* (K, MO, PRE).

EASTERN CAPE.—3324 (Steytlerville): Baviaanskloof near Patensie, (–CD), *Bayliss BRI B 546* (PRE). Grid ref. unknown: Karoo Poort, *Acocks 1004* (S); *Drège s.n.* (K); *Ecklon & Zeyher s.n.* (MO); *Herb. Thunberg s.n.* (UPS); *Herb. Swartzii s.n.* (S); Caput Bonae Spei, *Hiendlmayr s.n.* (M); Pigmentberg Mountain, *Levyns 2165* (BOL); Greg's Pass, *Levyns 1370* (BOL); Caput Bonae Spei, *Museum Botanicum Hauniense* (C); *Thunberg s.n.* (S); Caput Bonae Spei, *Thunberg s.n.* (SBT); *Zeyher s.n.* (M).

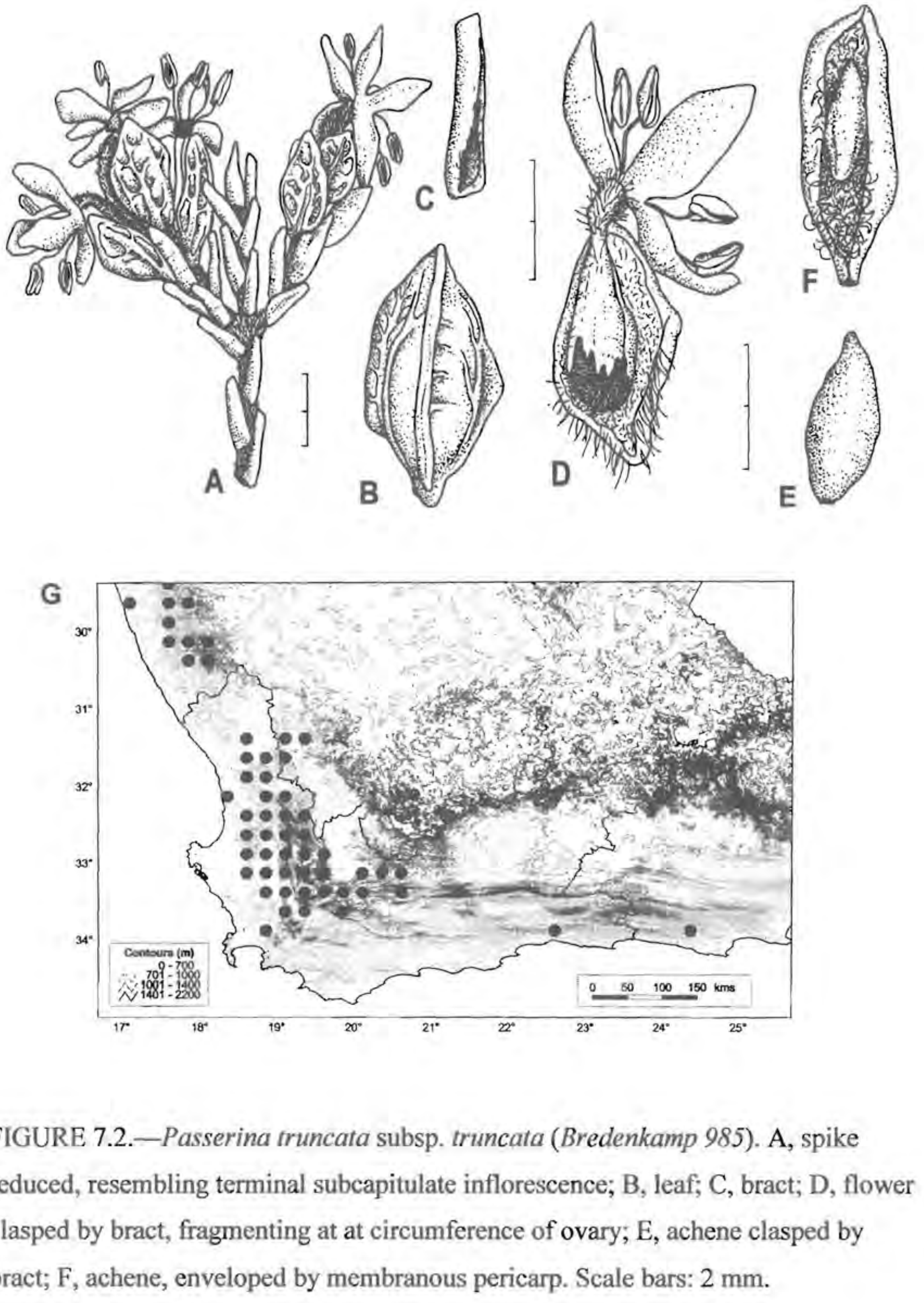

FIGURE 7.2.—*Passerina truncata* subsp. *truncata* (*Bredenkamp 985*). A, spike reduced, resembling terminal subcapitulate inflorescence; B, leaf; C, bract; D, flower clasped by bract, fragmenting at at circumference of ovary; E, achene clasped by bract; F, achene, enveloped by membranous pericarp. Scale bars: 2 mm.

G, known distribution of *Passerina truncata* subsp. *truncata*.

2b. subsp. **monticola** *Bredenk. & A.E.van Wyk* , subsp. nov., a subspecie typica praecipue habitu differt. *Frutices* vel fruticuli in habitu montano in fissuris rupium radicantibus; ramuli adscendentes, laxi, arcuati. *Folia* ad angulum 45° divergentia, anguste oblonga, carinata, apice truncata vel rotundata. *Bracteae* adscendentes, obovatae ad late obovatae, coriaceae, utrinque costae costatae, pallide virides.

TYPUS.—Western Cape, 3319 (Worcester): Robertson Division, Omklaar, (-DD), 1923, *Stokoe 22330* (PRE!, holo.; K!, iso.).

Shrubs or low stunted shrublets 0.2–1.5 m high, often rooted in rock crevices. *Stems* often stunted, branching profusely on younger growth, branchlets ascending, arcuate; younger branchlets densely whitish tomentose; cork fissured between yellowish leaf scars. *Leaves* diverging at an angle of ± 45°, abaxial surface laterally compressed and glabrous, plane shape narrowly oblong, length × depth (2.4–)2.6(–3.0) × 0.6–1.7 mm; base dilated; apex truncate to rounded, keeled. *Inflorescences* subcapitulate, ± ellipsoid, pale green. *Bracts* ascending, obovate to widely obovate; lamina adaxially concave (inside), abaxially convex (outside), villous on inside, glabrous on outside, coriaceous, ribbed, pale green, senescing to pale brown, base cuneate; main vein extending into obtuse to acute apex; length × depth (2.5–)2.9 × 1.5 mm. *Floral envelope* ± 4.9 mm long. *Hypanthium*: apex of ovary tomentose, neck tomentose, ± 0.7 mm long. *Sepals*: outer sepals concave, ovate, apex adaxially tomentose, abaxially glabrous; inner sepals widely obovate, adaxially tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 1.2 mm and those of antisepalous whorl ± 1.4 mm long; anthers 0.9 × 0.4 mm. *Ovary* 2.5 × 0.9 mm. Figure 7.3A–F.

## Diagnostic characters and relationships

*Passerina truncata* subsp. *monticola* can easily be distinguished from the typical subspecies by its growth form. Plants are often low shrublets rooted in rock crevices on mountain peaks. Stems are stunted, branching profusely on younger growth, the branchlets are ascending, lax and arcuate. The leaves spread at an angle of 45°, are narrowly oblong and the apex is truncate to rounded and keeled. Bracts retain the characteristic shape of subsp. *truncata*, but are ascending, smaller and pale green. Subsp. *monticola* is also distinguished from *P. quadrifaria* by its characteristic lax, arcuate branchlets.

### Etymology

The subspecific epithet *monticola* (= mountaineer) refers to the mountainous habit of the subspecies.

### Distribution and ecology

Subspecies *monticola* is distributed south of 32°S latitude and between 18°E and 20°E longitude. It occurs in the Northwestern and Southwestern Centres of the CFR. It grows in mountainous areas and is distributed from Clanwilliam, along the Cederberg Mountains, southwards along mountain ranges and summits to Table Mountain, Helderberg, Kogelberg, the Hex River Mountains and the Riviersonderend Mountains.

Plants are often found in rock crevices or in damp sheltered gullies. They also occur on western, southwestern and eastern slopes and on shale bands at an altitude of 1 667–2 000 m on Sneeukop (Goudini). The most common habitat is on mountain summits, e.g. Sneeuberg, Slanghoek Pile, Zebra Kop, Jonaskop and Buffelshoek, as well as on mountain peaks, e.g. Milner, Du Toits, Uitkyk and Bailey's Peaks, at altitudes of ± 2 000 m. Figure 7.3G.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Clanwilliam, (–BB), *Compton 1404* (NBG); Cederberg, Donkerkloof Kop, *Stokoe 64616* (PRE); E slopes of Kapteinskloof, *Pillans 7769* (BOL); Piketberg Mountain, summit of Zebra Kop, (–DB), *Pillans 7298* (BOL). 3219 (Wuppertal):

Cederberg Mountains, Uitkyk Peak, (–AC), *Esterhuysen 7380* (BOL); Cederberg Forest Reserve, Sneeukop, *Stehle 309* (NBG); Cederberg, *Stokoe s.n.* (NBG); *Stokoe 8040* (BOL); Cederberg Forest Reserve, Sneeuberg summit, *Taylor 6145* (PRE); Ceres border, Gideon's Kop, (–CB), *Stokoe s.n.* (NBG). 3318 (Cape Town): Table Mountain, Kasteel's Gully, (–CD), *Esterhuysen, 28574* (BOL); Jonkershoek, Langrivier, (–DD), *Kerfoot K5061* (NBG); The Twins, *Kruger 1754* (PRE). 3319 (Worcester): SW slopes of Sneeukop, (–AD), *Esterhuysen 3638* (BOL); Mostert's Hoek, *Esterhuysen 9822* (BOL); Hex River Mountains, Milner Peak, 6 000 ft, *Esterhuysen 28587* (BOL); Buffelshoek Peak, (–BD), *Esterhuysen 8416* (BOL); *Esterhuysen 27451* (BOL); Slanghoek Pile, summit, (–CA), *Esterhuysen 1744* (BOL); Worcester District, Mostert's Hoek, (–CB), *Esterhuysen 9921* (BOL); Goudini, Sneeukop, shale band slopes 5 000–6 000 ft, *Esterhuysen 28555* (BOL, K); Devil's Tooth, (–CC), *Esterhuysen 9542* (BOL); Adolph's Kop, *Esterhuysen 11046* (BOL); Wemmershoek, *Esterhuysen 11255* (BOL, K); Du Toits Peak, 6 000 ft, *Esterhuysen 30573* (BOL); Wemmershoek Peak, *Stokoe s.n.* (NBG); Jonaskop, near summit, (–DC), *Rourke 961* (MO, NBG); Wildepaardeberg, *Stokoe s.n.* (BOL); Robertson District, Onklaar, (–DD), *Stokoe 22330* (K, PRE). 3418 (Simonstown): near Wynberg Caves, (–AB), *Compton 6347* (NBG); Helderberg, (–BB), *Stokoe 17574* (BOL, PRE). 3419 (Caledon): W end of Riviersonderend Mountains, Olifantsberg, Boschiesveld, (–AB), *Esterhuysen 30910* (BOL); spur of Riviersonderend Mountains between Caledon and Robertson, 5 000 ft, *Stokoe s.n.* (BOL); Genadendal, Baviaanskloof, (–BA), *Marloth 6626* (NBG, PRE); *Stokoe 2520* (PRE); Kogelberg, (–BD), *Stokoe s.n.* (NBG). Grid ref. unknown: *Guthrie s.n.* (NBG); Tulbagh District, Bailey's Peak, *Stokoe s.n.* (NBG); Paarl District, top of Bailey's Peak near beacon, *Stokoe 8225* (BOL); Tulbagh, Little Winterhoek Mountains, *Stokoe s.n.* (BOL).

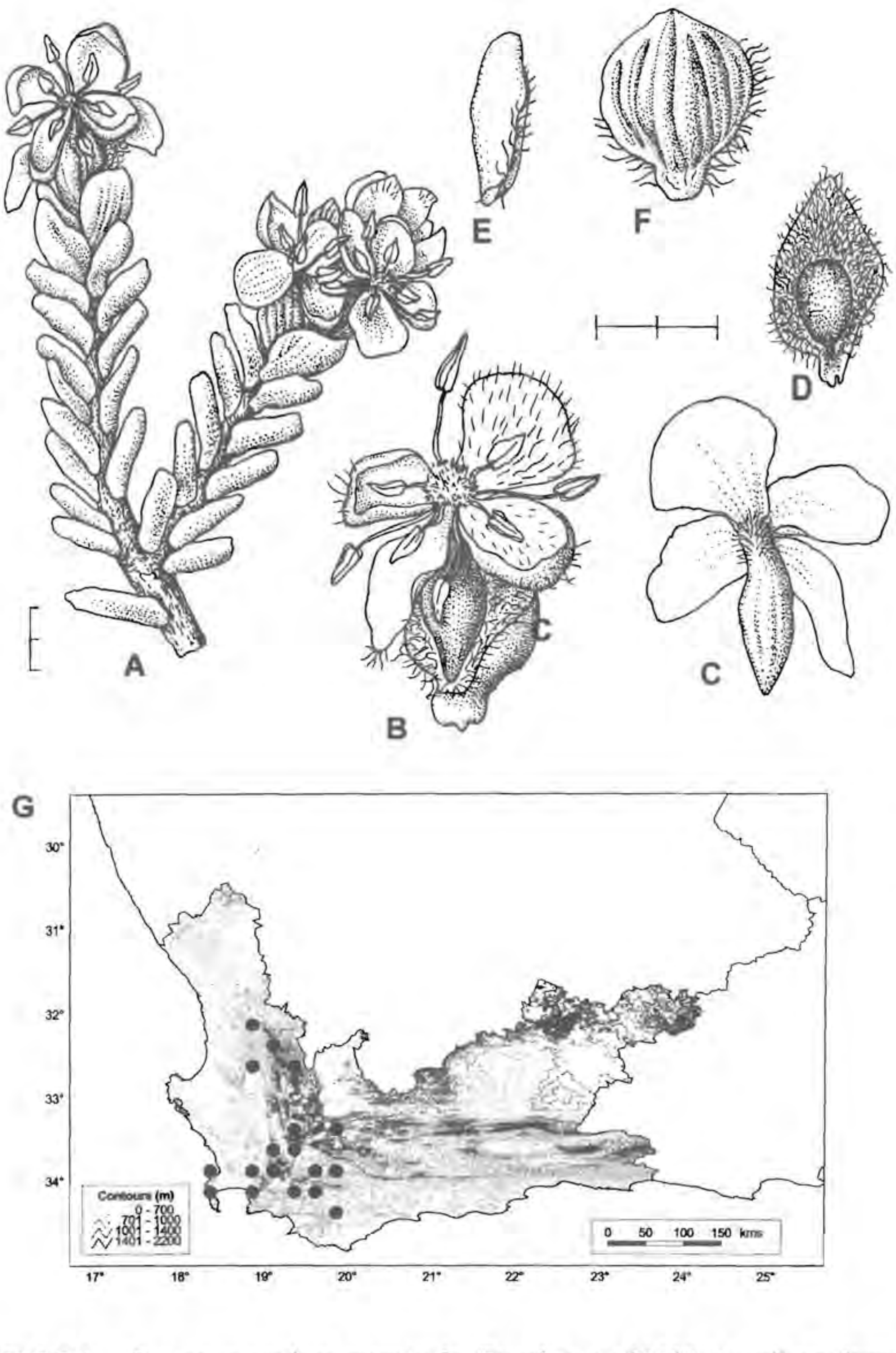

FIGURE 7.3.—*P. truncata* subsp. *monticola*, *Esterhuysen 28587*. A, spike reduced, resembling terminal subcapitulate inflorescence; B, flower clasped by bract; C, indumentum of hypanthium tube and glabrous abaxial surfaces of calyx lobes; D, fruit in tomentum of bract; E, leaf; F, bract. Scale bars: 2 mm.

G, known distribution of *P. truncata* subsp. *monticola*.

3. **Passerina quadrifaria** *Bredenk. & A.E.van Wyk*, sp. nov., *P. comosae* C.H.Wright affinis sed ramulis foliatis abbreviatis, internodis perbrevibus. *Folia* decussata, imbricata, ad angulum 45° divergentia, sessiles, basis rhombea, dilatata, accurate interordinata basibus foliorum nodorum proximorum, cymbiformes, circumscriptione lineari-lanceolata; lamina inverse ericoidea, pagina adaxialis concava, setosa, pagina abaxialis convexa, foliis juvenibus tomentosa; apex rotundatus; margines ciliati. *Bracteae* cymbiformes, circumscriptione ovatae vel late ovatae; lamina adaxialiter concava, comosa, abaxialiter convexa, sparsim pubescens ad tomentosa, ± tricostata utrinque costae, coriacea rugosaque, in marginem membranaceum expansa; basis cuneata; costa excurrens apicem rotundatum vel subacutum faciens; margines ciliati. *Flores* papyracei, tempore pollinationis luteo-rosei, postea rubescentes vel brunnescentes.

TYPUS.—Eastern Cape, 3324 (Steytlerville): Uitenhage District, Great Winterhoek Mountains, Cockscomb, (–BD), rocky ridge, 30 Nov. 1958, *Esterhuysen 28006* (PRE, holo.!; BOL!, K!).

*Passerina sp. nov. 3* Bredenk. & A.E.van Wyk 129: 70 (2000); 31,1: 56 (2001a); 31,2: 217 (2001b).

Low, often slender shrubs up to 1.0 m high, sometimes prostrate. *Stems* greyish brown, cork roughly fissured, grey-brown, with yellowish brown scabs often surrounding leaf scars; indumentum at growing point yellowish and villous, tomentose between leaf bases, flaking off with cork on older branchlets, becoming glabrous; leaf-bearing branchlets shortened, nodes closely arranged, internodes very short. *Leaves* spreading at an angle of 45°, plane shape linear-lanceolate, length × depth 4.0 × 2.5 mm; leaf base sessile, dilated, rhombic, exactly fitting between other leaf bases at alternate nodes; adaxial surface concave, setose, abaxial surface convex, tomentose in young leaves; apex rounded; margins ciliate. *Inflorescence* axes villous with yellowish hair. *Bracts* ovate to widely ovate in outline, length × depth (4.5–)4.9 × 1.5(–1.8) mm; lamina adaxially concave (inside), abaxially convex (outside), comose on inside, sparsely hairy to tomentose on outside, ± 3-ribbed on each side of main vein, coriaceous and rugose, extending into a membranous rim; base cuneate; main vein extending into a rounded or subacute apex, or the second form with a more rounded apex (resembling *P. montana*); margins ciliate. *Floral envelope* ± 5.9 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* glabrous at ovary, neck tomentose, ± 1.4 mm long. *Sepals*: outer sepals concave, ovate, apex abaxially setose; inner sepals obovate, adaxially tomentose in upper third, apex abaxially setose. *Androecium* with filaments of antipetalous whorl ± 1.1 mm and those of antisepalous whorl ± 2.2 mm long; anthers 0.7 × 0.2 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 1.6 × 1.0 mm. *Fruit* an achene, with pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in the sepals and androecium being shed. Figure 7.4A–F.

### Diagnostic characters and relationships

Both *Passerina quadrifaria* and *P. comosa* have bracts that are abaxially hairy, hence they are easily confused. Morphologically *P. comosa* is less robust, internodes are longer, leaves adhere closely to the stem and are generally more hairy and the bracts often have extended wings that are abaxially setose. These two species are geographically isolated, with *P. comosa* considered as a 'north-western endemic' of the Cape flora (Weimarck 1941), while the distribution of *P. quadrifaria* is along the mountain ranges of the southern Cape and western parts of the Eastern Cape Province.

All the specimens characterized by abaxially hairy bracts and occurring in mountainous areas of the Little Karoo and southern Cape showed considerable variation. In the present study all these specimens were grouped under *P. quadrifaria*, but two forms could be recognized within this species. The first form corresponds to the present species description. *Schlechter 5864*, *Keet 1067* and *Esterhuysen 10734*, *27971* and *27383* represent the second form, characterized by slightly longer internodes, smaller leaves and bracts with a more rounded apex (resembling *P. montana*). None of these characters are constant and many specimens represent intermediates between the two forms. Leaf anatomy does not provide additional characters to justify the recognition of these two forms at species level (Bredenkamp & Van Wyk 2000, 2001a).

*Passerina quadrifaria* could also be confused with stunted forms of *P. obtusifolia*, a species occurring in dryer areas of the Eastern Cape. The leaves of these plants also have a four-ranked appearance, but the shape and especially the obtuse apex of the leaves and the bracts clearly identify *P. obtusifolia*.

### Etymology

The specific epithet is derived from the Latin *quadrifarius* (= in four ranks). The name describes the decussate arrangement of the leaves, which almost gives the impression of a spinal column found in lower vertebrates.

### Distribution and ecology

*Passerina quadrifaria* is distributed in a belt between 33° and 34°S latitude and from 20° to 24°E longitude, on the mountain ranges of the southern and eastern parts of the Western Cape and the southern and western parts of the Eastern Cape, including the Langeberg, Swartberg, Kouga, Outeniqua, Tsitsikamma and Great Winterhoek Mountains. The range includes the Karoo Mountain, Langeberg and Southeastern Centres within the CFR. Plants grow at high altitudes (1 500–1 670 m), in rocky places, often on southeast-facing rocky slopes and the summits of peaks. According to Rebelo (1998) summer drought has a major influence on the vegetation of the Mountain Fynbos, possibly contributing to the xeromorphic appearance of *P. quadrifaria*, such as its shortened branchlets and internodes as well as sturdy, decussate and coriaceous leaves. On the northern side of the Swartberg Mountains, fynbos is replaced by karroid vegetation and it is in these areas that *P. quadrifaria* can easily be confused with *P. obtusifolia*, a species largely confined to more arid karoo conditions. Figure 7.4H.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3320 (Montagu): Heidelberg, Lemoenshoek Peak, SE slopes of Langeberg, 1500-1670 m, (–DD), *Esterhuysen 30876* (BOL). 3321 (Ladismith): Swartberg Mountains, Prince Albert side, (–AC), *Stokoe s.n.* in *SAM 59493* (NBG); Towerkop, SE aspect of Swartberg Mountains, (–BC), *Esterhuysen 26710*, (–BOL); Swartberg Pass, Prince Albert Division, (–BD), *Barnard s.n.* in *SAM 48187* (NBG); *Stokoe s.n.* in *SAM 51426* (NBG); Oudtshoorn Div. Swartberg Mountains, (–BD), *Stokoe s.n.* in *SAM 58589* (NBG). 3322 (Oudtshoorn) Prince Albert District, Swartberg summits, (–AC), *Pocock S.48* (PRE); *Stokoe 8676*, *8678*, *9302* (BOL, PRE); George District, Montagu Pass, (–CD), *Schlechter 5846* (BOL, G, GRA, M, PRE, TCD); Uniondale, summit of Mannetjiesberg at radio mast (DB), *Bredenkamp1550–1553* (PRE). 3323 (Willowmore): Knysna Division, Gouna, Hoogeberg, (–CC), *Keet 1067* (GRA, PRE).

EASTERN CAPE.—3323 (Willowmore): Uniondale Division, Smutsberg, (–DA), *Esterhuysen 10734* (BOL, K, NBG, PRE); Kouga Mountains, Saptoukop from Withoek, (–DA), *Esterhuysen 27971* (BOL); *Oliver 9927* (NBG); Uniondale Division, Peak Formosa, Tsitsikamma Mountains, (–DC), *Esterhuysen 27383* (BOL). 3324 (Steytlerville): Uitenhage Division, Great Winterhoek Mountains, Cockscomb, (–BD), *Esterhuysen 28006* (BOL, K, PRE); E peak of Kareedouw Pass 833 m, (–CD), *Fourcade 4889* (BOL).

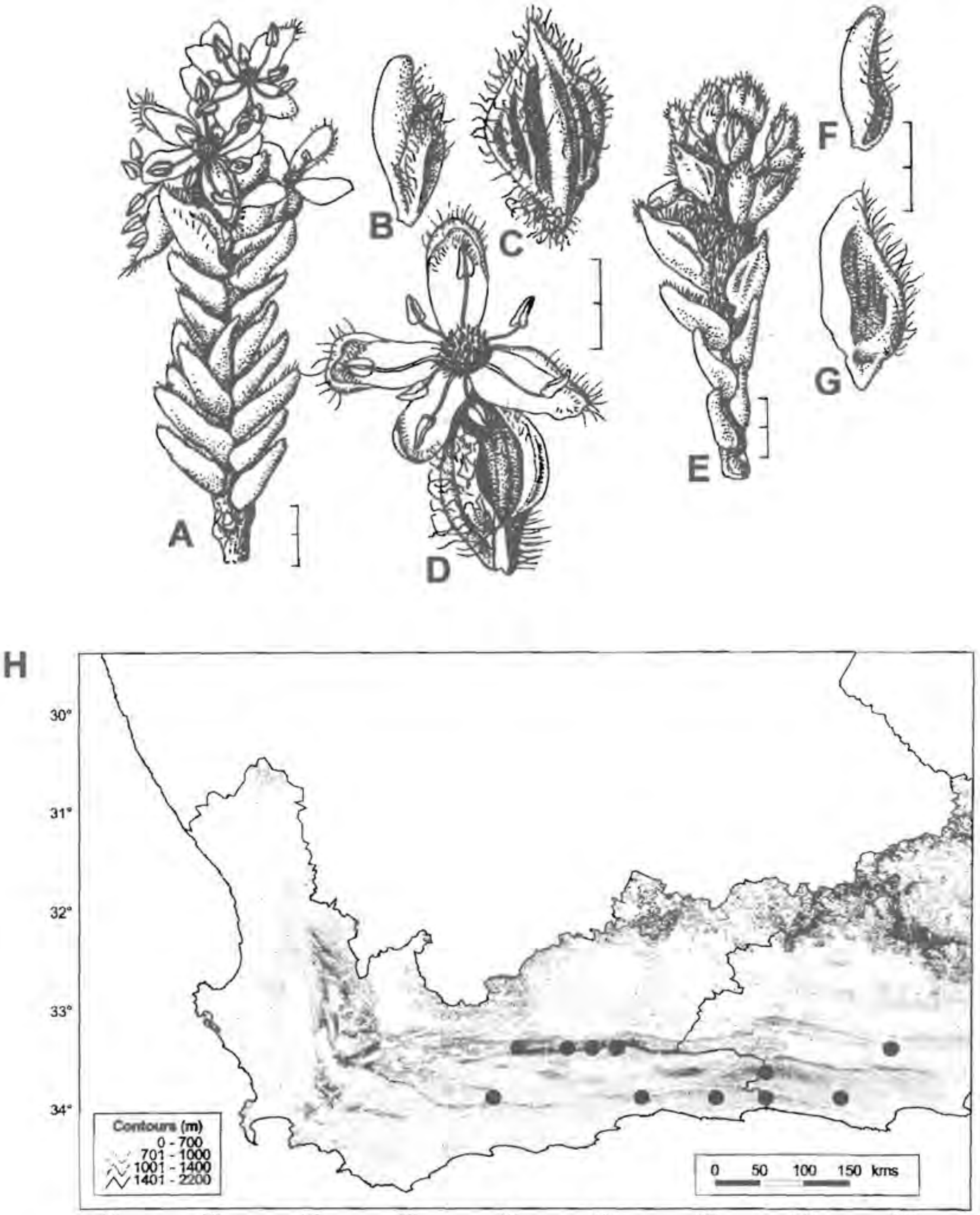

FIGURE 7.4.—*Passerina quadrifaria*, A–D form 1 (*Esterhuysen 28006*). A, spike reduced, resembling terminal subcapitulate inflorescence; B, leaf; C, bract; D, Flower clasped by bract. E–G form 2 (*Esterhuysen 10734*). E, inflorescence; F, leaf: G, bract. Scale bars: 2 mm.

H, known distribution of *P. quadrifaria*.

4. **Passerina montana** Thoday. Bulletin of Miscellaneous Information. Kew 4: 152 (1924a); Norl. & Weim.: 630 (1958); Bond & Goldblatt: 432 (1984); Hilliard & B.L.Burtt: 182 (1987). Type: Mooi River, *Wood 4036* [K!, lecto., designated by Thoday 10: 387 (1924b); BOL!, GRA!, PRE!].

*Passerina ericoides* sensu Meisn.: 401 (1840) pro parte, non L.; Meisn. 14: 562 (1857) pro parte; C.H.Wright: 12 (1915), pro parte.

*Passerina rigida* Wikstr. var. *tetragona* Meisn. 14: 563 (1857) pro parte quoad specim, circa Stormberg *Drège s.n.*

Small trees or shrubs (0.2–)1.0–2.0(–2.5) m high. *Stems* branching from base to up to growing points, young stems profusely branched, young branchlets ascending; branchlets terminally leafless and woolly, with conspicuous terminal scars after dispersal of fruit; bark greyish brown, younger branchlets densely white-tomentose, villous closer to growing points; bark on older branchlets shredding, greyish brown, remains of tomentum forming lengthwise strips; leaf scars conspicuous; older stems fissured lengthwise exposing greyish white sclerenchyma fibres; internodes mostly shorter than leaves. *Leaves* imbricate on young branchlets, closely appressed to stem, diverging at an angle of ± 0–5°, cymbiform, lamina inversely ericoid, adaxial surface concave, tomentose, abaxial surface laterally compressed and glabrous, plane shape linear to lanceolate; base sessile, dilated; apex acute, median vein prominent in upper third of leaf, incurved at apex; margins involute; length × depth 1.5–2.5(–4.0) × 0.6–0.8 mm. *Inflorescences* subcapitulate, ± ellipsoid. *Bracts* decussate, imbricate, sessile, appressed, ovate to obovate in outline; lamina adaxially (inside) concave and villous, abaxially (outside) convex and glabrous, thinly coriaceous, obscurely ribbed, yellowish green, margins of fruiting bracts turning red; base sessile; main vein extending into subacute apex; wings membranous, brownish; length × depth (3.2–)4.0 × 0.9(–1.6 mm). *Floral envelope* papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brownish; ± 5.8 mm long. *Hypanthium* glabrous at ovary, neck tomentose and ± 0.8 mm long, fragmentation at neck base. *Sepals*: outer sepals cymbiform, adaxially scantilly tomentose, abaxially glabrous; inner sepals obovate, adaxially tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 0.6 mm and those of antisepalous whorl ± 1.5 mm long; anthers 0.8 × 0.4 mm. *Ovary* 2.1 × 0.6 mm. *Fruit* an achene enveloped in beak-like, reddish, papyraceous hypanthium, fragmented at neck base; pericarp membranous and dry, 2.3 × 1.2 mm. Figure 7.5A–F.

### Nomenclatural notes

According to the concept of C.H. Wright (1915), *P. ericoides* is not only distributed along the southern coast of the Western Cape (present interpretation), but also along the coast to the Eastern Cape and further inland up to the present province Mpumalanga. However, most of the inland specimens cited by him have been classified as *P. montana* by Thoday (1924a). The interpretation of *P. corymbosa* by Wright (1915) posed the same problem, as *Wood 4036* (the lectotype of *P. montana*) was also placed in this taxon.

Meisner (1857) described *P. rigida* var. *tetragona* citing two Drège specimens, one from Ezelsbank and the other from Stormberg. The Ezelsbank specimen (*Drège 2971*, P, K) is *P. truncata*, but the Stormberg specimen could not be located. According to Gunn & Codd (1981), Drège crossed the Stormberg (3126BC, Queenstown) on 17 December 1832. The present author suspected that the Drège specimen would be *P. montana*, as it is common in this area. This suspicion is supported by *Sim 68* (from the Pirie Mountains in the King William's Town District), a syntype of *P. montana*, bearing the inscription '*P. rigida* Wiks – *tetragona*' and the Drège specimen from Stormberg is consequently regarded as *P. montana*.

### Diagnostic characters and relationships

Hilliard & Burtt (1988) noted two rather distinct forms of *P. montana* in KwaZulu-Natal. The first form is characterized by plants on rock platforms that are low, rounded bushes, 0.3–1.0 m high, with the tips of the branches erect, while those of the second form inhabit valleys and are riverside bushes of up to 2 m high, with open branches and pendulous branchlets. The present study, taking the whole distribution range of *P. montana* into consideration, recognises two forms. One, centred in the God's Window area of Mpumalanga, are rounded shrubs 0.5–2 m high, with many branchlets covered with smaller, decussate, imbricate leaves, bluish green in colour. The second form dominates in the Free State, Lesotho, KwaZulu-Natal and the Eastern Cape. These plants are more robust, with open branches and larger, yellowish green leaves and inflorescences, which are tinged pink. However, the two forms are not geographically distinct and intermediates are common. Both forms unequivocally show the specific characters and therefore we do not propose to give them formal taxonomic recognition. The leaf epidermal, anatomical and floral morphological studies (Bredenkamp & Van Wyk 2000, 2001a, 2001b) supplied no further evidence on which the two forms could be delineated.

### Etymology

The specific epithet is derived from the Latin *montanus* (= pertaining to or growing on mountains). This is a very appropriate epithet as *P. montana* is distributed along the Great Escarpment from the Eastern Cape to Zimbabwe.

### Common names

*Cooper 2302* (K), from Lesotho, reported the vernacular name *Likhabei* and *Staples 17* (PRE), from the Maluti Mountains in Lesotho, recorded the name *Lekaphu*. Story (1952) mentions the name *pakaan*. Von Breitenbach *et al*. (2001) used the names *berg-gonna* and 'mountain gonna'.

### Uses

Information on the specimen *Watt & Breyer-Brandwijk 1851*, collected at Thabaneng, states that the plants are used medicinally. However, Watt & Breyer-Brandwijk (1962) supplied no further details.

## Distribution and ecology

*Passerina montana* is a near-endemic to the Great Escarpment of southern Africa, with distant satellite populations in high-mountain areas of Angola, Namibia and the Northern Province of South Africa. It is distributed from Nyanga in Zimbabwe, along the escarpment to Manica and Sofala in Mozambique, the Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal, the Free State, Lesotho and the Eastern Cape. Outliers in Angola have been found on the escarpment of the Huilla Plateau near Lubango and the Cheila Mountains. Several specimens of this species have been collected at Moltkeblick on the Auas Mountains in Namibia. In the Northern Province *P. montana* is found in the Soutpansberg area and on the Blouberg, as well as on the summit of Krantzberg in the Waterberg Mountains. A single specimen (*Goossens 375*) was collected in the Pretoria District, but the species is currently probably extinct in this area, due to human impact. Figure 7.5G.

This species grows at altitudes of (900–)1 200–3 000 m. At Nyanga, *P. montana* is associated with *Erica mannii* (Hook.f.) Beentje and *E. hexandra* (S. Moore) Oliv., bordering on *Brachystegia* woodland and montane forest. In Mozambique and South Africa it has been found with *Widdringtonia nodiflora* (L.) Powrie and *Erica* species, bordering on montane forest. It is common amongst rocks on hills, mountain slopes, mountain tops, cliff ledges and rocky ridges. It also frequents stream courses and banks as well as river beds and banks, where the growth form has been reported as a shrub amongst rocks, a drooping bush over running water, a limply spreading bush in sand or dense bushes. These plants also grow in river valley forests and along plantations.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

ANGOLA.—1413: Lubango, Tundavala, ± 12 km from the cascades, (–CD), *Borges 112* (M, PRE); escarpment of the Cheila Mountains, *Mendes 866* (BM); Buraco do Bimbe, 220 m, *Mendes 3803* (K, M). 1513: Tundavala, in the proximity of the cascades, Mapunda River, (–BA), *Barbosa 9447* (K); Cheila Mountains, 10mi. W of Sa da Bandeira, *Kers 3240* (S).

ZIMBABWE.—1832 (Nyanga): Rhodes, Nyanga Estate, (–BA), *Brain 6950* (MO, PRE); *Chase 592* (BM, PRE); Nyanga, Chapungu Falls, *Dahlgren & Peterson 1661* (B, K); *Davies 48954* (PRE); *Eyles 8527* (K, S); *Eyles Herbarium 7945* (BM); *Fries, 2248, 2496* (K, MO); at Kuhera River, *Fries, Nordlindh & Weimarck 3077* (M); *Gilliland 2025* (BM); Nyanga, Pungwe Hills, *Hopkins s.n.* (K); Nyangani Mountains, *Hopkins B1580, 17165* (K, PRE); *Henkel s.n.* (K); *Humbert 15801* (NBG); *Le Munch 387* (K); *Linder 3980* (BOL, K, PRE); above Pungwe Falls, *Miller 3815, 3847* (K, PRE); Erin, *Miller 4644* (K, PRE); Nyanga Downs, *Rattray 909* (K); Troutbeck, *Robinson 1873* (K, MO); *Simon 657* (K, PRE); *Wild 1352* (K, PRE); Nyumkombe Forest, (–DA), *Gilliland 881* (BM); Nyumkombe Valley, *Gilliland 904 & 905* (BM, K); Odzani River, *Gilliland 1183* (BM); Manica, Umtali, Odzani River Valley, (–DC), *Teague 312* (BOL, K). 1932 (Melsetter): W slopes Mt Peni, Mermaid's Grotto Farm, (–DD), *Goldsmith 15/73* (K, MO, PRE).

MOZAMBIQUE.—Grid ref. unknown: Manica E Sofala, *Pedro & Pedragao 8095* (BOL, PRE); Manica Serra Zuira, 2 k da vacaria estrada Vila Perz, *Torre & Perreira 12683* (C).

NAMIBIA.—2217 (Windhoek): Ausberge, Moltkeblick, (–CA), *Giess 9014, 9429, 13136* (M, PRE); *Homan s.n.* (M); *Meyer 106, 9429* (M); *Rennie 2613* (BOL).

NORTHERN PROVINCE.—2229 (Waterpoort): Soutpansberg, Rushton, (–DD), *Raal & Raal 296* (PRE). 2230 (Messina): Venda, Dzambe Village, SE of Nwanedi Game Park, (–CB), *Hardy 6894* (PRE); Ngulumbi, Phiphidi Waterfall N bank of Nutshindudi, (–CD), *Glen & Glen 3911* (PRE); Sibasa District, Tate Vondo Forest Reserve, Tshirorha River Valley, *Hemm 1* (PRE); Phiphiti Waterfall, *Obermeyer TRV 30044* (PRE); Tate Vondo, Nzhelele River, *Van Wyk 2899* (PRE, PRU). 2328 (Baltimore): Blouberg, near Malabosch's Kraal, (–BB), *Van der Schijff 5376* (PRE). 2329 (Pietersburg): Blouberg Kloof, (–AA), *Codd 8772* (PRE); *Smuts & Pole-Evans 933* (BOL, K); Louis Trichardt, Hangklip, (–BB), *Bremekamp & Schweickerdt 417* (PRE); *Schlieben s.n.* (M); 40 mi. E of Haenertsburg, Iron Crown Mountains, (–DD), *Mogg 17383* (PRE). 2330 (Tzaneen): Entabeni Forest Reserve, (–AB), *Codd & Dyer 4473* (PRE); Tshakoma, *Obermeyer 1078* (PRE); Sebasa, *Smuts & Gillett 3179* (NBG); Woodbush Forest Reserve, (–CC), *Van Vuuren* 1632 (PRE); Letaba District, Cyprus Farm, *Renny 179* (PRE); Zoutpansberg District, Pepiti Falls, *Smuts & Gillett 3179* (PRE), Soutpansberg District, hill S of Berlin Mission, *Curson & Irvine 91* (PRE). 2427 (Thabazimbi): Waterberg, Bergfontein Farm, (–BC), *Jacobsen 3468* (PRE); Krantzberg; Groothoek Farm, *Westfall 716* (PRE); Marikele Nature Reserve, on top of Krantzberg, Bergfontein, (–CB), *Bredenkamp 1026* (PRE); Groothoek Farm, SE kloof, (–DA), *Westfall 756* (PRE). 2430 (Pilgrim's Rest): Platberg, The Downs, (–AA), *Rogers 21919* (PRE); Ararat Mountain, *Venter 7123* (PRE); Wolkberg Wilderness Forest Reserve, *Venter 11013* (PRE); Leboyana Peak area, Thabakgolo, (–AD), *Matthews & Van Rensburg 1036* (PRE).

GAUTENG.—2528 (Pretoria): Pretoria District, (–CA), *Goossens 375* (PRE).

MPUMALANGA.—2430 (Pilgrim's Rest): Ohrigstad Dam Nature Reserve, (–CC), *Jacobsen 1340* (PRE); Mariepskop, (–DB), *Keet s.n.* (NBG); *Killick & Strey 2386* (M, PRE); *Krynauw 789* (PRE); *Meeuse 9965* (PRE), 2 000–5 000 m, *Merxmüller 591* (M); *Van der Schijff 4478, 4836, 5592, 5845 & 6191* (K, PRE); *Venter 12721* (PRE); Mt Sheba Estate, (–DC), *Boucher 1862a & 1862b* (NBG); Ohrigstad Dam Nature Reserve, *Edwards 4058* (K, PRE); Mt Sheba Nature Reserve, *Forrester & Gooyer 203* (PRE); *Kerfoot 8102* (PRE); Ohrigstad Dam Nature Reserve, *Mauve 5246* (PRE); *Smit 22* (PRE); from World's View to God's Window, (–DD), *Bredenkamp 1022, 1023, 1024 & 1025* (PRE); 6.5 mi. from Pilgrim's Rest to God's Window, *Davidson & Mogg 32909* (PRE); Chum Falls to Belvedere, *Davidson & Mogg 32881* (UPS); Lisbon falls, *Davidson & Mogg 32859* (UPS); Vaalhoek, Erasmuskop, near grave of Oswald, *Perold & Fourie 2256* (PRE); Graskop Spruit, *Galpin 14573, 14578, & s.n.* (BOL, PRE); Lisbon Falls, *Jordaan 97* (PRE); Mac Mac Nature Reserve, *Kluge 1995* (PRE); God's Window, *Lambinon & Reekmans 82/157* (PRE); Kowyn's Pass, *Levyns 9409* (BOL); Lisbon falls, *Louw 2373* (NBG); 3 km from God's Window, *Meyer 1061* (PRE); Mac Mac, *Mudd s.n.* (K); Graskop, *Pole-Evans 129* (PRE); Graskop, top of gorge, *Prosser 2050* (PRE); Kowyn's Pass, *Rauh & Schlieben 9788* (M, PRE); *Rechinger A-4413* (M). 2530 (Lydenburg): Zwagershoek Farm, (–AB), *Obermeyer 258* (PRE); Hartebeestvlakte, *Kluge 2044* (PRE); 6 mi. NE of Dullstroom, (–AC), *Codd & De Winter 3237* (PRE); Santa 7.3 mi. from Dullstroom, (–AC), *Story 3896* (GRA, PRE); Schoemans Kloof, Somerset Farm, (–AD), *Smuts & Gillett 2162* (BOL, NBG, PRE); Long Tom Pass, (–BA), *Balsinhas & Kersberg 2114* (PRE); Mt Anderson, *Smuts & Gillett 2469* (PRE); 12 mi. from Lydenburg on Sabie road, *Story 3899 & 3900* (PRE); 7,6 km between Sabie and Hazyview, (–BB), *Deall 34* (PRE); Mac Mac Pools, *Hilliard & Burtt 18443* (PRE, S); Mt Anderson, *Humbert 11018* (NBG); Sabie, *Rogers 23675* (PRE); Wonderkloof Nature Reserve, (–BC), *Elan-Puttick 146* (PRE); Buffelskloof Nature Reserve, *Onderstall 919* (PRE); Lowveld Botanical Garden, (–BD), *Buitendag 104* (NBG, PRE); Witklip State Forest, *Kluge 797* (PRE); Pilgrim's Rest District, Rosehaugh, *Smuts 91* (PRE); Kaapsche Hoop, (–DB), *Nel 219* (PRE); *Onderstall 1269* (PRE); *Pole-Evans 986* (PRE); *Van der Merwe s.n.* (K, PRE); Crocodile River, *Pons s.n.* (PRE). 2531 (Komatipoort): Barberton District, Duivelskantoor, (–CB), *Thode 1639* (PRE).

SWAZILAND.—2631 (Mbabane): Helolotsha Valley, (–AA), *Kemp 1184* (MO, PRE); *Moss & Rogers 1263* (BM).

KWAZULU-NATAL.—2729 (Volksrus): W Slopes of Majuba Hill, (–BD), *Phillips 228* (PRE). 2730 (Vryheid): Utrecht District, Naauwhoek, (–AD), *Devenish 712* (BM, K, M, NBG, PRE); Great Winterhoek Mountains, (–CB), *Thode A292* (K, MO, PRE). 2731 (Louwsburg): Hlobane, (–CD), *Johnstone 543* (MO, PRE, S). 2828 (Bethlehem): Bergville District, Royal Natal National Park, Dooley Mountain, (–DB), *Galpin 10146* (PRE); Mont Aux Sources, (–DD), *Hutchinson, Forbes & Verdoorn 75* (PRE); in Tugela Gorge, *Schweickerdt 759* (PRE). 2829 (Harrismith): Van Reenen 5 000 ft, (–AD), *Wood 6601 & 11405* (BM, K); Klipriver, (–BC), *Sutherland s.n.* (K); Cathedral Peak area, (–CC), *Levyns 8274* (BOL); Little Tugela District, (–DC), *Hoffenthal 3464* (K); Klip River, *Curator Pretoria Botanical Garden s.n.* (PRE); *Stam 429* (PRE). 2830 (Dundee): Nkandla

District, 0.75 mi. W of Qudeni Beacon 88, (–DB), *Edwards 2239* (K, PRE). 2929 (Underberg): Bergville District, Champagne Castle, (–AB), *Edwards 1991* (PRE); Estcourt District, Giant's Castle Reserve, *Edwards 2276* (K, PRE); Bergville District, *Franks s.n.* (PRE); Cathedral Peak Forest, *Killick 1071 & 1585* (PRE); Champagne Castle, *Meebold 15158* (M); on slopes of Giant's Castle, *Symons 144* (PRE); Giant's Hut area, (–AD), *Ward 6944 & 6954* (PRE); Estcourt District, Stillerust Farm, *Wright 1029* (PRE); Estcourt pasture reserve, banks of Bushmans River, (–BA), *West 485* (PRE); Tabamhlope Mountain, *West 1392* (PRE); Estcourt District, Dalton Bridge, (–BB), *Acocks 10660* (PRE); Mooi River, *Wood s.n.* (NBG); Meteor Ridge, (–BC), *Mogg 3347 & 7083* (PRE); Mooi River, *Wood 4036* (BOL, K, GRA); Mpendle District, Mulangane Ridge, above Carter's Neck, *Hilliard & Burtt 16921* (M, PRE, S); Underberg District, Cobham Forest Reserve, Polola Valley, (–CB); *Hilliard & Burtt 13970 & 18071* (PRE); Sani Pass, (–DB), *Hilliard & Burtt 7139* (MO, S); Himeville, (–DC), *Marloth 11873* (PRE). 2930 (Pietermaritzburg): Mooi River, (–AA), *Wood 4036 & s.n.* (K); Dargle District, The Chestnuts Farm, (–AC), *Letty 269* (PRE); Howick District, Furth Farm, 40 km SW of Howick, *Curator Bloemfontein Museum 4* (PRE); district of Albert, (–AD), *Cooper 625* (BM, BOL, K, TCD); Umgeni Falls, (–CA), *Bayer 786* (PRE); Dargle Forest, *Moll 1228* (K, PRE). 2931 (Stanger): Mvoti River mouth, (–BA), *Moll 2466* (K). Grid ref. unknown: Drakensberg National Park, Tugela Gorge, *Acocks 1005* (S); Drakensberg summit, *Galpin 6825* (K); *Hilliard & Burtt 11726 & 13511* (K, S); Impendle District, Tilhitudlein Farm, *Huntley 125* (PRE); Natal 4 000-5 000ft, *Sutherland 185B* (TCD); Klip Rivier, *Sutherland s.n.* TCD; Movelo Hills, *Sutherland s.n.* (K).

FREE STATE.—2827 (Senekal): Korannaberg (CC), *Zietsman & Zietsman 427 & 512* (PRE); Clocolan, Hursley, (–C), *Stam 43* (PRE); Ficksburg District, Farm Westbury, (–DD), *Galpin, 14018 & s.n.* (BOL, PRE, S). 2828 (Bethlehem): Slabberts, Help Mij Plaas, (–AC), *Stam 174* (PRE); Mr Naude's farm, (–AD), *Theron 2182* (PRE); Golden Gate Highland, NW of Glen Reenen House, (–BC), *Liebenberg 7299* (PRE); Meltsetter Summit, *Roberts 3359* (PRE); Kestell, 'Korfshoek', (–BD), *Blom 275* (PRE); Ficksburg, Franschhoek, (–CA), *Ferreira 5* (PRE); Mt Morkel, *Repton 6253* (PRE); Fouriesburg District, Nelspoort Farm, E of Wittebergen, *Lutjeharms 6818* (PRE); Dunblane 335 Farm, W of Clarens, W flank of Mt Spur, (–CB), *Scheepers 1831* (MO, PRE); Golden Gate, Zuluhoek, bottom of valley, (–DA), *Bredenkamp 889* (PRE); summit of Mt Meltsetter, *Bredenkamp 890 & 891* (PRE); Brandwag Rock, Gertenbach & Groenewald 9104 (PRE); Golden Gate National Park, *Liebenberg 7299* (K, NBG); Witsieshoek, (–DB), *Junod TRV 17326* (PRE); *Thode s.n.* (NBG); Witsieshoek, (–DB), *Van der Zeyde s.n.* (MO, S). 2829 (Harrismith): Manyenyeza Mountain, Rensburgkop Farm, (–AC), *Jacobsz 664* (PRE); Kerkenberg, *Jacobsz 1379 & 1482* (PRE); Platberg Botanical Garden area, *Jacobsz 2603* (NBG, PRE); Platberg slopes, *Putterill s.n.* (PRE); *Sankey 69* (K, MO); *Van der Zeyde s.n.* (NBG); Van Reenen, *Wood 12179* (NBG); Kerkenberg, (–CA), *Jacobsz 313* (PRE). 2926 (Bloemfontein): Thaba Nchu, (–BB), *Mostert 1185* (PRE); *Peeters, Gericke & Burelli 387 & 407* (MO, PRE); *Roberts 1953 & 1954* (PRE). 2927 (Maseru): Ladybrand, on top of mountain, (–AB), *Bredenkamp 893 & 894* (PRE); *Rogers 788* (PRE); Leliehoek, *Zietsman 323* (PRE). 3027 (Lady Grey): Zastron District, mountain summit, (–AC), *Heydoorn 10* (PRE); Trans-Garipina, Kornetspruit, Gariep & Caledon Rivers, foot of Wittebergen, (–AD), *Zeyher 117.11* (S); between Drakensberg and Wittebergen, *Mellersh 617* (TCD).

LESOTHO.—2828 (Bethlehem): Leribe, mountain slopes, (–CC), *Dieterlen 49* (K, MO, NBG, PRE, S); Butha Buthe, from Motenge to Oxbow, *Hedberg & Hedberg* 82060 (UPS); Oxbow, Tsehlanyane, *Herbst 5269* (PRE); 2 mi. from Oxbow, kloof leading to Khatibe, *Lubke 274* (PRE, M); Ox Bow, (–DC), *Hebblethwaite s.n.* (GRA); Lekhapu, *Jacot-Guillarmod 3824* (GRA); 8 km from New Oxbow Inn road to Moteng Pass, Tsehlanyane River, *Killick 4485* (PRE). 2927 (Maseru): Maseru District, mountain road, (–AD), *Jacot-Guillarmod 3225* (K, PRE); Ha Khotso, (–BB), *Gormley & Barber 23* (PRE); Masoeling, *Jacot-Guillarmod 1546* (PRE); Blue Mountain Pass, (–BC), *Schmitz 8265* (PRE); Molimo-Nthuse, between Bushmen's and Blue Mountain Passes, (–BD), *De Kruif 1158* (PRE); between God Help Me Pass and Blue Mountain Pass, *Hilger 22* (M, PRE); Blue Mountain Pass, *Hilliard & Burtt 17703* (PRE, S); God Help Me Pass, *Killick 4225* (MO, PRE); Bushmans Pass, *Werdermann & Oberdieck 1560* (K); Thaba Morewa Mission, (–CD), *Dieterlen 1247* (NBG, PRE); Thabaneng, *Watt & Brandwijk 1851* (PRE); S of Roma, 3 km E of Quaba, (–DB), Hilger 83/8 (M, PRE); Roma, Hanging Valley, *Schmitz 56* (PRE); bridle path, hill slope, (–DB), *Jacot-Guillarmod 1792* (PRE). 2928 (Marakabei): Mamalapi, (–AC), *Jacot-Guillarmod 765 & 780* (PRE); Likolobeng, *Compton 21236* (NBG); Lehaha-La-Sekhonyana, (–AD), *Jacot-Guillarmod 230* (PRE). 2929 (Underberg): Sehlabathebe Nature Park, Matsa-A-Mafikeng area at cave, (–CC), *Beverly 72* PRE; Sesiu Valley, Sehlabathebe National Park, *Hoener 1635 & 1846* (MO, PRE, S); Bushmans Pass, *Werdermann & Oberdieck 1560* (B, K, PRE). 3028 (Matatiele): Ntibokho, Rafanyanes Valley, junction Lehaha-La-Sekhonyana, bridle path and cut-off to Bokong (-AB), *Jacot-Guillarmod 298* (PRE); upper Quthing, gorge after Makope's, (–AC), *Schmitz 8314* (PRE); Transkei/Lesotho border, Qachasnek, (–BA), *Jacot-Guillarmod 9842 & 9886* (GRA, PRE). Grid ref. unkown: experimental area Thaba Tsoeu, *Archibald 677* (GRA); Machoeka 9 000 ft, *Bryce s.n.* (K); Chalabisa, *Compton 21048* (NBG); Mequalleng, *Cooper 702* (BM, BOL, K, M, PRE, TCD); Orange Free State & Basutoland, *Cooper 842* (BOL, K); Basutuland, *Cooper 2302* (K); Maluti Mountain, *Staples 17* (PRE).

EASTERN CAPE.—3026 (Aliwal North): Elandshoek Farm 40 km S of Aliwal North, (–DC), *Dold 1617* (GRA); Elandshoek, *Story 2071* (MO, PRE). 3027 (Lady Grey): Witteberg, Jouberts Pass, (–BC), *Hilliard & Burtt 12213* (PRE, S); Wittebergen, Lady Grey, (–CA), *Barber 745* (GRA); Lady Grey District, *Gerstner 119 & s.n.* (PRE); Jouberts Pass, *Werger 1806* (MO, PRE); Jouberts Pass, (–CB), *Werger 1054* (PRE); Karringmelkspruit Gorge, (–CC), *Jacot-Guillarmod 7854* (GRA, PRE); Jouberts Pass, 2 km up from Glen Doon, (–CD), *Welman 798* (PRE); Moshesh's Ford, 21 mi. from Barkley East, (–DD), *Edwards 4187* (K, MO, PRE); along road S of Lundean's neck, 1 km S of Fetcani Glen Farm track, *Phillipson 624* (MO, UPS). 3028 (Matatiele): Ramatselanes Gate, escarpment, (–BB), *Bayliss 1349 & 1362* (PRE); Maclear District, Naude's Neck Pass, (–CA), *Acocks 12175* (PRE); *Dold 2053* (GRA); *Hilliard 5191* (MO, PRE); *Seutloali 94* (PRE); *Thomas s.n.* (GRA); *Werdermann & Oberdieck 1129* (K, PRE); Naude's Neck, between Maclear and Rhodes, (–CC), *Van Wyk 6704* (PRE, PRU). 3029 (Kokstad): Mt Fletcher District, Kokstad to Franklin Road, (–CB), *Hilliard & Burtt 7220* (PRE). 3030 (Port Shepstone): Port Shepstone, (–CB), *Burtt-Davy 2410* (BOL). 3126 (Queenstown): Majuba Neck, Sterkspruit, (–AA), *Hepburn 85* (GRA); Molteno, Broughton, (–AC), *Flanagan 1635 & 1892* (K, NBG, PRE, S); near Predikantskop, road to Burgersdorp, (–BA), *Edwards 4196* (K, PRE); Predikantskop, deviation from Jamestown Road, Farm Spitskop, *Bredenkamp 895* (PRE); Jamestown, Vogelfontein Farm, (–BB), *Compton 2241* (NBG); Andriesberg near Bailey, (–DA), *Galpin 2028* (K, PRE); near top of Hangklip Mountain, (–DD), Roberts *1973 & 2001* (PRE); Mt Shepstone, *Bayliss 1432* (PRE); Hangklip Mountain, *Roberts 1973* (PRE). 3127 (Lady Frere): Indwe, (–AD): *Sim 2595* (K); Transkei, Xalanga District, Cala commonage, (–BC), *Dold 840* (GRA); Enqcobo, (–DB), *Esterhuysen 29153* (BOL). 3128 (Umtata): Ugie, Pomona, (–AA), *Gill 240* (BOL). 3226 (Fort Beaufort): Tarka District, near Spring Valley P.O., (–AD), *Acocks 12125* (PRE); Stockenstroom, Katberg, (–BB), *Dyer 752* (GRA, K, PRE); Katberg, near the gorge, (–BC), *Dyer 753 & 754* (GRA, K, PRE); *Hutchinson 1624* (PRE, K); Amatole Mountains, Hogsback, Cathcart Road, near Klipplaat River crossing, (–BD), *Phillipson 1140* (K, PRE); Cathcart District, Fairford, *Catterell 41* (PRE); Farm Glencoe, *Palmer 1417* (GRA); Katberg, (–DA), *Hutchinson 1624* (BM); Keiskamma Hoek Dist, Amatola Range, top of range NW of Cata Forest Reserve, (–DB), *Story 3667* (PRE). 3227 (Stutterheim): Hogsback District, Stockenstroom, (–CA), *Compton s.n.* (NBG); Victoria East District, Hogsback, *Levyns 9553* (BOL); *Rattray s.n.* (PRE); Keiskammahoek District, Wolf-Mnyameni Watershed, *Story 3778* (GRA PRE); King William's Town District, mountains, (–CD), *Rattray 382* (BOL); Pirie Mountain, *Sim 68* (K PRE). 3326 (Grahamstown): Kenton-on-Sea, (–DA), *Botha 2610* (PRE). 3327 (East London): (–BB), *Sim 1471* (K). Grid ref. unknown: *Dunne s.n.* (BM); Drakensberg, Barkley East District, summit Doodmans Krans Mountain, *Galpin 6825* (PRE); Victoria East Hogsback, *Giffen s.n.* GRA; Bushmans River Pass, *Thode s.n.* (NBG); *Wager TRV 10772* (PRE).

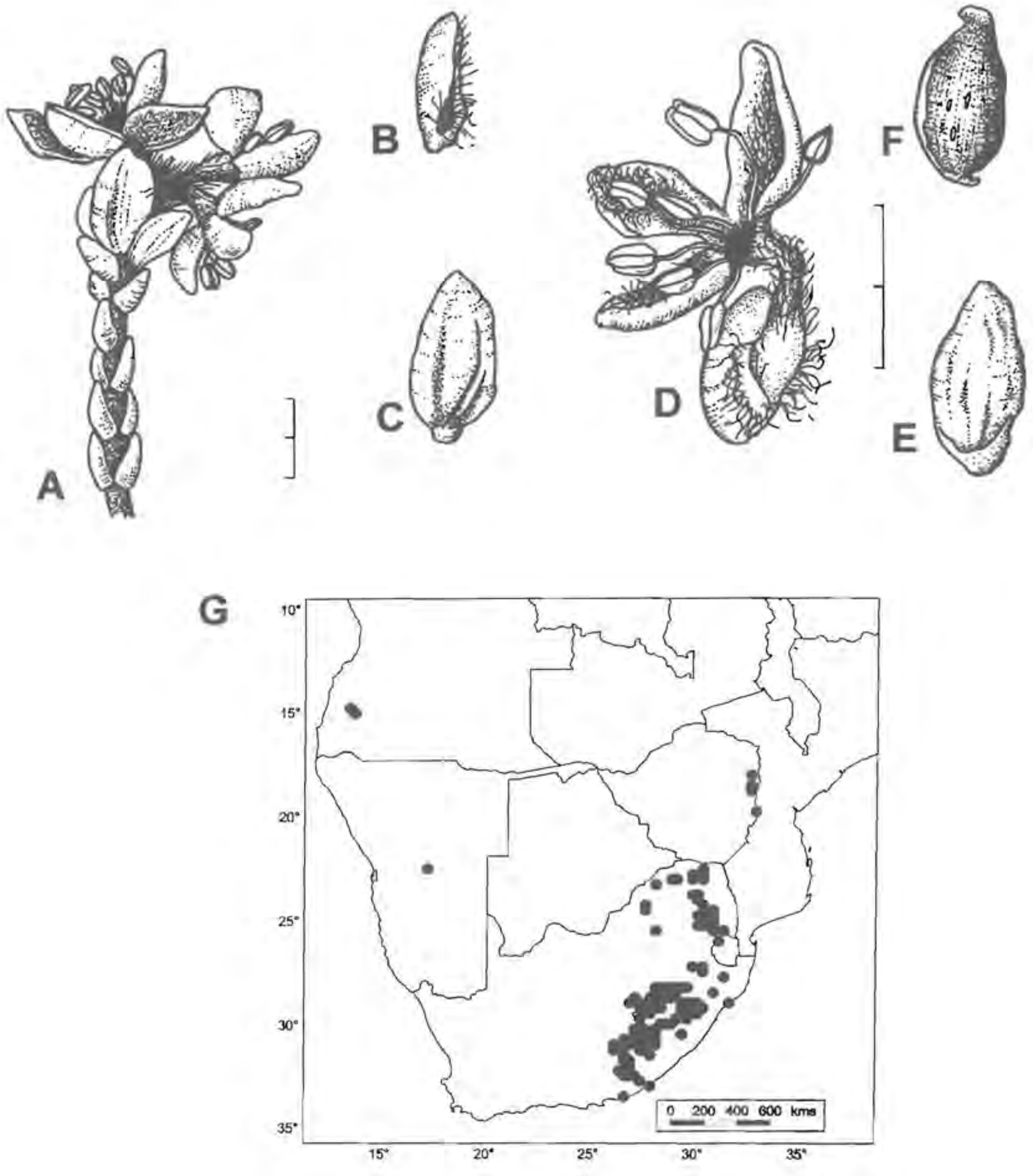

FIGURE 7.5.—*Passerina montana* (*Bredenkamp 893*). A, spike reduced, resembling terminal subcapitulate inflorescence; B, leaf; C, bract; D, flower clasped by bract; E, achene, enveloped by membranous pericarp; F. achene in lateral view. Scale bars: 2 mm.

G, known distribution of *Passerina montana*.

5. **Passerina burchellii** *Thoday*. Bulletin of Miscellaneous Information. Kew 4: 155 (1924a); Bond & Goldblatt: 432 (1984); Goldblatt & Manning: 683 (2000). Type: Western Cape, Caledon Division, mountain tops of Baviaanskloof near Genadendal, *Burchell 7761* [K, lecto.!, designated by Thoday 10: 387 (1924b); M!, P!].

*Passerina tetragona* Burchell MS. in Herb. Kew, non Steud. fide Thoday 4:156 (1924a).

Low, erect, many-stemmed shrublets, branching mostly on new growth, ± 0.3 m high, from a common rootstock. *Stems* greyish brown, cork fissured, grey-brown, scabrous, surrounding prominent leaf scars; indumentum at growing point densely white-tomentose, flaking off with cork on older branchlets, which become glabrous. *Leaves* imbricate, overlapping ± 50%, diverging at an angle of 30°, plane shape rhombic, length × depth 2.8(–3.5) × 1.5 mm, adaxial surface concave, villous, abaxial surface convex, glabrous; base sessile, cuneate; apex subacute, bearded; margins brownish setose. *Inflorescences* with spikes extended, number of spikes often reduced, spikes sometimes solitary, 6–12-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* appressed, rhombic, length × depth (3.2–)3.5 × 1.5 mm; lamina adaxially concave (inside), abaxially convex (outside), villous inside, glabrous outside, coriaceous and smooth, extending into a smooth wing, dark green when fresh, dark brown in dried specimens; base cuneate; main vein extending into acute, bearded apex; margins brownish setose, involute. *Floral envelope* ± 4.7 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* glabrous at ovary, neck tomentose, ± 0.8 mm long. *Sepals*: outer sepals cymbiform, midrib adaxially and apex abaxially setose; inner sepals obovate, adaxially tomentose, apex abaxially setose. *Androecium* with filaments of antipetalous whorl ± 0.7 mm and those of antisepalous whorl ± 1.5 mm long; anthers 0.5 × 0.3 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 1.6 × 0.6 mm. *Fruit* an achene, pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in sepals and androecium being shed. Figure 7.6A–D.

### Nomenclatural notes

Although Thoday (1924a) cited *P. rigida* var. *comosa* Meisn. partly (ex MS. in Herb. Kew) in synonymy under *P. burchellii*, the specimens cited by Meisner (1857) in the description of the var. *comosa* all belong to *P. pendula* (Eckl. & Zeyh.) Thoday.

### Diagnostic characters and relationships

Bearded sepals, leaves and bracts distinguish this species from *P. pendula*.

### Eponymy

This plant was named in honour of the explorer and botanist W.J. Burchell, who collected in Caledon and as far north as Tulbagh between 1810 and 1811. During this trip *Burchell 7761*, the lectotype of *P. burchellii*, was collected on the summit of the mountains of Baviaanskloof near Genadendal.

### Distribution and ecology

*Passerina burchellii* is endemic to the Southwestern and Langeberg Centres within the CFR. It is common on mountain summits of the Villiersdorp and Genadendal Districts, with outliers on southeastern rocky slopes of Towerkop in the Swartberg Mountains at Ladismith. This species occurs at altitudes of 1 333–2 167 m, often covered in mist. It is found in small groups on sandy loam, between boulders and rocks on upper south- or southeast-facing slopes. Figure 7.6E.

*Conservation status*: because of small population size, the conservation status is considered as Vulnerable (VU D2) (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3319 (Worcester): Blokkop, above Villiersdorp, (–CC), *Esterhuysen 35415* (BOL); Jonaskop, (-DC), *Bredenkamp 1545, 1546* (PRE); *Esterhuysen 36404* (BOL); *Stokoe s.n.* (NBG, PRE); *Stokoe 2800, 2802, 22329* (BOL, K, NBG, PRE). 3321 (Ladismith): Towerkop, (–CA), *Esterhuysen 26714* (BOL, K). 3419 (Caledon): Genadendal mountain summits, (–BA), *Bolus 687* (BM, BOL, HAL, K, NBG, P, PRE, UPS, W); mountain tops of Baviaanskloof, *Burchell 7761* (K, M); Robertson, Galgeberg, *Esterhuysen 34537* (BOL, K, S); Genadendal, Kanonkop, *Esterhuysen 35616* (BOL, K); top of Baviaanskloof, *Stokoe 2542, 3199* (PRE, K). Grid ref. unknown: Caledon, E of Villiersdorp "Silverstream", *Esterhuysen 33533a* (BOL M); *Niven Laubert s.n.* (S).

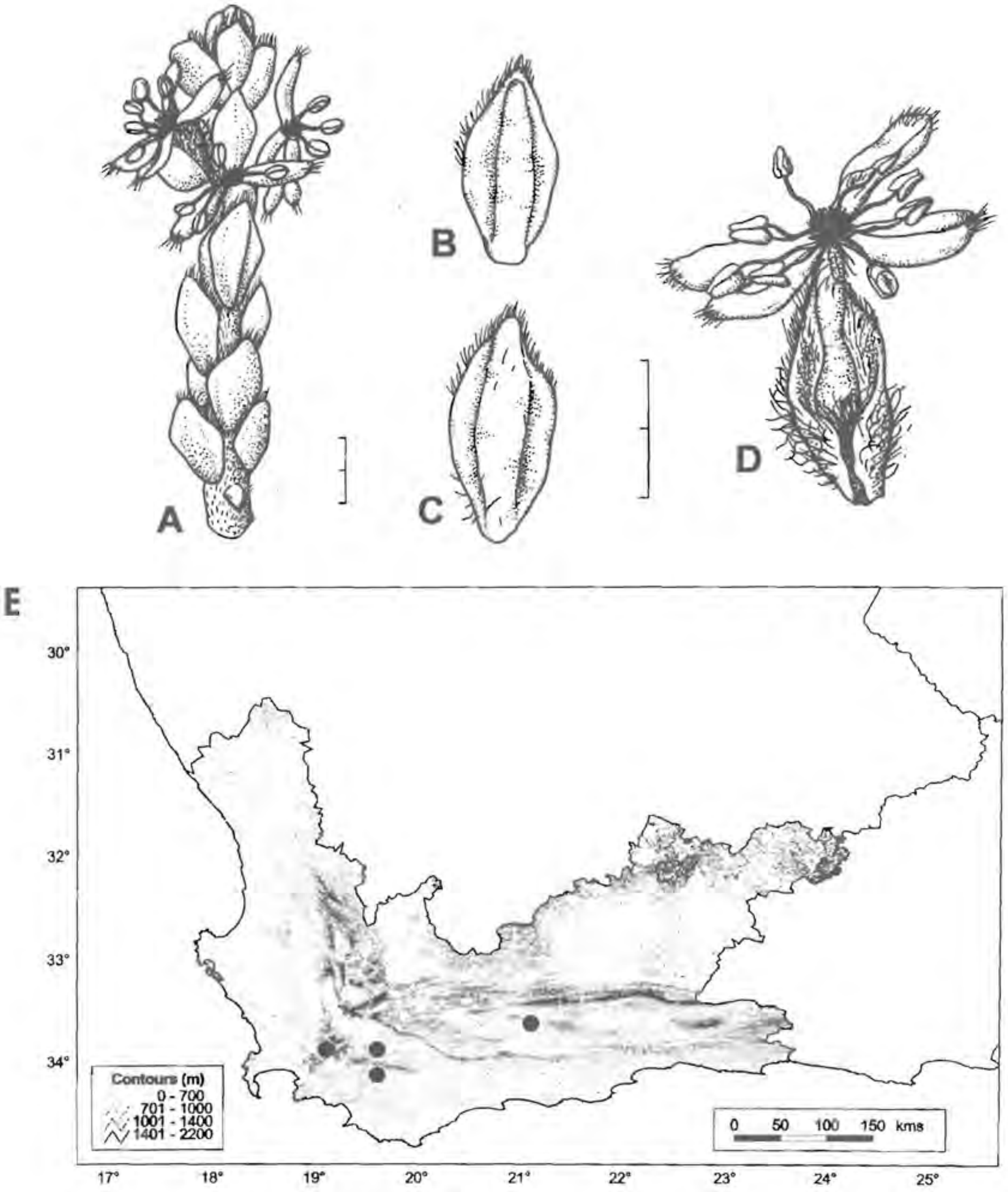

FIGURE 7.6.—*Passerina burchellii* (*H. Bolus 687*). A, flowering inflorescence; B, leaf; C, bract; D, flower clasped by bract. Scale bars: 2 mm.
E, known distribution of *Passerina burchellii*.

6. **Passerina ericoides** *L.* Systema naturae 12,2: 733 (1767); Burm.f.: 12 (1768); L.: 236 (1771); L.: 374 (1784); Willd.: 430 (1799); Poir.: 41 (1804); Wikstr. 39: 325 (1818); Meisn.: 401 (1840) pro parte minore; Steud.: 274 (1841); C.A.Mey.: 49 (1843); C.H.; Meisn. 14: 562 (1857) pro parte minore; Wright: 12 (1915) pro parte; Thoday 4:166 (1924a); Bond & Goldblatt: 432 (1984); Hilliard & B.L.Burtt: 182 (1987); Goldblatt & Manning: 683 (2000). Type: *Passerina ericoides, Linnean Herbarium 504.5* [LINN, lecto.!, designated by Thoday 4:148 (1924a)].

*Chymococca empetroides* Meisn. 14: 565 (1857); Harv.: 325 (1868); Bol. & Wolley-Dod: 315 (1904); C.H.Wright: 15 (1915); Thoday 4:166 (1924a). *Passerina filiformis* L. var. *crassifolia* Eckl. & Zeyh. fide Meisn. 14: 565 (1857). Type: *Eckl. & Zeyh. herb. no. 39* (G!, lecto., here designated; BOL!, MO!, P!, W!).

*Passerina glomerata* sensu Meisn. 14: 562 (1857), non Thunb.: 75 (1794); *Lachnaea conglomerata* L. sensu Meisn. 14: 562 (1857).

Low, rounded, many-stemmed shrublets, branching profusely on new growth, 0.3–1.2 m high, older branchlets indurate, young branchlets lax, often arcuate. *Stems* light greyish brown, cork fissured lengthwise, grey-brown, whitish scabrous, surrounding prominent leaf scars; indumentum at growing point densely white strigose, flaking off with cork on older branchlets, which become glabrous. *Leaves* slightly succulent, imbricate, overlapping ± 50%, diverging at an angle of 45°, plane shape oblong, length × depth 2.5–2.8 × 0.6–0.7 mm, adaxial surface concave, villous, abaxial surface convex, glabrous, greyish green, smooth; base sessile, dilated; apex obtuse to subacute; margins glabrous, basally sparsely setose. *Inflorescences* with spikes usually extended, 6–12-flowered, arrangement subterminal, axis white strigose, proliferating growth common. *Bracts* spreading at an angle of 60° (flowering) or 90° (fruiting), oblong to lanceolate, length × depth 3.6 × 1.5 mm; lamina adaxially concave (inside), abaxially convex (outside), villous inside, glabrous outside, smooth, wings absent, greyish green, slightly succulent; base dilated; apex obtuse to subacute; margins glabrous, basally sparsely setose, involute. *Floral envelope* ± 5.0 mm long, coriaceous and greenish during pollination, dehydrated after shedding of pollen, turning red. *Hypanthium* ovate-oblong at ovary, strigose, neck strigose, ± 0.6 mm long. *Sepals* globose when young, concave, widely obovate, outer and inner sepals adaxially puberulent, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 0.5 mm and those of antisepalous whorl ± 1.3 mm long; anthers large, 0.9 × 0.7 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.1 × 1.7 mm. *Fruit* a fleshy red berry, 5.3 × 4.0 mm, enveloped by persistent, loosely arranged hypanthium, fragmenting over widest circumference of fruit, the fragmented hypanthium, sepals and androecium being shed. *Seed* 2.9 × 1.6 mm. Figure 7.7A–G.

### Nomenclatural notes

In the *Catalogue of the Linnaean Herbarium*, Savage (1945) made the following inscription 'Tulb. list c. 1769. n.1. det. L.—*Blaeria ericoides*'. This refers to consignments of bulbs, seeds and herbarium specimens that Rijk Tulbagh sent to Van Royen, the Burmans at Amsterdam and Linnaeus at Upsala (Gunn & Codd 1981). Jackson (1917–1918) published a list of 203 of the specimens sent to Linnaeus around 1769 and identified by him. The first inscription on the list is the provisional name *Blaeria ericoides*, which Savage (1945) believed to be the *P. ericoides* specimen at LINN, but there is no numbering or any other indication on the specimen to link it with Tulbagh's list (Jackson 1917–1918). As Linnaeus had already described *P. ericoides* in 1767, the specimen at LINN is probably not part of the Tulbagh collection. Thoday (1924a) clearly regarded the specimen at LINN, named by Linnaeus, as the type of *P. ericoides*. As no other original elements exist, *P. ericoides* LINN 504.5 is regarded as a lectotype designated by Thoday (1924a).

Thunberg (1825a) accepted Wikström's concept of *P. glomerata*, occurring at Hout Bay in the Cape, and cited *P. ericoides* in synonymy, causing confusion about the identity of the latter taxon. Meisner (1840) reinstated *P. ericoides*, but the concept of this taxon became even more doubtful in the light of the cited distribution. In 1857 Meisner retained his concept of *P. ericoides*, occurring at Uitenhage, Port Elizabeth, Witbergen and Onderbokkeveld, and placed *P. glomerata* and *Lachnaea conglomerata* in synonymy under *P. ericoides*. This revision by Meisner (1857) was largely followed by Wright (1915). Because of his incorrect concept of the taxon, Meisner (1857) was confronted with material from Table Bay and Standvallei with red berries, which he then named *Chymococca empetroides*, based especially on the fleshy fruit. Thoday (1924a) was justified in placing this name in synonymy under *P. ericoides* as the descriptions of these taxa coincide and as the fleshy fruit of *C. empetroides* is not unique, but is also found in *P. rigida*. The concept of *P. ericoides*, occurring along coastal dunes mainly in the Cape Peninsula and adjacent coastal areas of the Western Cape, was clarified by Thoday (1924a) and is also accepted in the present study.

### Diagnostic characters

*Passerina ericoides* is characterized by greenish flowers, with a coriaceous, strigose hypanthium and the fruits are fleshy red berries. The leaves are greyish green and oblong, with an obtuse apex. The bracts are leaf-like, larger and lanceolate.

### Etymology

The specific epithet *ericoides* refers to the ericoid appearance of this species indicated by the phrase 'corollae tubus globosus, inflatus—unde et Ericam refert flore', which was used by Linnaeus (1767) in his original description of the species.

### Common names

Willdenow (1799) introduced the vernacular name *heideartiger Vogelkopf*, and the common names 'Christmas berry' or *dronkbessie* were documented by Smith (1966).

### Uses

Marloth (1925) remarked that *P. ericoides* was laden with bright, scarlet fruits and that it was often employed as a Christmas decoration. The juicy pulp has a somewhat unpleasant taste, but appears to be harmless (*dronkbessie*). As early as

(1919) Sim recommended *P. ericoides* as a useful shrub for planting in coastal areas exposed to sea winds. This species occurs on coastal dunes and on the banks of lagoons in the Cape Peninsula and adjacent coastal areas of the Western Cape. The plants are excellent sand binders as they have an extensive root system from which resprouting often takes place. Because human impact and invasion of alien vegetation along the coast of the Cape Peninsula are very high, rehabilitation and conservation of coastal dunes is of vital importance. *P. ericoides* plants are ideally suited to combat erosion of coastal dunes and can be used as a substitute in coastal areas where alien vegetation is cleared. In their research on the coastal erosion of the Milnerton beaches, Biggs *et al.* (2001) made use of *P. ericoides*, occurring on the mobile dunes of this area as a natural monitor to indicate coastal erosion.

**Distribution and ecology**

*Passerina ericoides* ranges from Melkbosstrand along the coast of the Cape Peninsula to De Mond in the Bredasdorp District. It is endemic to the Southwestern and Agulhas Plain Centres within the CFR. This species occurs on littoral sand between rocks, or in dune valleys between the primary and secondary dunes. Figure 7.7H.

According to a note on the specimen *Taylor 4042*, *P. ericoides* forms part of the Coastal Fynbos (Acocks 1988), currently divided by Rebelo (1998) into the Laterite Fynbos of the Elim Flats, the Limestone Fynbos on calcareous sands overlying the limestone and associated calcretes of the Bredasdorp Formation, and the Sand Plain Fynbos from the Olifants River Mouth to Muizenberg on the West Coast lowlands. According to Rebelo (1998) the southernmost centre of the Sand Plain Fynbos is almost engulfed by the Cape Town Metropolitan Area and the area between Milnerton and Malmesbury must rank as one of the world's hottest spots for the loss of plant biodiversity.

*Conservation status*: as a large portion of the coast along the Cape Peninsula is affected by human impact and invasion by alien vegetation associated with the

Cape Town Metropolitan Area, the conservation status of *P. ericoides* is considered as Near Threatened (NT) (IUCN Species Survival Commission 2000).

### Specimens examined

WESTERN CAPE.—3318 (Cape Town): valley between Melkbosstrand and Duinefontein, (–CB), *Glen 1089* (PRE); Milnerton, (–CD), *Andraea 385, 385b* (NBG PRE); Blaauwberg Beach, beacon 41, (–CD), *Boucher 3973* (PRE); Sands of Table Bay, (–CD), *Bowie 1* (BM); Milnerton Beach, higher dunes, (–CD ), *Bredenkamp 956* (PRE); *Garside 502* (K); Blouberg Strand, (–CD), *Giess 1293* (M); *Pole-Evans 4373* (PRE); Zoutrivier, (–DA), *Zeyher 42* (NBG). 3418 (Simonstown): Blaawbergstrand, (–AB), *Acocks 19066* (K, PRE); Noordhoek, (–AB), *Barker 2726* (NBG); Kalk Bay, (–AB), *Bolus 4498* (BM, K); Fish Hoek bay, (–AB) *Bolus 4498* (BOL); Miller's Point, (–AB), *Gillett 3457* (NBG); between Smith's farm and Vasco da Gama, (–AB), *Hutchinson 663* (K, PRE); Simonstown, (–AB), *MacOwen 3404* (K); Muizenberg, (–AB), *Marloth 5648* (B, PRE); Miller's Point, (–AB), *Meebold 15154* (M); Noordhoek, (–AB), *Salter 7051* (K); Witsand, (–AB), *Smuts 1134* (PRE); Strandfontein, (–AB), *Van Zinderen Bakker 12* (NBG); Fish Hoek, (–AB), *Wall s.n.* (S); Simonstown, (–AB), *Wolley-Dod 1878* (BOL, K); Simonstown Bay, (–AB), *Wright s.n.* (C, P); Cape Maclear, (–AD), *Bredenkamp 962* (PRE); Buffels Bay, (–AD), *Compton 10633* (NBG); Cape Peninsula, Olifantsbos, (–AD), *Compton 22289* (NBG, S); Cape of Good Hope Nature Reserve, (–AD), *Taylor 9871* (NBG, PRE); dunes near Strandfontein, (–BA), *Acocks 690* (S); Macassar Beach, (–BB), *Taylor 6211* (NBG, PRE); *Downing 401* (NBG, PRE); near Hangklip Lighthouse, (–BD), *Boucher 1691* (NBG); near Rietvalley, (–DC), collector unknown (BOL, P, W). 3419 (Caledon): Mossel River near Hermanus, (–AC), *Guthrie 17414* (BOL ); Hermanus, (–AC), *Krause s.n.* (NBG);*Walters 247, 1084* (C, NBG); 3 mi. E of Hangklip Coast at Stony Point, (–BD), *Pillans 8513* (BOL); Melkbosch Strand, (–BD), collector unknown (S); Pearly Beach, (–CB), *Acocks 22784* (PRE); *Taylor 4042* (K, M, PRE); Pearly Beach Holiday Resort, (–DA), *Boucher 856* (K, NBG, PRE). 3420 (Bredasdorp): Struis Bay, (–CA), *Levyns 3100* (BOL); Arniston sand dunes, (–CA), *Martin s.n.* (GRA); Quoin Point, (–CA), *Rycroft 2135* (NBG); De Mond, (–CA), *Walsh s.n.* (NBG). Grid ref. unknown: *Corneliussen 1875* (C); Herb. S. Dreyer, *Ecklon s.n.* (C); locality doubtful, *Ecklon & Zeyher 39* (BOL, G, MO, P, W); *Harvey 691* (BM); Herb. Regium Monacense, Caput Bonae Spei, *Hiendlmayr s.n.* (M); Herb. Schreberianum, *Swartz s.n.* (M); Caput Bonae Spei, *Laubert s.n.* (S); *Linnaeus 504.5* (LINN); *Marloth s.n.* (PRE); Museum Botanicum Hauniense (C); Cape, *N.J.A. s.n.* (S); *Pappe s.n.* (NBG); locality unknown, *Zeyher s.n.* (NBG).

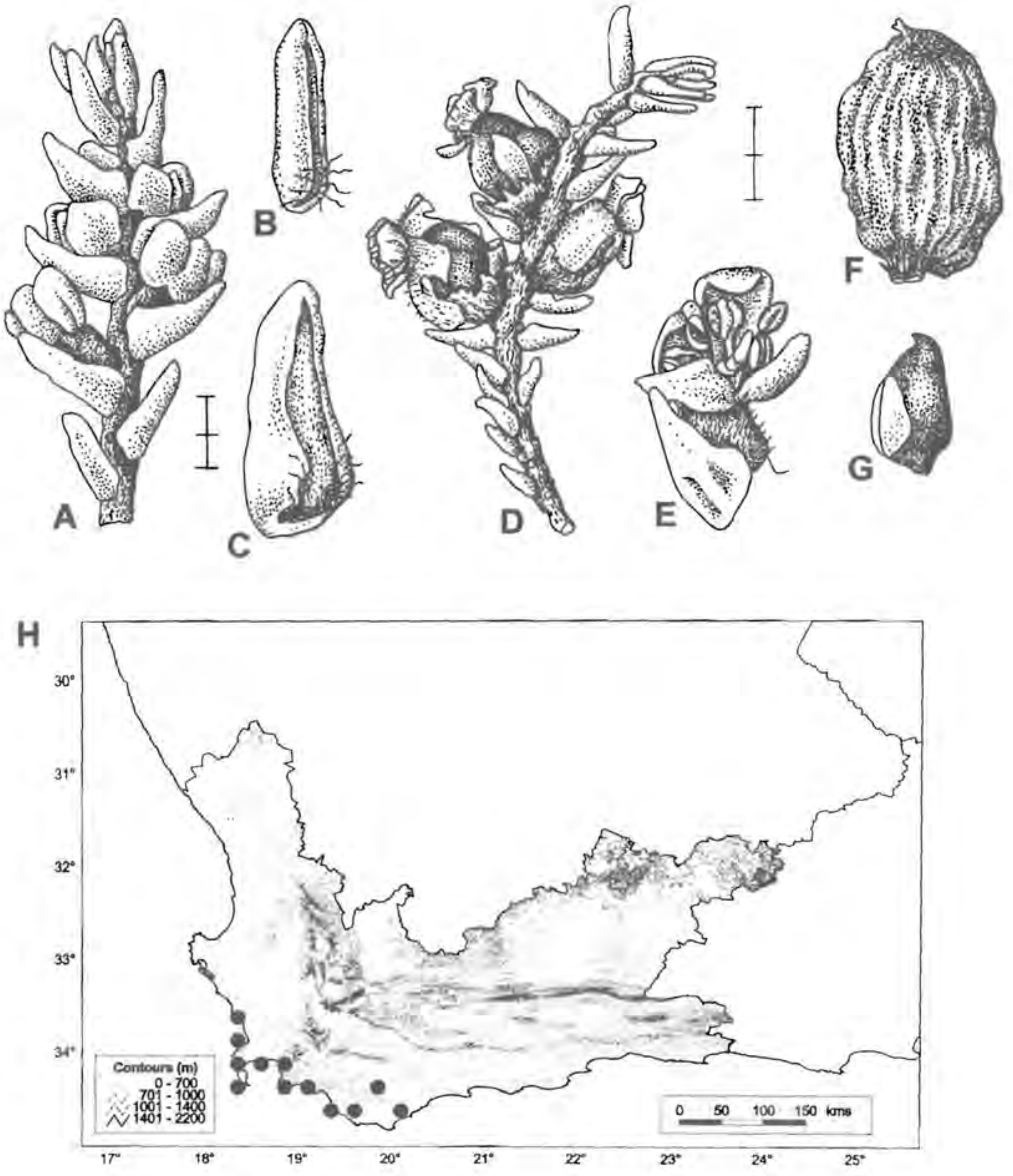

FIGURE 7.7.—*Passerina ericoides* (*Bredenkamp 962*). A, young inflorescence; B, leaf exposing adaxial surface; C, bract exposing adaxial surface; D, fruiting branchlet; E, flower enveloped by bract; F, fleshy one-seeded berry; G, seed with black tegmen and white fragment of endocarp. Scale bars: 2 mm.

H, known distribution of *Passerina ericoides*.

7. **Passerina rigida** *Wikstr.* in Kunglinga Svenska Vetenskapsakademiens Handlingar 39: 326 (1818); Meisn.: 402 (1840); Steud.: 274 (1841); Drège: 208 (1843); C.A.Mey.: 49 (1843); Meisn. 14: 563 (1857); C.H. Wright: 13 (1915); Thoday 4:165 (1924a); Palmer & Pitman: 1585 (1972); Coates Palgrave: 649 (1977); Bond & Goldblatt: 433 (1984); A.E.van Wyk & P.van Wyk (1997). Type: Hab. ad Promont bonae spei [Cape Peninsula], *Prof. Sparrman s.n., Herb. Thunb. 9578* (UPS, holo.!; M!, S!).

*Passerina eriophora* Gand.: 418 (1913); Thoday 4:165 (1924a). Types: KwaZulu-Natal, Stanger, Natal, in ora prope Durban [coast near Durban], *Wood 1712* (K!, lecto., designated by Thoday 4:165 (1924a), BM!, BOL!, M!, W!); *Wood 6592* (S!).

*Passerina ericoides* sensu Meisn. 14: 562 (1857) pro parte quoad specim. *Drège s.n.* (MO!), non L.

Many-stemmed, much branched, robust shrubs of (0.6–)1.0–2.0(–3.04) m tall on coastal dunes; secondary and tertiary branches ascending, conical in appearance, formation of branchlets profuse, decussate, older branchlets self-pruning, lax or arcuate, 60–100 mm long, progressively shortening towards growing point, young branchlets ascending, 5–60 mm long, growing point nodding, fertile branchlets often pendulous and secund. *Stems* greyish brown, bark stringy; cork grey-brown; branchlets and growing points densely white-tomentose, tomentum forming lengthwise patterns with cork on older branchlets, which later become glabrous. *Leaves* imbricate, overlapping ± 50%, appressed, plane shape lanceolate to ovate, length × depth 1.6–2.5 × 0.1–1.1 mm, adaxial surface concave, villous, abaxial surface convex, glabrous, greyish green, smooth, often covered by salt crystals; base sessile, dilated; median vein in distal half visible as a keel, forming acute apex; margins villous. *Inflorescences* with spikes usually extended, 6–10-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* appressed, ascending in fruit, widely ovate, length × depth (2.6–)3.4 × 1.4(–1.9) mm; lamina adaxially concave (inside), abaxially convex (outside), villous inside, glabrous outside, smooth, with 2 or 3 shallow folds on each side of main vein, wings absent, greyish green, coriaceous; base dilated; apex with distinct, short, acute point; margins tomentose, involute. *Floral envelope* ± 4.0 mm long, membranous and yellow during pollination, dehydrated after shedding of pollen, turning red. *Hypanthium* glabrous at ovary, neck tomentose, ± 0.8 mm long. *Sepals*: outer sepals cymbiform, midrib adaxially tomentose, abaxial surface glabrous, inner sepals obovate, adaxially tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 0.5 mm and those of antisepalous whorl ± 1.5 mm long; anthers, 0.8 × 0.4 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.2 × 1.4 mm. *Fruit* a fleshy yellow berry, 2.6 × 2.3 mm, enveloped by persistent, loosely arranged hypanthium, fragmenting over widest circumference of fruit, the fragmented hypanthium, sepals and androecium being shed. *Seed* 1.4 × 1.1 mm. Figure 7.8A–I.

### Nomenclatural notes

In his description of *P. rigida*, Wikström (1818) clearly indicated the specimen of Sparrman, in the Thunberg Herbarium, as the type. This specimen bears the inscriptions *Passerina glomerata* β and epithet *rigida* in pencil. Thoday (1924a) identified the handwriting of the pencilled 'rigida' as Wikström's, comparing it to signed letters in the library at Kew. Wikström's handwriting was also confirmed in the present study, using examples published by Burdet (1979). According to Stafleu & Cowan (1986), original specimens of the Thunberg Herbarium (to which Sparrman also contributed) were donated to UPS and the duplicates were sent to S. Thus three other *Sparrman s.n.* specimens of Herb. Swartzii, Herb. Wikströmii and Herb. Gaströmii, housed at S, and a fourth one from Schreber's herbarium, housed at M, are duplicates. As Wikström clearly indicated the specimen in the Thunberg Herbarium as the type, we regard it as the holotype and the other four Sparrman specimens as isotypes.

### Diagnostic characters and relationships

*Passerina rigida* can easily be distinguished as robust, rigid shrubs of mostly 1.0–2.0 m high. The ascending branches are conical in shape due to many branchlets that are pendulous when fertile. The flowers are yellow and membranous and bright yellow berries are borne subterminally. The leaves are narrowly lanceolate to ovate and the apex is acute, with the main vein visible as a blunt keel. The bracts are widely ovate with the apex acute. This species is easily distinguished from *P. paleacea* which occurs on secondary dunes and is distributed mainly along the southern coast of the Western Cape. Plants of the latter species are less robust, reaching a maximun height of 1.5 m, characterized by an abundance of subcapitulate inflorescences and the fruits are dry (achenes).

### Etymology

The epithet *rigida* refers to the rigid, ascending branches, characteristic of the growth form of this plant.

### Common names

Smith (1966) recorded the vernacular names *gonnabas* and *seekoppiesgonna*, while both Palmer & Pitman (1972) and Coates Palgrave (1977) added the name 'dune gonna'. Palmer & Pitman (1972) also listed the names *ishoba* and *unyenyevu*. The names 'dune-string', *duinetaaibos* and *gonnabos* were used by Lubke & Van Wijk (1998). *Duin-gonna*, 'dune gonna', *inwele*, *unyenyevu* are names given by Von Breitenbach *et al.* (2001).

### Uses

*Passerina rigida* is a pioneer of the coastal dunes along large portions of the South African coast. Because these robust plants are excellent sand binders and are completely adapted to maritime winds and salt spray, they can be used in the rehabilitation of coastal dunes in disturbed areas. *P. rigida* has an extensive root system from which resprouting commonly takes place. The yellow berries are an important food source for animals inhabiting coastal areas, especially birds.

### Distribution and ecology

*Passerina rigida* is distributed from Witsand River Mouth on the western coast of the Cape Peninsula, along the coastline of South Africa to Lake Sibayi on the northeastern coast of KwaZulu-Natal. It is endemic to the coastlines of KwaZulu-Natal, the Eastern Cape and the Western Cape. The specimen *Taylor 4143*, recorded as far North as Lambert's Bay on the West Coast, is regarded as an outlier as no other specimens have been recorded in the grid 3318. Thoday (1924a) mentioned *Bowker s.n.* from Somerset, *Cooper 2301* from Albany and *Ecklon & Zeyher s.n.* (*SAM 19801*) as specimens from inland localities. In recent years more cases of *P. rigida* growing along sandy banks of rivers adjacent to the coast have been noted. Figure 7.8J.

This species occurs on littoral sand dunes and hammock dunes just above the level of spring tide. It is also found in marshy places and on sandy banks of river mouths and lagoons. A stunted form is present on shallow marine sand over limestone and on rocky hills facing the sea. Lubke & Van Wijk (1998) regard *P. rigida* on the southern and Eastern Cape coast as a pioneer found in bush clumps or bush pockets on rear dunes. According to them, there are often no pioneer communities on the vast dune sands and the first vegetation encountered as one moves away from the shore is dune thicket, in which *P. rigida* is one of the dominant shrubs. *Passerina* species occurring on littoral dunes in the Western Cape are found mainly in Coastal Fynbos (Acocks 1988). From the southern Cape coast to Port Alfred, Dune Fynbos and Dune Thicket form a mosaic as well as a successional series between the two vegetation types (Lubke & Van Wijk 1998).

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

KWAZULU-NATAL.—2732 (Ubombo): Lake Sibayi, near Mabibi, (–BC), *Stephen 455* (PRE); between Island Rock and Mabibi, (–BD), *Ward 2167* (PRE); Mtunzini Farm, (–DC), *Van Wyk 2517*

(PRE, PRU); Mtunzini District, beach area, (–DD), *Eicker 1* (PRE); *Worsdell s.n.* (NBG). 2832 (Mtubatuba): St Lucia, (–AD), *Buff 760610-2/1* (WU); Maphelane Nature Reserve, (–AD), *Fokkens 5* (PRE); St Lucia, (–AD), *Jacobsen 1381* (PRE); *Strey 6769* (PRE); *Ward 7211* (PRE); St Lucia Park, 600 m N of bridge, (–BA), *Ward 4374* (PRE); Richards Bay, (–CC), *Gafney 11* (MO, PRE); Isipingo Beach, (–DD), *Gillett 1207* (PRE); near Durban, (–DD), *Wood 9139* (NBG). 2931 (Stanger): Mvoti River Mouth, (–BA), *Moll 2466* (K, PRE); Durban, (–CC), *Kuntze s.n.* (K); bluff at Durban, (–CC), *Meebold 15755* (M); Beachwood, (–CC), *Mitchell, Pammenter & Spencer B 4(11)* (PRE); near Port Natal, (–CC), *Sutherland s.n.* (K); Durban, (–CC), *Wilms 2277* (K); Durban, sandy hills near sea, (–CC), *Wood 1712* (BM, BOL, K); *Wood 5786* (M, MO); *Wood 6592* (S); *Wood 9139* (BOL); *Wood s.n.* (PRE). 3030 (Port Shepstone): Winkle Spruit, (–BB), *Rudatis 1505* (K, NBG); Isipingo Beach, (–BB), *Smuts s.n.* (NBG); Isipingo North, (–BB), *Ward 549* (PRE); between Port Shepstone and Margate, (–CD), *Acocks 1006* (S); Margate Beach, (–CD), *Bayer 1307* (MO); Port Shepstone, (–CD), *Burtt-Davy 2410* (K); Uvongo, (–CD), *Mogg 13220* (K PRE).

EASTERN CAPE.—3129 (Port St Johns): Embotyi Mouth, (–BC), *Miller 2701* (PRE); Msikaba River, (–BD), *Van Wyk 1545* (PRE, PRU); Umgazi River Mouth, (–CB), *Taylor 8998* (PRE, S); Port St Johns, (–CB), *Wall s.n.* (S); Tshani River Mouth, (–CC), *Snyman s.n.* (GRA); Port St Johns, (–DA), *Acocks 10967* (PRE); *Bayliss 6017* (PRE); *Comins 1930* (PRE); *Galpin 9353* (K, PRE); *Hutchinson 1748* (K, PRE). 3130 (Port Edward): Umtamvuna Bridge, (–AA), *Bredenkamp 1013, 1014* (PRE); Umtamvuna Lagoon, (–AA), *Crawford 384* (PRE); Leisure Bay, (–AA), *Euckermann 7889* (PRE); Palm Beach, (–AA), *Weigend 2341* (M); Umtamvuna River, (–AB), *Botha & Coetzee 1605* (PRE). 3227 (Stutterheim): Nahoon, (–DC), *Nanni 123* (PRE); Bonza Bay, (–DD), *Compton s.n.* (S). 3228 (Butterworth): Kei Mouth, (–CB), *Flanagan 418* (NBG, PRE); Kentani District, coast, (–CB), *Pegler 234* (PRE); N side of Nxaxo Mouth, (–CB), *Ward 5735* (PRE); Gonubrie Springs, (–CC) *Levyns 10832* (BOL); Kwelega, (–CC), *McKitterick 12* (GRA); Cefane River, (–CC), *O'Callaghan 1003* (GRA); Cintsa, New East London, (–CC), *Quickelberge A7758* (GRA). 3323 (Willowmore): Nature's Valley, Groot River Mouth, (–DC), *Parsons 182* (NBG); Koega River, (–DC), *Zeyher 3777* (NBG); Tsitsikama Forest, Elandsbos River, (–DD), *Bower 602* (PRE). 3324 (Steylerville): near mouth of Swartkops River, (–DD), *Zeyher 405* (TCD, GRA); *Zeyher 1025* (BM). 3325 (Port Elizabeth): Sundays River, (–AA), *Hendricks 13* (GRA); *Rivers-Moore s.n.* (GRA); Maitland River Mouth, (–CD), *Boucher 3363* (NBG); Uitenhage, (–CD), *Ecklon & Zeyher s.n.* (S); *Pappe s.n.* (S); Humewood, (–DC), *Dahlstrand 148* (MO); Markman industrial area, (–DC), *Dahlstrand 2949* (NBG, PRE); Humewood, (–DC), *Holland 3699* (BOL); Port Elizabeth, (–DC), *Kemsley 141* (GRA, NBG); *Long 798* (K, PRE); Amsterdam Hoek, (–DC), *Noel s.n.* (GRA); Coega River, (–DC), *Olivier 2027* (PRE); Cape Receife, (–DC), *Olivier 3024* (GRA); Humewood, (–DC), *Paterson 1123* (GRA); Port Elizabeth, (–DC), *Potts BLF 288* (GRA, PRE). 3326 (Grahamstown): Somerset, near Kowie, (–BC), *Bowker s.n.* (K); Kowie, salt vlei dunes, (–BC), *Martin s.n.* (GRA); Alexandria District, fore dunes, (–CB), *Gilfillan 7* (GRA); Bushmans River Mouth, (–CB), *Johnson 1069* (GRA); Alexandria, (–CB), *Osborne 126* (GRA); Cape Padrone, (–CD), *Jacot-Guillarmod & Brink 41* (GRA, PRE); Kenton-on-Sea, (–DA), *Abrahams s.n. & A7759* (GRA, MO, PRE); Bushmans River Mouth, (–DA), *Archibald 4552/52* (GRA, PRE); Kenton-on-Sea, (–DA), *Bredenkamp 899* (PRE); Boknes, (–DA), *Burrows 3395* (GRA); Bushmans River mouth, (–DA), *Cooper 15* (GRA); *Johnson 1069* (K, PRE); Dias Cross Memorial, (–DA), *Retief 1194* (MO, PRE); Port Alfred, (–DB), *Bayliss 650* (K, MO, M, PRE); Port Alfred, (–DB), *Bredenkamp 898* (PRE); Kowie West, (–DB), *Britten 5014* (GRA); Kowie River, (–DB), *Germishuizen 1527* (PRE); spring between Port Alfred and Kasuka, (–DB), *Gibbs Russell 4094* (PRE); Bathurst, (–DB), *Hoole J1* (GRA); Port Alfred, (–DB), *Rogers 28018* (GRA); *Theron G.C. 1076* (PRE, K); *Theron G.K. 282* (PRE); *Tyson s.n.* & *TRV 17233* (PRE). 3327 (Peddie): East London, (–BB), *Fouche s.n.* (PRE); *Galpin 3363* (PRE); *Hilner 184* (PRE); Kleinmond River near western bank, (–CA), *Bredenkamp 897* (PRE); Tharfield Farm, between Riet and Kleinmond Rivers, (–CA), *Lubke 2312* (GRA); Kleinmond East, (–CA), *Van Wyk 3167* (PRE, PRU). 3424 (Humansdorp): W of Tsitsikama River, (–AB), *O'Callaghan 1425* (NBG); between Kromme and Tsitsikama Rivers, (–AB), *District Forest Officer 97* (GRA); Duineveld between Slang and Kromme Rivers, (–BA), *Sim 1* (GRA); Kromme Bay, (–BB), *Acocks 21455* (M, PRE); Jeffreys Bay, (–BB), *Bredenkamp 911, 913* (PRE); Sea Vista, (–BB), *Lubke 1782* (GRA); Slang River, (–BB), *Phillips 1622, 3363A & B* (K, PRE); Jeffreys Bay, (–BB), *Stopp 70* (M).

WESTERN CAPE.—3218 (Clanwilliam): Lambert's Bay, (–AB), *Taylor 4143* (NBG). 3322 (Oudtshoorn): Wilderness, (–DC), *Mogg s.n.* (PRE). 3418 (Simonstown): Witsand River Mouth, (–AB), *Hugo 1912* (C, M, PRE); Cape Flats, (–BA), *Van Rensburg 459* (NBG); Betty's Bay, (–BD), *Bohnen 94.04* (PRE); *Botha 372* (PRE); Kogel Bay, (–BD), *Boucher 470* (K); near Hangklip Lighthouse, (–BD), *Boucher 1690* (NBG, PRE); Rooiels, Hangklip, (–BD), *Parsons 60* (NBG); Palmiet River Mouth, (–BD), *Van Rensburg STE 2147* (PRE). 3419 (Caledon): Hermanus, (–AC), *Marloth 13012* (PRE); *Purcell s.n.* (NBG); Mossel River, (–AD), *Guthrie 17413* (BOL); Walker Bay, (–AD), *Taylor 8367* (NBG); Voëlklip, (–AD), *Taylor 9879* (NBG, PRE); *Williams 1008* (K, M); Cape Hangklip, (–BD), *Levyns 10867* (BOL). 3420 (Bredasdorp): Swellendam, (–AB), *Ecklon & Zeyher s.n.* (NBG); De Hoop Nature Reserve, (–AD), *Burgers 2924* (NBG); Slang River, (–BC), *Fourcade 1806* (NBG); Lekkerwater, (–BC), *Paterson-Jones 697* (NBG); *Taylor 9905* (NBG, PRE); Slang River, (–BD), *Fourcade 1806* (K, PRE); Waenhuiskrans, (–CA), *Bredenkamp 948* (PRE); De Mond, Heuning River, (–CA), *Boucher 1677* (PRE); Struis Bay, (–CA), *Levyns 3101* (BOL); Waenhuiskrans, (–CA), *Taylor 10171, 10249* (MO, NBG, PRE); Die Mond Forest Station, (–CA), *Van Breda 1037* (PRE); Waenhuiskrans, (–CA), *Van der Westhuizen 144, 147* (PRE). 3421 (Riversdale): Stilbaai, (–AD), *Bohnen 4911, 8147* (NBG, PRE); *Bredenkamp 935* (PRE); *Muir 14* (PRE); *Taylor 10144* (NBG, PRE); Stilbaai, (–BC), *Van Schalkwyk 46* (PRE). 3422 (Mossel Bay): Hartenbos River Mouth, (–AA), *Parsons 322* (NBG PRE); Sedgefield, (–BB), *Anderson 76* (PRE); Gericke Point, (–BB), *Hugo 1992* (NBG, PRE). 3423 (Knysna): Buffalo Bay, (–AA), *Duthie 533* (NBG); *Keet 873* (NBG); Groen Vlei, (–AA), *Levyns 10291* (BOL); Knysna Heads, (–AA), *Oldevig-Roberts 120* (S); Keurboomsrivier Strand, (–AB), *Codd 3602* (PRE, K); Plettenberg Bay Lagoon, (–AB), *Marsh 1327* (NBG, PRE); S of Keurboomsrivier Lagoon, (–AB), *O'Callaghan 839* (NBG, PRE); Plettenberg Bay, (–AB), *Rogers 26774, 26790* (PRE); Keurboomsrivier Strand, (–AB), *Taylor 2953* (PRE). Grid ref. unknown: *Burchell 4049, 7463* (K); Albany, *Cooper 2301* (K); *Drège s.n.* (K, MO); *Ecklon & Zeyher s.n.* (BREM); Transkei, Casino, *Frankish 253* (MO); *Gerrard 95* (K); *Herb. Thunberg 9578* (UPS); Caput Bonae Spei, *Hutton s.n.* (TCD); *Laubner s.n.* (K); Caput Bonae Spei, *Museum Bot. Hauniense s.n.* (C); KwaZulu-Natal, *without collector s.n.* (TCD); Caput Bonae Spei, *Herb. Schreber*, *Sparrman s.n.* (M);

Caput Bonae Spei, *Herb. Swartzii*, *Sparrman s.n.* (S); Caput Bonae Spei, *Herb. Wikströmii*, *Sparrman s.n.* (S); Caput Bonae Spei, *Herb.Gaströmii*, *Sparrman s.n.* (S); KwaZulu-Natal, Manzingwenya, *Vahrmeijer & Tolken 252* (PRE).

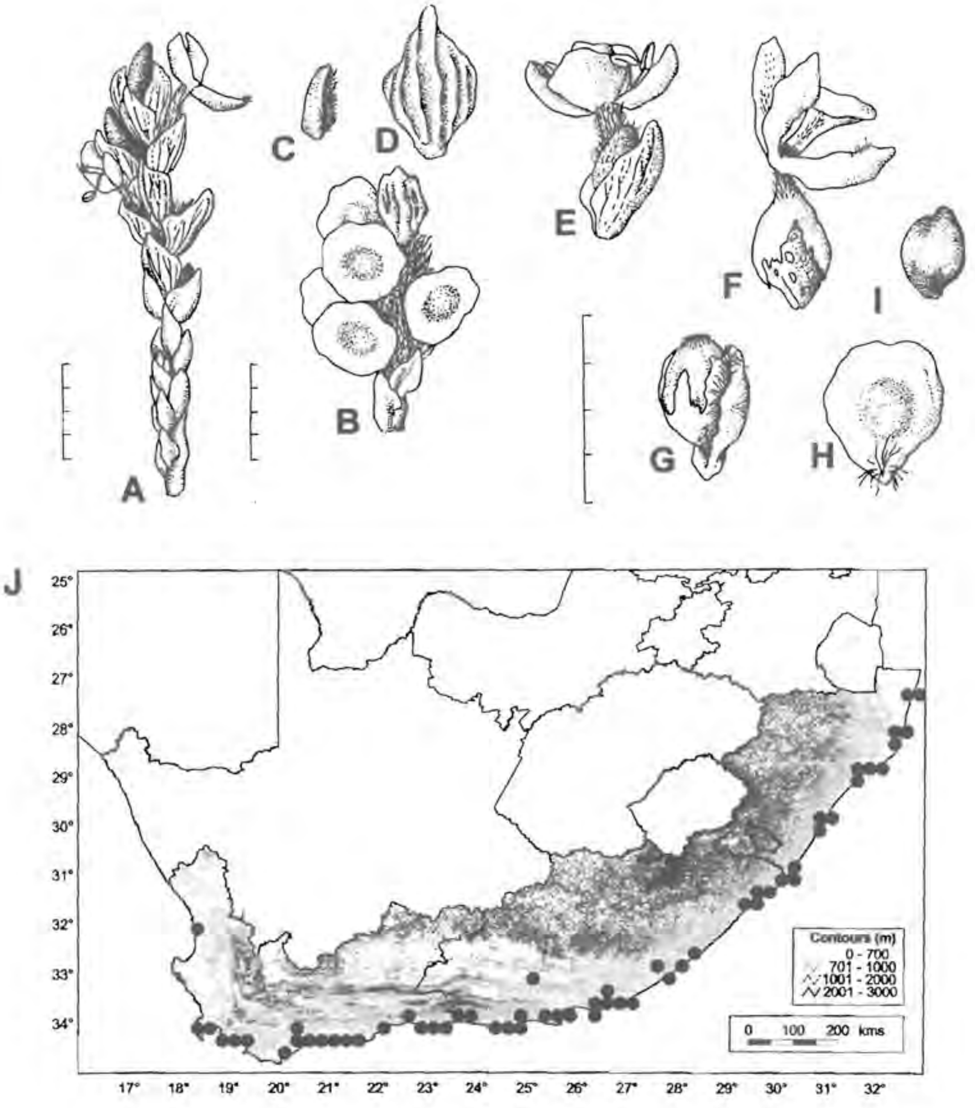

FIGURE 7.8.—*Passerina rigida* (*Bredenkamp 1013*). A, flowering inflorescence; B, fruiting inflorescence; C, leaf; D, bract; E, flower clasped by bract; F, hypanthium fragmenting at circumference of ovary; G, fruit clasped in tomentum of bract; H, fruit, a yellow, fleshy berry; I, seed. Scale bars: 4 mm.

J, known distribution of *Passerina rigida*.

8. **Passerina nivicola** *Bredenk.* & *A.E.Van Wyk*, sp. nov., *P. comosae* C.H.Wright affinis sed bracteis circumscriptione late obovatis, basi cuneatis, rubrofusis in alabastro, lamina utrinque glabra, chartacea, alis bullatis, membranaceis, marginibus ciliatis dimidio superiore, costa crassa, ventraliter tomentosa in apicem subacutum extensa, caespite apicali pilorum. *Hypanthium* circa ovarium extra tomentoso. *Sepala* tempore pollinationis membranacea, lutea vel luteorosea; sepalis exterioribus apice setosis, sepalis interioribus utrinque glabris.

TYPUS.—Western Cape, 3319 (Worcester): Ceres District, Waboomberg, 1760 m, (–DD), 12 November 1989, *E.G.H. Oliver 9281* (PRE!, holo.; NBG!, iso.).

*Passerina sp. nov. 1* Bredenk. & A.E.van Wyk 129: 70 (2000); 31,1: 56 (2001a); 31,2: 217 (2001b).

Low rounded shrublets or shrubs 0.3–0.5 m high. *Stems* greyish brown, younger branchlets greyish tomentose, cork finely fissured, grey-brown. *Leaves* imbricate on young branchlets, sessile, closely appressed to stem, cymbiform, cigar-shaped, often slightly dilated apically; plane shape linear-lanceolate, length × depth (2.5–)3.1(–4.5) × (0.5–)0.6(–0.7) mm; lamina inversely ericoid, adaxial surface concave, tomentose, abaxial surface convex, glabrous; base sessile; apex rounded, with an apical tuft of hair, tinged red; margins sometimes ciliate. *Inflorescences* polytelic synflorescences; main florescences and co-florescences spicate. *Bracts* tinged red in bud stage, enveloping flowers and fruits, largest after anthesis of flowers, becoming more coriaceous and rounded at fruit set, decussate, imbricate, cymbiform, plane shape widely obovate, length × depth (3.1–)3.5 × 1.4(–1.9) mm; lamina, adaxial surface (inside) concave, abaxial surface (outside) convex, glabrous on outside, chartaceous; main vein strongly developed, tomentose on inside, extending to form a subacute apex, with an apical tuft of hair; wings glabrous, bullate, membranous; margins ciliate in distal half; base cuneate. *Floral envelope* petaloid, ± 5.3 mm long, during pollination membranous and yellow or yellow-pink, after pollination papyraceous, turning red. *Hypanthium* ovary tomentose, neck ± 1.2 mm long, tomentose on outside, inside often hairy; after fruiting dehydration and torsification of tissue causing fragmentation of neck base and shedding of sepals and androecium. *Sepals* 4, imbricate in bud, flexed in flower, outer sepals cymbiform, abaxially setose at apex, inner sepals widely ovate, glabrous on both surfaces. *Androecium* filaments of antipetalous whorl ± 0.4 mm and those of antisepalous whorl ± 1.2 mm long. *Ovary* ± 1.7 × 0.5 mm. *Fruit* enveloped by persistent, loosely arranged hypanthium fragmented at neck base; a 1-seeded berry, pericarp membranous and dry. *Seed* 2.2 × 1.2 mm. Figure 7.9A–E.

### Diagnostic characters and relationships

*Passerina nivicola* can easily be distinguished from *P. comosa* by its glabrous leaves and red-tinged bracts, which are glabrous outside, with bullate, membranous wings. The flowers are yellow or yellow-pink and membranous at pollination, with outer sepals abaxially setose at apex, inner sepals glabrous on both surfaces.

### Etymology

The specific epithet is a compound of the Latin *nivalis* (= pertaining to snow) and *cola* (= dweller), thus *nivicola* (= a dweller in the snow). The name refers to the occurrence of this species at high altitudes, where the plants are often covered by snow; specimens collected during the present study were dug from the snow in mid-October.

### Uses

Plants growing on the level area south of the beacon on Waboomberg were conspicuously stunted, possibly because they were covered by a layer of snow, but it was also obvious that these plants had been grazed by livestock.

### Distribution and ecology

Restricted mostly to mountainous areas, *Passerina nivicola* is possibly still under-collected. The most northerly record is from Sneeukrans on the Roggeveld

Escarpment, an area covered by Escarpment Mountain Renosterveld (Rebelo 1998). The species was more extensively collected in the Ceres District and also further south in the Worcester District, in Mountain Fynbos or Central Mountain Renosterveld (Rebelo 1998). Figure 7.9F.

Plants on Waboomberg (altitude 1760 m) occur in low restioid or graminoid veld on sandy loamy soil, are somewhat stunted and attain a height of ± 0.3 m, possibly due to the effect of snow. Based on the bracts that are morphologically similar, the plants growing lower down, along the road leading up the mountain, are regarded as the same species. These plants reach a height of up to 0.5 m, are more robust and the bracts are more coriaceous. Information from *Grobler 540* (PRE), indicates that this species occurs on shale flats at Kareevlakte near Ceres.

*Conservation status*: Least concern [LC] (IUCN Species Survival Commission 2000). This species is rare, but does not qualify for Red List status under IUCN (2000) guidelines.

### Specimens examined

WESTERN CAPE.—3220 (Sutherland): Roggeveld Escarpment, Quaggasfontein Farm on road to Uitkyk, Sneeukrans W of Sutherland, (–AB), *Goldblatt & Manning 8627* (PRE). 3319 (Worcester): Ceres, Kareevlakte, (–AD), *Grobler 540* (PRE); Ceres, Waboomberg, (–AD), *Bredenkamp 1044–1047* (PRE); Vlei N of FM tower, *Cillie 9* (NBG); Level area S. of Beacon, *Oliver 9281* (NBG, PRE); Ceres, Baviaansberg, (–BA), *Compton 8718* (NBG); Worcester District, Tafelberg, (–CC), *Pillans 17159* (BOL, K); *Pillans sn* (K).

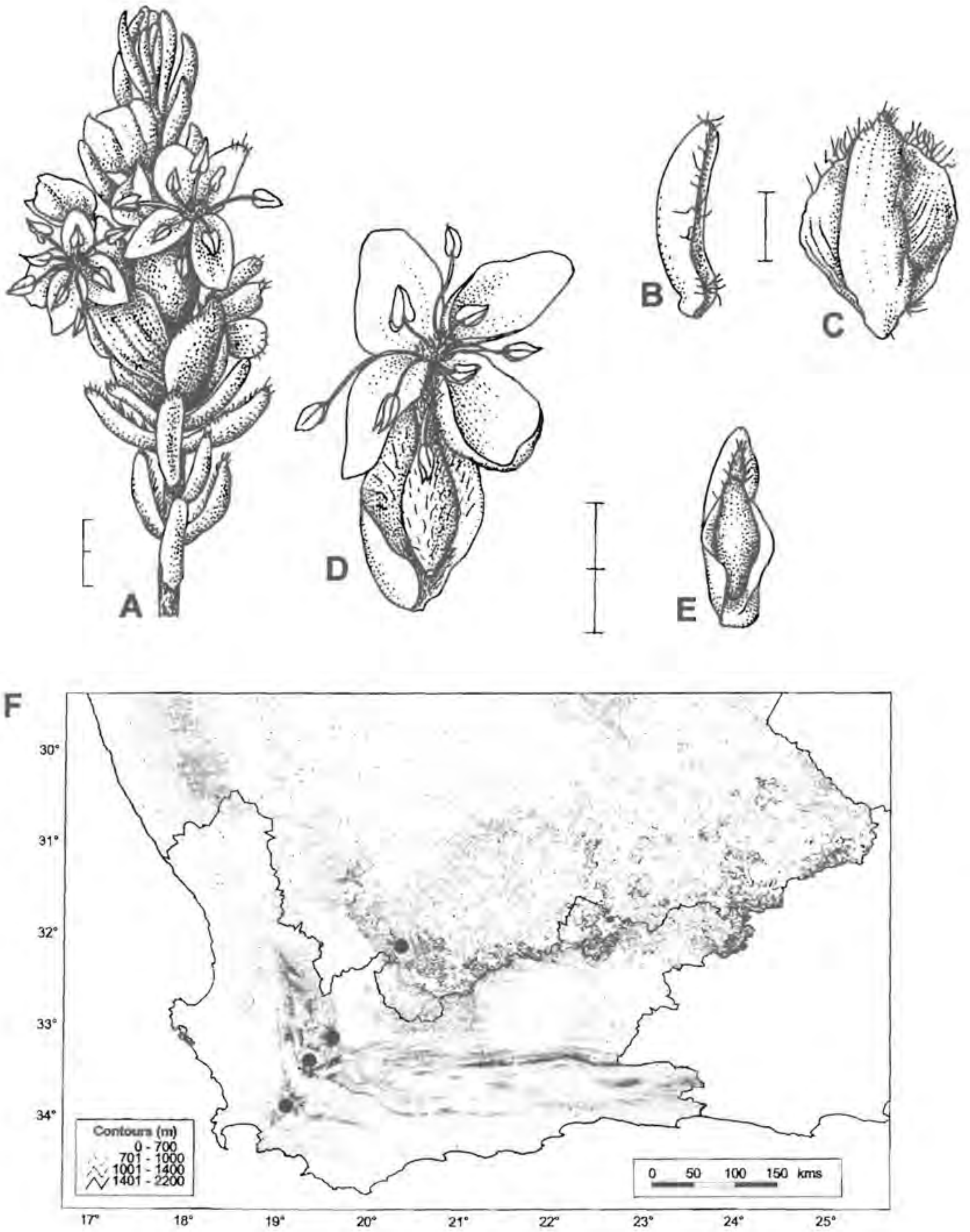

FIGURE 7.9.—*Passerina nivicola* (*Oliver 9281*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract; E, fruit enveloped by persistent floral bract. Scale bars: A, D, E, 2 mm; B, C, 1mm.

F, known distribution of *P. nivicola*.

9. **Passerina esterhuyseniae** *Bredenk. & A.E.van Wyk*, sp. nov., *P. comosae* C.H.Wright affinis. *Bracteae* galeiformes, circumscriptione obovatae; lamina adaxialiter concava, abaxialiter convexa, intra setosa, extra glabra, tenuiter chartacea, laevis, concolorans, brunneola, in marginem membranaceum vel in alas membranaceas expansa; basis cuneata; costa excurrens apicem subacutum vel acutum faciens; margines ciliati dimidio superiore. *Flores* membranacei, tempore pollinationis flavidi, postea rubri ad brunnei.

TYPE.—Western Cape, 3218 (Clanwilliam): N Cederberg Mountains, (–BB), Groenberg near Pakhuis, along base of high rugged rock, rocky slopes, ± 1167 m, 27-12-1956, *Esterhuysen 26859* (BOL, holo.!).

*Passerina sp. nov. 2* Bredenk. & A.E.van Wyk 129: 70 (2000); 31,1: 56 (2001a); 31,2: 217 (2001b).

Shrubs or shrublets 0.3–0.5 m high. *Stems* greyish brown, younger branchlets greyish tomentose, cork finely fissured, grey-brown, displaying whitish sclerenchyma fibres at scars. *Leaves* imbricate on young branchlets, closely appressed to stem, cymbiform, plane shape linear-lanceolate, length × depth ± 2.0 × 0.5 mm; lamina inversely ericoid, adaxial surface concave, setose, abaxial surface convex, glabrous; base sessile; apex rounded into subacute point; margins sometimes ciliate. *Inflorescences* polytelic synflorescences; main florescences and co-florescences spicate. *Bracts* enveloping flowers and fruits, largest after anthesis of flowers, becoming more coriaceous and rounded at fruit set, decussate, imbricate, sessile, helmet-shaped, widely obovate in outline, length × depth ± 3.1 × 2.4 mm; lamina adaxially concave (inside), abaxially convex (outside), setose on inside, glabrous on outside, thinly chartaceous, smooth, concolorous, brownish, extending into a membranous rim or membranous wings; base cuneate; main vein extending to form a subacute to acute apex; margins ciliate in distal half. *Floral envelope* constituting hypanthium (fused calyx and androecium) and sepals; membranous and yellowish during pollination, dehydrated after shedding of pollen, becoming papyraceous, turning red to brown, ± 4.6 mm long. *Hypanthium* a membranous cylindric tube, indumentum at ovary and neck tomentose, neck ± 0.7 mm long, abscission tissue and articulation plane absent. *Sepals* 4, petaloid; imbricate in bud, flexed in flower, outer sepals concave oblong with apex adaxially tomentose, abaxially setose; inner sepals concave, obovate with apex adaxially glabrous, abaxially setose. *Androecium* filaments of antipetalous whorl ± 0.4 mm and those of antisepalous whorl ± 1.2 mm long. *Ovary* 1.8 × 0.5 mm. *Fruit* enveloped by persistent, loosely arranged hypanthium fragmenting over widest circumference of fruit, the fragmented hypanthium, sepals and androecium being shed; an achene with pericarp membranous and dry, 2.5 × 1.2 mm. Figure 7.10A–G.

### Diagnostic characters and relationships

*Passerina esterhuyseniae* can easily be distinguished from *P. comosa* by its helmet-shaped bracts, which are widely obovate in outline. The concolorous, brownish bracts are thinly chartaceous and smooth in texture, the lamina extends into a membranous rim or membranous wings and the main vein elongates forming a subacute to acute apex. The flowers are membranous and yellowish during pollination and red to brown after shedding of the pollen.

### Eponymy

This species is dedicated to Elsie Esterhuysen who diligently collected especially the high-mountain flora of the Northern, Western and Eastern Cape Provinces.

### Distribution and ecology

*Passerina esterhuyseniae* has been collected on the northern Cederberg Mountains at Groenberg near Pakhuis and at Konpoort. It is endemic to the Northwestern Centre within the CFR. The northern Cederberg area is covered by Mountain Fynbos (Rebelo 1998). This species grows at the peaks of mountain tops at altitudes of ± 1 167 m, or against rocky slopes amongst high rugged rocks. Confined mostly to mountainous areas, this species is still under-collected. *Pillans 7689* (BOL) collected on slopes near the road SE of Redelinghuis has been classified under *P. esterhuyseniae*, although these plants seem to be more robust and grow at lower altitudes. Figure 7.10H.

*Conservation status*: as the population size of this species is probably very small or restricted, the conservation status is Near Threatened (NT) (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Piquetberg District, SE of Redelinghuis, slopes near road, (–AD), *Pillans 7689* (BOL); N Cederberg Mountains, Groenberg near Pakhuis, (–BB), *Esterhuysen 26859* (BOL); slopes of peak at Konpoort, (–BB), *Esterhuysen 12189* (BOL).

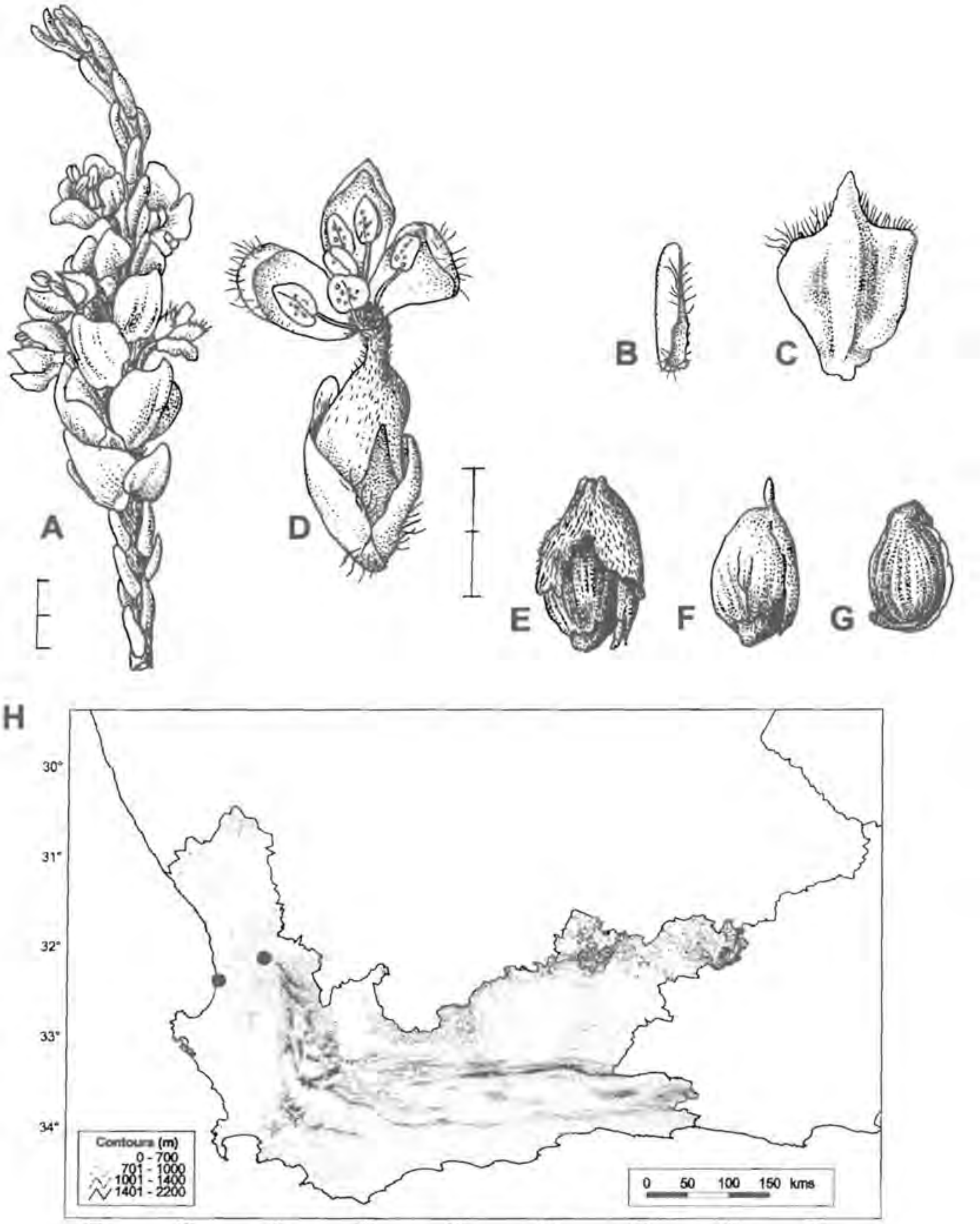

FIGURE 7.10.—*Passerina esterhuyseniae* (*Esterhuysen 26859*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract showing fragmentation of hypanthium at circumference of fruit. E, fruit with remnants of hypanthium; F, achene, enveloped by membranous pericarp; G. Achene in lateral view. Scale bars: 2 mm.

H, known distribution of *Passerina esterhuyseniae*.

10. **Passerina comosa** (Meisn.) C.H.Wright. Flora capensis 5,2: 11 (1915); Thoday 4:158 (1924a); Bond & Goldblatt: 432 (1984); Goldblatt & Manning: 683 (2000). Type: Little Namaqualand; Khamiesberg Range, between Pedros Kloof and Leliefontein, 3 000–4 000 ft., *Drège 2570* [K!, lecto., designated by Thoday 10: 388 (1924b); PRE!].

*Passerina filiformis* L. var. *comosa* Meisn.: 399 (1840); Meisn. 14: 562 (1857); C.H.Wright: 11 (1915); Thoday 4:158 (1924a). Type: as above.

*Passerina falciformis* Drège: 68 (1843) nom. nud.

Small shrubs, (0.3–)0.6–0.9(–1.06) m high, branches often virgate. *Stems* grey-brown, cork fissured lengthwise, grey-brown, surrounding prominent leaf scars; indumentum of young branches densely white or yellowish tomentose, flaking off with cork on older branchlets, which become glabrous. *Leaves* imbricate, overlapping ± 20%, diverging at an angle of 20°, plane shape linear to narrowly lanceolate, length × depth (2.7–)3.0(–4.0) × 0.6–0.9 mm, adaxial surface concave, villous, abaxial surface convex, tomentose to villous, rugose or warty with bases of fallen hairs; base sessile; apex obtuse to subacute; margins glabrous, basally setose. *Inflorescences* with spikes usually extended, 6–12-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* appressed, widely ovate, length × depth (3.0–)5.5 × 1.5(–1.8) mm; lamina adaxially concave (inside), abaxially convex (outside), villous inside, tomentose to villous outside, coriaceous, rugose with bases of fallen hairs, ± 3-ribbed on each side of main vein, margins submembranous or wings extended and abaxially setose to villous; base sessile; apex acute; margins glabrous, basally setose, involute. *Floral envelope* ± 7.3 mm long, yellow-pink during pollination, dehydrated after shedding of pollen, turning red. *Hypanthium* glabrous at ovary, neck tomentose, ± 0.9 mm long. *Sepals*: outer sepals cymbiform, inner sepals elliptic, outer and inner sepals adaxially glabrous, abaxially tomentose. *Androecium* with filaments of antipetalous whorl ± 0.7 mm and those of antisepalous whorl ± 1.5 mm long; anthers 0.7 × 0.4 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.7 ×

1.0 mm. *Fruit* an achene with pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in the sepals and androecium being shed. Figure 7.11A–D.

### Diagnostic characters and relationships

*Passerina comosa* and *P. quadrifaria* both have abaxially hairy bracts and are easily confused. However, these two species are geographically segregated, with *P. comosa* considered as a 'north-western endemic' of the Cape flora (Weimarck 1941)., while *P. quadrifaria* is endemic to the Karoo Mountain and Southeastern Centres. Morphologically *P. comosa* is less robust, internodes are longer, leaves adhere closely to the stem and are generally more hairy and the bracts often have extended wings that are abaxially setose to villous.

### Etymology

The epithet *comosa* refers to the hairs on the abaxial surface of the leaves, bracts and sepals, which are characteristic of this species.

### Distribution and ecology

*Passerina comosa* ranges from mountain summits and slopes of the Kamiesberg to Calvinia in the Northern Cape. In the Western Cape it is distributed in the area between 33° and 34°S latitude and from 19° to 21°E longitude, with *Primos 41* (PRE) as the most easterly outlier. This species is endemic to the Northern Cape, as well as the Northwestern, Southwestern and Karoo Mountain Centres within the CFR. It occurs on the Roggeveld, Witteberg and the Klein Swartberg mountain ranges. This species is found in sand among rocks, on rocky ledges, on mountain summits, or on SW facing slopes at altitudes of 1 000–1 200 m. Figure 7.11E.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

NORTHERN CAPE.—3018 (Kamiesberg): between Pedroskloof and Leliefontein, (–AB), *Drège 2570* (K, PRE); NE of Leliefontein, (–AC), *Adamson 1515* (PRE); hills E of Leliefontein, (–AC), *Levyns 1515* (BOL). 3119 (Calvinia): between Calvinia and Middelpos, (–BD), *Goldblatt 4380* (MO, NBG).

WESTERN CAPE.—3319 (Worcester): Waterfall, Bergfläche von Bächen durchschnitten, 1 000–2 000 ft, (–AB), *Ecklon & Zeyher s.n.* (C, UPS); Roggeveld, Uitkyk Farm, (–AB), *Marloth 9695* (PRE); Tafelberg, (–CC), *Pillans 17158* (NBG); Stettynsberg, SW slopes, (–CD), *Esterhuysen 11148* (BOL). 3320 (Montagu): Tweedside, (–AB), *Compton 22870* (C, NBG); Witteberg Rocks, Tweedside Slopes, (–AB), *Levyns 2371* (BOL); Tweedside mountain near Matjesfontein, (–AB), *Marloth 10817* (NBG, PRE); Laingsburg, Cabidu, (–BB), *Compton 22218* (NBG, S); Concordia Valley, (–CC), *Michell 333* (PRE); Montagu District, near Concordia, (–CD), *Thoday 212, 212A* (BOL, K, NBG). 3321 (Ladismith): Prince Albert, Klein Zwartebergen, (–AC), *Andraea 1222, 1227* (NBG, PRE); *Curator Pretoria Botanical Garden P42* (PRE); Prince Albert District, Seweweekspoort Mountain, (–AD), *Andraea 1288, 1288A* (PRE); *Barnard s.n.* (NBG); Klein Swartberg above Sand River, N slopes, first slope W of Seweweekspoort Peak, (–AD), *McDonald 2125*, (–NBG); *Stokoe 1790, 1811* (PRE). 3322 (Oudtshoorn): Prince Albert District, Klein Zwartberg, N and S side on ledges, (–BC), *Primos 41* (PRE). Grid ref. unknown: *Burchell 7129* (K); no locality, 1839, *Drège s.n.* (S); *Drège s.n.* (BM, NBG, S); Trinity College, *no collector s.n.* (TCD); *Tyson 77* (GRA).

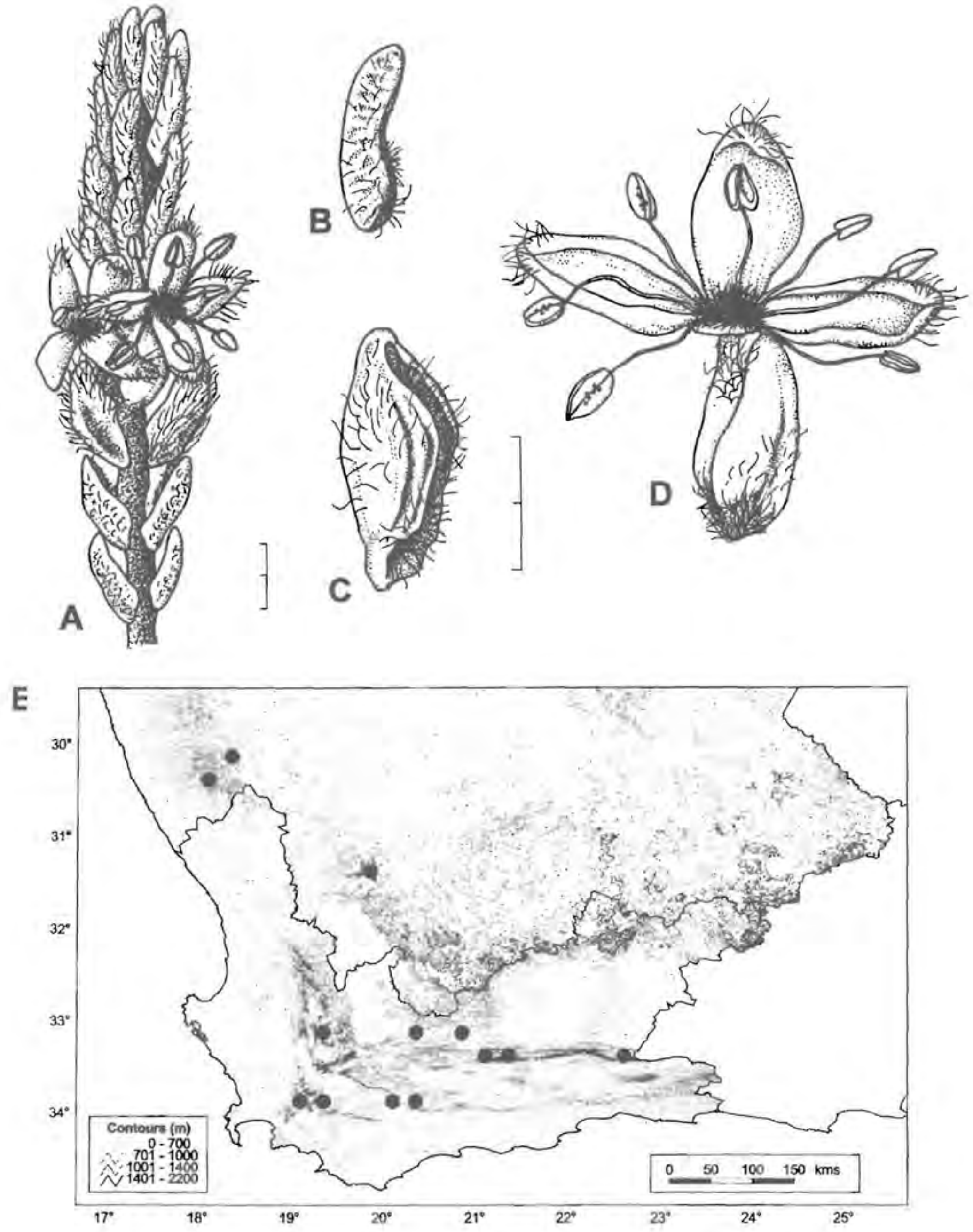

FIGURE 7.11.—*Passerina comosa* (*Andraea 1288*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract. Scale bars: 2 mm.

E, known distribution of *Passerina comosa*.

11. **Passerina pendula** *Eckl. & Zeyh.* ex *Thoday*. Bulletin of Miscellaneous Information. Kew 4: 155 (1924a); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 684 (2000). Type: Uitenhage Division, Zwartkops River, *Ecklon & Zeyher 7381* [K!, lecto., designated by Thoday 10: 387 (1924b); BREM!, P!, PRE!, WU!].

*P. pendula* Eckl. & Zeyh. fide Drège: 210 (1847b) nom. nud.; Meisn. 14: 563 (1857) nom. nud.

*Passerina rigida* Wikstr. var. *comosa* Meisn.: 402 (1840); Drège: 584 (1847a); Meisn. 14: 563 (1857); C.H.Wright: 13 (1915) pro parte; Thoday 4:155 (1924a). Lectotype as above.

Erect, many-stemmed shrubs, 1.0–1.5 m high, young branchlets often pendulous. *Stems* greyish brown, indumentum of young stems densely white-tomentose, flaking off on older branchlets, which become glabrous, remaining indumentum forming lengthwise patterns with grey-brown cork, brown leaf scars prominent. *Leaves* greyish green, imbricate, overlapping ± 25%, appressed, plane shape rhombic, length × depth 2.5–3.4 × 1.0–1.2 mm, adaxial surface concave, comose, abaxial surface convex, softly coriaceous and smooth, glabrous; base sessile, abruptly tapered; apex subacute; margins brownish setose. *Inflorescences* with multiflowered main and co-florescences; spikes usually extended, 6–16-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* greyish green when fresh, grey-brown in dried specimens, appressed, rhombic, length × depth (3.0–)4.2 × 1.0 (–1.5) mm; lamina adaxially concave (inside), abaxially convex (outside), comose inside, glabrous outside, softly coriaceous and smooth, wings membranous; base cuneate; apex obtusely angled; margins brownish setose. *Floral envelope* ± 6.5 mm long, membranous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* glabrous at ovary, neck tomentose, ± 0.6 mm long. *Sepals*: outer sepals cymbiform, adaxially scantily tomentose, abaxially glabrous; inner sepals oblong, adaxially scantily tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 1.5 mm and those of antisepalous whorl ± 2.0 mm long; anthers 0.8 × 0.4 mm, subbasifixed, 2-thecous and 4-locular.

*Ovary* 2.0 × 0.7 mm. *Fruit* an achene with pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in the sepals and androecium being shed. Figure 7.12A–D.

## Nomenclatural notes

*Passerina pendula*, ascribed to Ecklon & Zeyher, was first published as a *nomen nudum* by Drège (1847b). This name was placed in synonymy under *P. rigida* var. *comosa* by Meisner (1857). Wright (1915) partly followed Meisner's interpretation of *P. rigida* var. *comosa*, but in the citation of the specimens he added all those that were later published as *P. burchellii* by Thoday (1924a). In his revision of *Passerina*, Thoday (1924a) reinstated the name *P. pendula* Eckl. & Zeyh. ex Meisn., as the varietal name 'comosa' had already been used at species level by Wright (1915). The present study regards Thoday's publication of *P. pendula* as valid, as it is accompanied by a Latin diagnosis, a description of the species and it was published in 1924. As *P. pendula* Eckl. & Zeyh. ex Meisn. was based on a *nomen nudum*, and since Thoday ascribed the name to Ecklon & Zeyher, the correct author citation for this species is *P. pendula* Eckl. & Zeyh. ex Thoday.

## Diagnostic characters and relationships

*Passerina pendula* is distinguished from *P. burchellii* by being taller (up to 1.5 m), much branched shrubs with pendulous branchlets, with grey-green, softly coriaceous and smooth leaves and yellow-pink membranous flowers that are abaxially glabrous and adaxially scantily tomentose.

## Etymology

The specific epithet *pendula* refers to the pendulous branchlets of these shrubs as seen in their natural habitat.

## Distribution and ecology

*Passerina pendula* is endemic to the Southeastern Centre within the CFR. It is distributed on hills and slopes from the Kouga Mountains in the Western Cape to the Langkloof Mountains and the Great Winterhoek Mountains in the Eastern Cape. The species is also distributed along watercourses as it occurs in the KwaZunga Catchment Basin and on the banks of the Upper Swartkops River as well as the Bushmans River at Port Elizabeth. *P. pendula* grows at altitudes of (133–)383–600 m. On mountain slopes it is often found in a belt above Valley Thicket and below Mountain Fynbos. It grows in sand or shallow, gravelly, sandy loam. The plants are frequent throughout the natural range of the species and a number of populations are conserved in the Groendal Nature Reserve at Uitenhage. Figure 7.12E.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3323 (Willowmore): Uniondale District, Kouga Mountains, (–CB), *Esterhuysen 10733* (BOL); Misgund, (–CD), *Esterhuysen 6962* (BOL); Langkloof below Ongelegen and Misgund, (–CD), *Fourcade 1708* (BOL, K, NBG, PRE).

EASTERN CAPE.—3324 (Steytlerville): Kouga Mountains, Drinkwaterskloof, (–CA), *Euston-Brown 41* (BOL); Humansdorp, Kouga Hills at Sewefontein, (–CB), *Esterhuysen 6678* (K, NBG); Zuur Anys, along road to Kouga, (–CB), *Fourcade 3043* (MO, PRE); channel of Swartkops River, (–DB), *Zeyher 1025* (NBG, TCD); Uitenhage, Swartkops River, valley and hills adjacent to farm of Paul Maré, (–DB), *Ecklon & Zeyher 3781* (G, HAL, P, PRE, S, W, WU); *Zeyer 44* (G, NBG, S, W); Swartkops River, (–DB), *Ecklon & Zeyher 7381* (BREM, K, P, PRE, WU). 3325 (Port Elizabeth): Upper Swartkops River, Groendal Wilderness area, KwaZunga Ridge, (–CA), *Scharf 1067* (PRE); Farm Rietvlei, (–CA), *Scharf 1596* (NBG, PRE); Uitenhage District, Groendal Nature Reserve, Spitskop Road, (–CB), *Bredenkamp 908, 909* (PRE); Great Winterhoek Mountain Range, Matthew's Place Farm, (–CB), *Scharf 1958* (PRE); *Scharf 1959* (K, PRE); near Uitenhage, (–CD), *Ecklon & Zeyher s.n.* (C, S, UPS); Groendal Wilderness area, Ten Stop Hill, (–CD), *Olivier 3197* (PRE); Groendal Wilderness area, catchment basin, (–CD), *Scharf 1013* (PRE); Krakakamma, between Port Elizabeth and Van Stadensberg, (–CD), *Zeyher 3780* (G, P, S, W); Uitenhage, banks of Boesmans River, (–CD), *Zeyher 41* (G, S); Port Elizabeth, (–DC), *Rob & Fries 3395* (UPS, S).

3424 (Humansdorp): Enon conglomerat, Farm Boshoek, (–BB), *Cowling 796* (GRA); 7 mi. N of Humansdorp, (–BB), *Schonland 3054* (GRA, PRE).

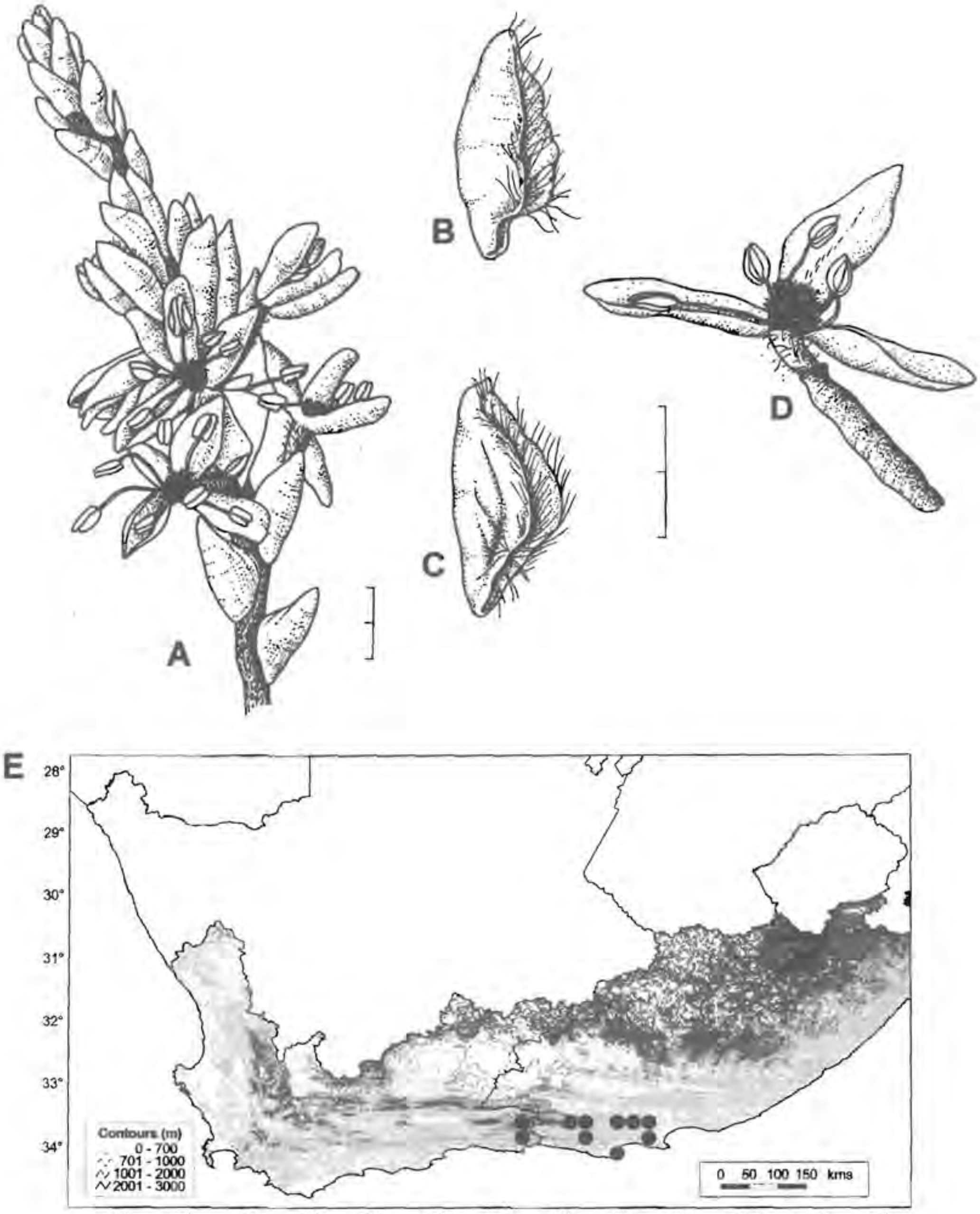

FIGURE 7.12.—*Passerina pendula* (*Bredenkamp 908*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower. Scale bars: 2 mm.

E, known distribution of *Passerina pendula*.

12. **Passerina galpinii** *C.H.Wright*. Flora capensis 5,2: 10 (1915) as *P. galpini*; Thoday 4:161 (1924a); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 683 (2000). Type: Western Cape, Riversdale District, Melkhoutfontein, about 600 ft, 7 October 1897, *Galpin 4491* (K, holo.!; PRE!).

Stunted or erect, much branched shrubs, (0.1–)0.3–1.0(–1.2) m high. *Stems* light greyish brown, indumentum of young stems greyish brown tomentose, cork grey-brown, fissured lengthwise, with sclerenchyma fibres protruding between fissures, leaf scars rounded. *Leaves* greyish green, imbricate, overlapping 10%–25%, diverging at an angle of 30°, plane shape linear, incurved towards apex, length × depth 2.9–4.5 × 0.5–0.8 mm, adaxial surface concave, comose, abaxial surface convex, chartaceous, glabrous; base sessile; apex subacute to obtuse; margins glabrous, involute. *Inflorescences* with spikes subterminal, usually congested, 8–10-flowered, axis whitish tomentose, proliferating growth common. *Bracts* appressed, oblate, length × depth (3.6–)4.5 × 1.1(–2.2) mm; lamina greyish green, adaxially concave (inside), abaxially convex (outside), chartaceous, glabrous outside, midrib extended into leaf-like point, tomentose inside; wings straw-coloured, membranous, broadly rounded, bullate; base cuneate; apex subacute; margins glabrous, involute. *Floral envelope* ± 5.3 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* pubescent at ovary, neck pubescent, ± 1.0 mm long. *Sepals*: outer sepals concave elliptic, glabrous, inner sepals obovate, abaxially glabrous, apex margin adaxially tomentose. *Androecium* with filaments of antipetalous whorl ± 1.4 mm and those of antisepalous whorl ± 2.1 mm long; anthers 0.6 × 0.5 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.0 × 1.1 mm. *Fruit* an achene with pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at circumference of ovary, resulting in the sepals and androecium being shed. Figure 7.13A–D.

### Nomenclatural notes

*Passerina galpini* C.H.Wright (1915), published with a full description, but without a Latin diagnosis, was accepted by Thoday (1924a). In the present study the specific epithet is corrected to '*galpinii*' and the name accepted as validly published by Wright, as the starting date for a Latin diagnosis as prerequisite for valid publication is 1 January 1935 (Greuter *et al*. 2000).

### Diagnostic characters and relationships

*Passerina galpinii* is distinguished by its characteristic bracts, which are oblate, with the midrib extended into a leaf-like point. The lamina is cymbiform, greyish green, chartaceous and glabrous, with the midrib adaxially tomentose. The wings are straw-coloured, membranous, broadly rounded and bullate. The distribution of this species is also diagnostic as it is endemic to the Agulhas Plain Centre within the CFR.

### Eponymy

*Passerina galpinii* was named in honour of the botanist E.E. Galpin. The holotype of this name, *Galpin 4491*, was collected on 7 October 1897. At this time, Galpin organised a collecting trip from Port Elizabeth via the Humansdorp, Knysna, George, Riversdale, Swellendam and Caledon Districts to Cape Town and increased his collecting numbers from 3531 to 4846. All these specimens were probably identified at the Bolus Herbarium in Cape Town, where he also spent a few weeks (Gunn & Codd 1981).

### Common name

Rebelo (1998) mentions the vernacular name *Elim gonna* for this species.

## Distribution and ecology

*Passerina galpinii* is endemic to the Agulhas Plain Centre within the CFR. It is distributed on stony flats, coastal limestone deposits and limestone hills, from Elim to Bredasdorp, Arniston, Stilbaai, Melkhoutfontein, Albertinia and Mossel Bay; it grows at altitudes of 0–290 m. Plants reach a height of ± 1.2 m on stony flats, but become stunted on southeast-facing slopes of limestone hills, overlooking the sea. The plants are frequent in their natural environment. They are conserved in the De Hoop and Potberg Nature Reserves and several private nature reserves. The vegetation of the area is threatened by large stands of *Acacia cyclops* (*rooikrans*), an alien invasive tree. Figure 7.13E.

*Passerina galpinii* is associated with Laterite Fynbos (Rebelo 1998), occurring on the Elim Flats of the Western Cape, which is characterized by gravelly, lateritic and seasonally waterlogged soils. The present study also indicates the presence of this species in Limestone Fynbos, where it occurs on coastal limestone deposits.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3419 (Caledon): Bredasdorp, The Poort, (–DB), *Compton 9066, 14743* (NBG); between Elandspoort and Elim, (–DB), *Levyns 9726* (BOL); De Hoop Nature Reserve, (–AD), *Bredenkamp 946, 947* (PRE); *Van der Merwe 1108* (PRE). 3420 (Bredasdorp): Potberg Nature Reserve, (–BC), *Burgers 2259* (PRE); Hamerkop Farm, (–BC), *Van Wyk 1920* (PRE, PRU); De Hoop, Witwater, (–BD), *Morley 21* (PRE); Hamerkop Farm, (–BD), *Van Wyk 1736* (M, PRE); Arniston, (–CA), *Acocks 22608* (K, PRE); Bredasdorp Poort, (–CA), *Esterhuysen 3016* (BOL); *Esterhuysen 23322* (MO); Bredasdorp District, Klipbrug, (–CA), *Henrici 3701* (BOL); Soetendalsvlei, (–CA), *Henrici s.n.* (NBG); between Bredasdorp and Elim, (–CA), *Leighton 21113* (BOL); Meulvlei Farm, (–CA), *Rosenberg & Rutherford 308* (NBG); 5 mi. inland near Arniston,

(–CA), *Taylor 3803* (PRE). 3421 (Riversdale): 4.5 mi. S of Vermaaklikheid, (–AC), *Acocks 24213* (K, NBG, PRE); Puntjie, Duivenhok's River Mouth, (–AC), *Boucher 2224* (NBG); Puntjie, (–AC), *Bredenkamp 939* (PRE); hills between Riversdale and Stilbaai, (–AC), *Goldblatt 4144* (MO, NBG, PRE); Stilbaai, (–AD), *Bohnen 4012* (C, PRE); Stilbaai Rifle Range, (–AD), *Bohnen 4065* (NBG, PRE); road to Riethuiskraal, (–AD), *Bredenkamp 932* (PRE); Kafferkuil's River at Stilbaai Rifle Range, (–AD), *Bredenkamp 933, 934* (PRE); Riversdale District, Melkhoutfontein, (–AD), *Galpin 4491* (K, PRE); road between Riversdale and Stilbaai, (–AD), *Levyns 9511* (BOL); Melkhoutfontein, (–AD), *Muir 2441* (PRE); Stilbaai, (–AD), *Strauss s.n.* (NBG); Albertinia, Ystervarkpunt Coastal Stoop, (–BC), *Willemse 805* (NBG, PRE). 3422 (Mossel Bay): close to light house at Mossel Bay, (–AA), *Bredenkamp 923* (PRE). Grid ref. unknown: *Ecklon s.n.* (S); Duineveld Limestone hill, *Levyns 9674* (BOL).

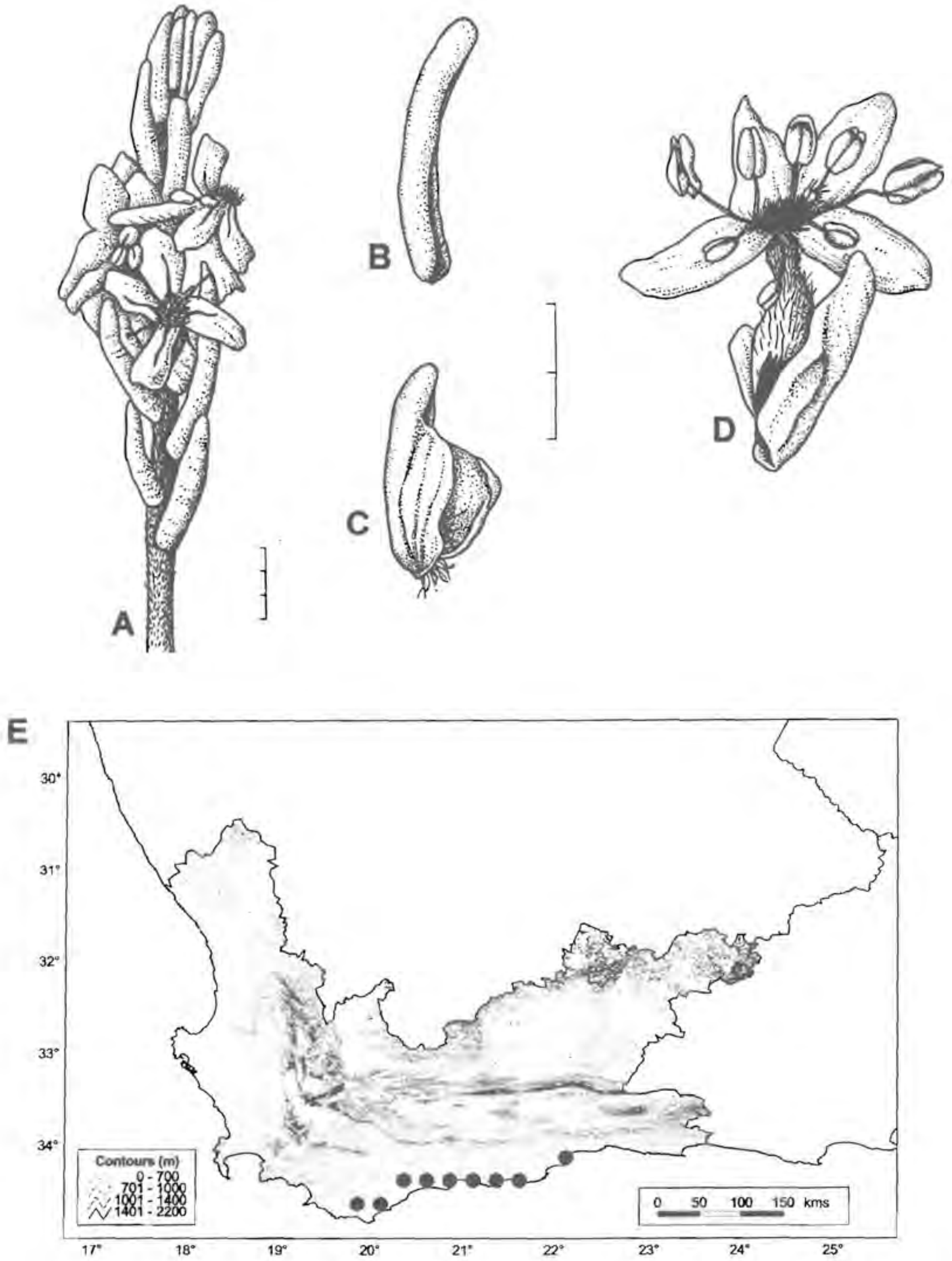

FIGURE 7.13.—*Passerina galpinii* (*Bredenkamp 946*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract, hypanthium fragmenting at circumference of ovary. Scale bars: A 3 mm; B, C, D 2 mm.

E, known distribution of *Passerina galpinii*.

13. **Passerina drakensbergensis** *Hilliard & B.L.Burtt*. Annals of the Kirstenbosch Botanic Gardens 15: 233 (1987); Hilliard & B.L.Burtt: 88 (1988). Type: KwaZulu-Natal, Harrismith, Bergville District, Cathedral Peak Forest Reserve, Ndedema River, 6 000 ft, 5 November 1985, *Hilliard & Burtt 18570* (E, holo.; K!, M!, P!, PRE!, S!).

Erect, many-stemmed shrubs, ± 2.0 m high, much branched. *Stems* grey-brown, indumentum of young stems closely white-tomentose, flaking off on older branches, forming lengthwise patterns with patches of yellowish brown cork, leaf scars prominent. *Leaves* greyish green (glaucous), imbricate, overlapping ± 15%, appressed, plane shape linear to lanceolate, longitudinaly folded and somewhat keeled, length × depth (3.5–)4.2–5.5(–6.5) × 0.8–2.0 mm, adaxial surface concave, tomentose, abaxial surface slightly convex, rugose, glabrous; base sessile, abruptly narrowed; apex subacute, sometimes incurved; margins setose. *Inflorescences* with multiflowered main and co-florescences; spikes usually extended, 8–12-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* greyish green (glaucous), appressed, lanceolate, length × depth 4.75–6.0(–7.0) × 1.5 mm; lamina folded lengthwise and keeled, adaxially concave (inside), abaxially slightly convex (outside), villous inside, glabrous outside, coriaceous, obscurely ribbed and reticulately veined; base cuneate; apex obtuse to acute; margins sometimes narrowly membranous. *Floral envelope* ± 5.9 mm long; papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* scantily tomentose at ovary, neck tomentose, ± 1.7 mm long. *Sepals*: outer and inner sepals concave lanceolate, outer sepals adaxially glabrous, abaxially tomentose; inner sepals adaxially and abaxially tomentose. *Androecium* with filaments of antipetalous whorl ± 1.2 mm and those of antisepalous whorl ± 2.0 mm long; anthers oblong, 0.9(–1.25) × 0.3 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.4 × 0.9 mm. *Fruit* an achene with pericarp membranous and dry, 2.5 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in the sepals and androecium being shed. Figure 7.14A–D.

## Diagnostic characters and relationships

*Passerina drakensbergensis* is characterized by appressed leaves, up to 6.5 mm long. The bracts are lanceolate, up to 7.0 mm long, the apex is obtuse to acute without a leaf-like point and membranous wings are absent. It can easily be confused with *P. montivaga* and *P. montana*, both occurring in the northern KwaZulu-Natal Drakensberg area. *P. montivaga* has longer leaves (up to 8 mm) and bracts with the midrib extended, forming a straight or filiform, leaf-like point. The wings are ovate with margins hairy in distal half, or obtrullate, narrowing abruptly into the midrib. *P. montana* can be separated by its terminal subcapitulate spikes and short leaves (up to 4.0 mm long), which are linear to lanceolate, with a dilated base and with a prominent median vein in the upper third of the leaf, incurved at the acute apex. The bracts are ovate to obovate in outline.

*Passerina montivaga* is a fynbos element which possibly originated in the southern Cape and dispersed eastwards. Both this species and *P. montana* are distributed from the Eastern Cape via the Drakensberg Mountains northwards to Zimbabwe. Although the distribution of *P. drakensbergensis*, *P. montivaga* and *P. montana* overlap in the northern part of the KwaZulu-Natal Drakensberg, significant trends in the geographical and altitudinal ranges of these species have been identified.

## Etymology

The specific epithet refers to the location of this species in the northern KwaZulu-Natal Drakensberg.

## Distribution and ecology

*Passerina drakensbergensis* is endemic to the Bergville District in the northern KwaZulu-Natal Drakensberg. It has been collected from the Royal Natal National Park to Giant's Castle Game Reserve at altitudes between 1 500 and 1 980 m. It is frequent at Cathedral Peak above Ndedema Gorge, where it is found in a marginal belt between forest and grassland. It also grows along streams and riverbanks and on mountain slopes. Figure 7.14E.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

KWAZULU-NATAL.—2828 (Bethlehem): Bergville District, Royal Natal National Park, path to Mahai Falls, (–DB), *Edwards 973*, *974* (BOL, PRE). 2829 (Harrismith): Bergville District, Cathedral Peak Forest Station, above Ndedema River, (–CC), *Hilliard & Burtt 18570* (K, M, P, PRE, S); *Levyns 8236* (BOL); Ndedema Gorge near burning plots, (–CD), *Bredenkamp 1018–1021* (PRE). 2929 (Underberg): Cathedral Peak Forest, upper Indumeni River Valley, (–AB), *Killick 1973* (PRE); in Ndedema Valley, (–AB), *Killick 2289* (PRE); Giant's Castle Game Reserve, Loembazo area, (–AB), *Trauseld 860* (PRE); Estcourt District, Tabamhlope Mountain, (–BA), *West 181* (PRE); Giant's Castle Game Reserve, Mlombazo Stream, (–BB), *Trauseld 435* (PRE).

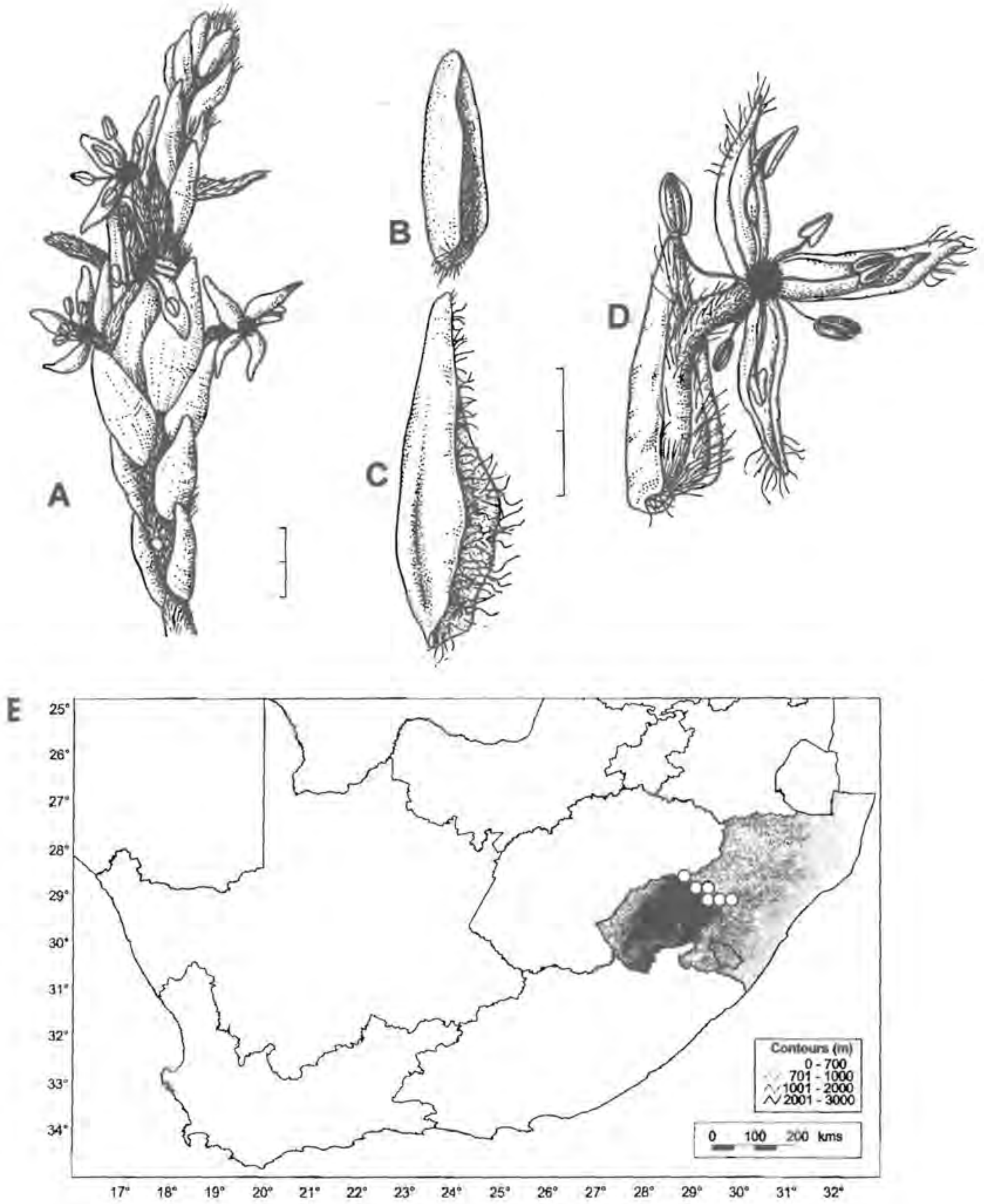

FIGURE 7.14.—*Passerina drakensbergensis* (*Bredenkamp 1021*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract. Scale bars: 2 mm.

E. known distribution of *Passerina drakensbergensis*.

14. **Passerina corymbosa** *Eckl.* ex *C.H.Wright*. Flora capensis 5,2: 14 (1915); Thoday 4:162 (1924a). Type: Western Cape, Bredasdorp, Zwellendam, Pupas Valley, Voormansbosch and Duivelsbosch, Keurboomsrivier, October, *Ecklon & Zeyher 40* (*70.10*) (B, holo.†; W!, lecto., here designated; MO!, S!).

*Passerina filiformis* L. var. *vulgaris* Meisn.: 399 (1840); Meisn. 14: 562 (1857): Drège: 87 (1843). *P. vulgaris* (Meisn.) Thoday 4: 162 (1924a); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 684 (2000). Type: locis subhumidis secus rivulum, prope Paarlberg, alt. 1 000–1500 ped. [subhumid locality along river, near Paarlberg, alt. 1 000–1 500 ft], Nov.–Dec. 1839, *Drège s.n.* [K, lecto., designated by Thoday 10: 388 (1924b); S!, W!].

*Passerina filiformis* sensu C.H.Wright: 11 (1915) pro parte, non L.

Much branched shrubs, (0.3–)1.0–1.5(–2.5) m high, younger branchlets leafy, older ones leafless, often arcuate, indurate. *Stems* often arising from a woody, underground rootstock, greyish brown, indumentum of young stems closely whitish tomentose, forming lengthwise patterns with cork on older branches, which gradually become glabrous; cork fissured lengthwise, with sclerenchyma fibres protruding between fissures; leaf scars oblate. *Leaves* greyish green, drying greyish brown, ascending, diverging at an angle of ± 40°, imbricate, overlapping up to 50%, laterally compressed, plane shape linear to narrowly lanceolate, length × depth (2.0–)3.2–4.4 (–10.0) × 0.5–0.8 mm, adaxial surface concave, tomentose, abaxial surface glabrous; lamina longitudinaly folded, midrib distinct and somewhat keeled, with 2 or more lateral veins visible as faint striae when fresh, base sessile; apex tapered or acute; margins glabrous, involute. *Inflorescences* with multiflowered main and co-florescences; spikes usually extended, 10–16-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* greyish green, ascending, rhombic to obtrullate, distictly angled, length × depth (4.4–)5.1 × 1.4(–1.7) mm; lamina folded lengthwise and keeled, adaxially concave (inside), abaxially slightly convex (outside), shortly villous inside, glabrous outside, coriaceous; wings coriaceous, distinctly 4- or 5-ribbed; base cuneate; midrib shortly extended into an acute apex; margins glabrous, involute. *Floral envelope* ± 6.2 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* glabrous at ovary, neck scantily tomentose, ± 1.6 mm long. *Sepals*: outer sepals cymbiform, inner sepals obovate, outer and inner sepals adaxially scantily tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 0.7 mm and those of antisepalous whorl ± 1.4 mm long; anthers ovoid, 0.9 × 0.4 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.1 × 1.1 mm. *Fruit* an achene with pericarp membranous and dry, 2.6 × 1.5 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in the sepals and androecium being shed. Figure 7.15A–G.

## Diagnostic characters and relationships

*Passerina corymbosa* can be distinguished by its greyish green leaves and grey-brown stems of which the older branchlets are leafless, often arcuate and indurate. The leaves are laterally compressed with the distinct midrib somewhat keeled. The rhombic to obtrullate (diamond-shaped) bracts are always conspicuously angled and distinctly 4- or 5-ribbed. The most diagnostic leaf anatomical character of *P. corymbosa* is the presence of a hypodermal sclerenchymatous sheath, illustrated by Bredenkamp & Van Wyk (2001; see x.x). This species has always been confused with *P. filiformis sensu lato*, which has inconsistently been distinguished by longer, filiform leaves. In the Western Cape *P. filiformis* subsp. *filiformis* is separated by widely obovate bracts, narrowing abruptly into a filiform point. Where the distribution of *P. corymbosa* and *P. montivaga* overlap in the southern Cape, the latter species is distinguished by bracts with ovate wings and margins that are hairy in the distal half. In the Eastern Cape *P. montivaga* is distinguished by obtrullate bracts narrowing abruptly into a straight, leaf-like point.

## Etymology

Of all the species in the genus, *Passerina corymbosa* is the most common, as it is adapted to a wide range of habitats mostly in the Western and Eastern Cape Provinces. The specific Latin epithet *corymbosa* (= with a cluster of flowers or of fruits) is indicative of the 10–16-flowered, extended spikes usually arranged in multiflowered main and co-florescences.

### Common names

According to Van Wyk & Gericke (2000), *P. corymbosa* (formerly known as *P. vulgaris*) can also be called *bakkersbos*, a name that commemorates an era when the official bakers in the Cape used this plant to heat up their outside ovens.

### Uses

From an agricultural point of view, Story (1952) described *P. corymbosa* at Keiskammahoek as an unpalatable bush, which remained undamaged from grazing, among the few closely cropped specimens of *Cliffortia linearifolia* Eckl. & Zeyh. and *C. paucistaminea* Weim. However, the value of *P. corymbosa* as a pioneer, and also in combatting erosion, cannot be underestimated. This species is commonly found along roadsides and in other disturbed places. It is one of the most successful species for the rehabilitation of embankments along newly built roads in the Western and Eastern Cape Provinces. The plants are resprouters from woody, underground rootstocks and are excellent sand binders, often found on coastal sand dunes. Considering the human impact and invasion of alien vegetation along the Cape coast, *P. corymbosa* would be a natural pioneer, combatting erosion in areas where alien vegetation is cleared.

### Distribution and ecology

Except for a few outliers, *P. corymbosa* is endemic to the Western and Eastern Cape Provinces, and all the phytogeographic Centres within the CFR. Although this species is distributed from Clanwilliam to Cape Town and eastwards to East London, it most commonly occurs in an area between the coast and the 33°S latitude and from 18° to 29°E longitude. *Gerstner 105* (PRE), collected near Compasberg in the Lady Grey District, represents the most northerly distribution of *P. corymbosa* in the

Eastern Cape. The specimens collected in KwaZulu-Natal are regarded as outliers, representing remnants of a former wider distribution. *Hilliard 4081* (PRE), collected at the Ellesmere Farm in Ngome (KwaZulu-Natal), is an anomalous specimen, with a greyish appearance, infected by fungi and recorded from cliff faces. This specimen was classified as *P. corymbosa* on the basis of the angular bracts and the leaves that are laterally compressed. The other two specimens, *Herb. Poeppig s.n.*, probably collected before 1868, and *Rudatis 1204* (PRE), collected in 1910, represent populations that have possibly succumbed to human impact. Figure 7.15H.

*Passerina corymbosa* is a species with a wide habitat spectrum. It most commonly occurs as a pioneer along roadsides over the whole range of its distribution. The species is found in stony areas on mountain slopes, peaks and mountain passes. Along the coastal region, it is often found on the rear dunes. It also grows in river valleys and on the banks of river mouths. This species is common in the whole of the Fynbos Biome of the CFR. In the Eastern Cape it is found in all the above-mentioned habitats, but also in grassland. Story (1952) reported that *P. corymbosa* is found in sourveld and mixed grassveld but that it showed no sign of advancing into the sweetveld. In open grassland this species is often clustered along streambanks or on rocky areas. *P. corymbosa* occurs at a range of altitudes, from sea level up to 1 300 m.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

KWAZULU-NATAL.—2731 (Louwsburg): Ngome; Ellesmere Farm, (–CD), *Hilliard 4081* (K, PRE). 2931 (Stanger): Port Natal, (–CC), *Herb. Poeppig s.n.* (M, PRE). 3030 (Port Shepstone): Dumisa Station, Alexandra, (–AD), *Rudatis 1204* (K, PR, PRE, S).

EASTERN CAPE.—3027 (Lady Grey): Lady Grey, (–CA), *Gerstner 105* (PRE). 3124 (Hanover): Near Compasberg, (–DC), *Levyns 9603* (BOL). 3126 (Queenstown): Gwatyn, Junction Farm, (–DD), *Galpin 8279* (PRE). 3224 (Graaff-Reinet): Koudeveld Mountains, SE of Doornbosch, (–AA), *Oliver 5226* (PRE); Sneeuberg, (–AA), *Collector unknown 170* (S); Summit of Oudeberg, (–CC), *Bolus 170* (BOL, K). 3226 (Fort Beaufort): Mitchell's Pass, (–DB), *Marloth 10693* (PRE). 3227 (Stutterheim): Keiskammahoek, Wolf River Plateau, (–CA), *Stayner 24* (GRA, PRE); near beacon, *Lanyokwe 97*, (–CA), *Story 3885* (GRA); Mount Coke, (–CD), *Sim 1380, 1499* (C, NBG). 3228 (Butterworth): Sea shore near Kei River Mouth, (–CB), *Flanagan 1478* (BOL); East London, Gonubie Springs, (–CC), *Levyns 10833* (BOL). 3323 (Willowmore): Grootwes River, Nature's Valley, (–DC), *Parsons 169* (PRE); Kouga, Braam River near Joubertina, (–DD), *Esterhuysen 16295* (PRE). 3324 (Steytlerville): Opkoms, off Long Kloof, (–CA), *Bayliss 6117* (PRE); Harkerville, (–CD), *Bredenkamp 916* (PRE); Baviaanskloof, near Cambria, (–DD), *Van Wyk 390* (PRE). 3325 (Port Elizabeth): Zuurberg District, Melkhoutboom Cave, (–BC), *Louwrens A7763* (GRA); Zuurberg Mountains, (–BC), *Lubke s.n.* (GRA); Uitenhage District, Groendal, Spitskop Road, (–CB), *Bredenkamp 907* (PRE); Enon, (–CB), *Thode 1120* (PRE); Van Staden's Pass, (–CC), *Toughton 156* (GRA); Cockscomb, Great Winterhoek Mountains, (–CD), *Esterhuysen 27139a* (BOL); Port Elizabeth, German school, (–DC), *Drège 285* (GRA); Port Elizabeth, (–DC), *Drège TRV 10800* (PRE); St George's Park, (–DC), *Long 790* (GRA, PRE); driftsands Port Elizabeth, (–DC), *Sim 20* (K). 3326 (Grahamstown): Howison's Poort, (–AC), *Britten 2562* (GRA); Woest Hill, Albany, (–AD), *Bayliss 5035* (B, MO); Grahamstown, Gunfire Hill, (–AD), *Bredenkamp 901* (PRE); Albany, (–AD), *Dyer 963–966* (GRA, PRE); Grahamstown, Far Away, (–AD), *Jacot-Guillarmod 10003* (GRA, PRE); stony slopes near Grahamstown, (–AD), *MacOwen 103* (GRA, K, TCD); Howison's Poort, (–AD), *Reed 35* (GRA); Albany District, Highlands Road, Slaai Kraal Farm, (–AD), *Wells 2998* (PRE); Settler's Dam Road, *Bayliss 5289* (MO); Botha's Hill, drift between Grahamstown and Fort Brown, (–BA), *Britten 5522* (PRE); Botha's Ridge, (–BA), *Dyer 970* (PRE); Andries Vosloo Kudu Reserve, (–BA), *White 95* (GRA); Grahamstown, old municipal quarry, (–BC), *Bayliss BRI.B.32* (GRA, MO, PRE); Grahamstown, (–BC), *Bayliss 2468* (B, MO, NBG); Hillview road 33, left hand side of road, (–BC), *Bredenkamp 902* (PRE); Botha's Hill, (–BC), *Bredenkamp 903* (PRE); Grahamstown, (–BC), *Breijer TRV 16898* (PRE); Gunfire Hill, (–BC), *Britten 5489* (PRE); Farm Gretua, (–BC), *Dacombe s.n.* (GRA); Fish River Mouth, (–BC), *Dold 1099* (GRA); bush past Hamilton Dam, (–BC), *Dyer 179, 180* (PRE); Penrock Farm, (–BC), *Dyer 597* (GRA, K, PRE); Botha's Ridge, (–BC), *Dyer 962, 967, 968* (GRA, K, PRE); Hope's Garden Hill, (–BC), *Galpin 251* (PRE); Signal Hill, (–BC), *Levyns 3763* (BOL); Mountain Drive, (–BC), *Marloth 10912* (PRE); Grahamstown, (–BC), *Noel 322* (GRA); Milner Dam, (–BC), *Ramsay 1592* (GRA); Gunfire Hill, (–BC), *Rennie 480* (BOL, GRA); Grahamstown, (–BC), *Sim 19659* (PRE); *Van Dam TRV 23994* (PRE); Blaauwkrantz Drift, (–BD), *Britten 2828* (PRE); Grahamstown, (–BD), *Wirminghaus 178* (GRA); Bushmans River Poort, on Witteberg, (–CB), *Archibald 5583* (PRE); Waai Heuwel, (–CB), *Archibald 5727* (PRE); Tootabi, (–CB), *Archibald 6053* (PRE); Hopewell, (–DA), *Acocks 23848* (PRE); Boknes, (–DA), *Botha 2618* (PRE); Southwell District, (–DA), *Britten 2239* (PRE); Boknes Strand, (–DA), *Burrows 3066* (GRA); Kariega Park, (–DA), *Burrows 3956* (GRA); Kowie, (–DB), *Britten 5008* (GRA, PRE); Port Alfred, (–DB), *Hutton 1603* (K); Bathurst District, (–DB), *Sidey 3595, 3801* (PRE, S). 3327 (Peddie): 2.6 km to Kiwane from main Peddie–East London Road, (–BA), *Bredenkamp 896* (PRE); East London, (–BB), *Breijer TRV 16577* (PRE); East London, Potter's Pass, (–BB), *Jacot-Guillarmod & Brink 29* (GRA). 3423 (Knysna): Stormsriver Mouth, (–BB), *Rourke 3000* (NBG). 3424 (Humansdorp): Witte Els Beach, (–AB), *Fourcade 952* (BOL, GRA); 100 m from turn-off to Jeffreys Bay en route to N2, (–BB), *Bredenkamp 912* (PRE); St Francis Bay, (–BB), *Cowling 51* (GRA); *Lubke 1861* (GRA); 18.4 mi. from Humansdorp to Cape St Francis, (–BB), *Marsh 1361* (PRE). 3425 (Skoenmakerskop): Cape Receife, (–BA), *Olivier 2988* (GRA); near Skoenmakerskop, (–BA), *Theron 631* (PRE).

WESTERN CAPE.—3218 (Clanwilliam): between Paleisheuwel and Leipoldtville, (–AB), *Werdermann & Oberdieck 476* (B, PRE); Clanwilliam, slopes down Langvlei, SE of Swartboskraal, (–BB), *Bean & Viviers 1508* (BOL); Piquetberg, 9.5 mi. NE of Velddrif, (–CC), *Acocks 19810* (NBG); Piquetberg, (–DA), *Marloth 6218* (PRE); Het Kruis, (–DA), *Stokoe s.n.* (NBG). 3222 (Beaufort West): Nuweveld, W slopes of Gert Adrian's Kop, (–BA), *Bremer 299* (BOL). 3318 (Cape Town): Hopefield District, 16.8 mi. NW of Ysterfontein, (–AB), *Acocks 20714* (PRE); Darling, Zonquasfontein Farm, (–AB), *Boucher 3301* (PRE); Hopefield, (–AB), *Letty 142* (PRE); Ysterfontein, (–AC), *Van Rensburg 151* (PRE); Platteklip, (–AD), *Marloth 2756* (PRE); near Mamre to Darling Road, (–CB), *Boucher 2449* (PRE); near Melkbosstrand, (–CB), *Esterhuysen 781* (MO); Kirstenbosch, (–CD), *Barker 349* (PRE); Camps Bay, (–CD), *Bredenkamp 957, 958* (PRE); Table Mountain, (–CD), *Ecklon 508* (BOL, HAL, M, PR, PRE, S, W,); Table Mountain, (–CD), *Ecklon 590* (S); Kirstenbosch, (–CD), *Forbes 160* (PRE); Newlands, (–CD), *Hafström s.n.* (S); Kirstenbosch, cultivated, (–CD), *Hilger 83/60* (M); Devil's Peak, (–CD), *Marloth 1585* (PRE); Pipe Track, (–CD), *McKinnon s.n.* (NBG); Kirstenbosch Reserve, (–CD), *Meebold 15151* (M); Cape Town, (–CD), *Meebold 15159* (M); *Pappe s.n.* (GRA); slopes above Camps Bay, (–CD), *Pillans 2792* (BOL); slope of Kirstenbosch Ridge, (–CD), *Pillans 8030* (BOL); Kirstenbosch Reserve, (–CD), *Schmidt 567* (M); Oranjezicht, (–CD), *Thoday 42* (NBG); Camps Bay, (–CD), *Thoday 52* (BOL, NBG); Kirstenbosch, (–CD), *Wall s.n.* (S); Table Mountain, (–CD), *Zeyher s.n.* (C); Cape Town, *Burchell 473* (K); Burgers Post Farm, near Pella, (–DA), *Boucher & Shepherd 4828* (PRE); Paarl, (–DB), *Bolus 2924* (K); Paarl Mountain, (–DB), *Cummings s.n.* (GRA); *Drège s.n.* (S, W); *Van der Merwe 964* (PRE); Wellington District, (–DB), *Wawra 3* (PRE); Milnerton, intersection of Malmesbury, Parow Roads, (–DC), *Boucher 3243* (PRE); E slope of Table Mountain at Constantia, (–DC), *Ecklon & Zeyher 37* (MO, S); Newlands, (–DC), *Ecklon & Zeyher 3782* (NBG, W); Kraaifontein, Beecroft Farm, (–DC), *Esterhuysen 961* (BOL); Constantia Road, (–DC), *Hafström s.n.* (S); Cape Town, (–DC), *Pappe s.n.* (NBG); Bellville, (–DC), *Rogers 17281* (BM); Table Mountain, (–DC), *Wall s.n.* (S); Constantia Neck, (–DC), *Wall s.n.* (S); Stellenboschberg, W foot below Donkergatkloof, (–DD), *Boucher 1955* (PRE); Jonkershoek Valley, Black Bridge, (–DD), *Brown 490* (PRE); Jonkershoek Forest Reserve, below Lambrechtsbos, (–DD), *De Kock 134* (PRE); Jonkershoek, Swartboschkloof, (–DD), *McDonald 819* (NBG, PRE); Stellenbosch District, (–DD), *Potts 1281* (PRE); Assegaaibos, (–DD), *Van der Merwe 1225* (PRE). 3319 (Worcester): Tulbagh Kloof, (–AA), *King 1* (M, PRE); Piquetberg, 9.5 mi. from Velddrift, (–AC), *Acocks 19810* (K, PRE); Watervalberg, Kleitjieskraal Forestry Plantation, (–AC), *Bredenkamp 974* (PRE); pass between Wolseley and Ceres, (–AC), *Bredenkamp 979, 980* (PRE); Waterfall Forest Station, Tulbaghweg, (–AC), *Fellingham 202* (PRE); Tulbagh Kloof, (–AC), *King 1* (BM, MO); Tulbagh, (–AC), *Levyns 2550* (BOL); Wolseley, banks of Breede River, (–AC), *Marloth 6189* (PRE); N of Wellington, Elandskloof Mountains, (–AC), *Stokoe s.n.* (NBG); Worcester, Tulbagh Waterfall,

(–AC), *Zeyher 34* (NBG); Mitchell's Pass, 12 km SW of Ceres along road to Tulbagh, (–AD), *Greuter 21845* (B, PRE); Ceres, (–AD), *Meebold 15153* (M); Bains Kloof, (–CA), *Gentry 18995* (PRE); *Germishuizen 4077* (PRE); Du Toits Kloof, (–CA), *Maguire 1127* (M); Bains Kloof, (–CA), *Thoday 13* (NBG); Worcester at Waterfall, (–CB), *Ecklon 1.11* (B, S); Orchard Siding, (–CB), *Rogers 16701* (K); Worcester, Waterfall, (–CB), *Zeyher s.n.* (MO); Wemmershoek Mountains, (–CC), *Davidson 24904* (PRE); Franschhoek, (–CC), *Phillips 1294* (NBG); Zachariashoek Catchment, Kasteelkloof, (–CC), *Van Wilgen 163* (PRE); Villiersdorp in Botanical Garden, (–CD), *Bredenkamp 964, 965* (PRE); Botha's Halt, *Van Breda 679* (PRE). 3320 (Montagu): Laingsburg District, Witteberg Kloof, (–BC), *Compton 3005, 3166, 5915* (BOL, K); Cogman's Kloof, (–CC), *Kuntze s.n.* (K); *Michell 24* (PRE); Barrydale Mountains, (–DC), *Barnard s.n.* (NBG). 3321 (Ladismith): Matjiesvlei, Huis River, (–BC), *Bayliss 5023* (M, MO); Towerkop, (–CA), *Wurts 1211* (NBG); road between Riversdal and Stilbaai, (–CB), *Bredenkamp 931* (PRE); Witwater, en route to Korentherivier Dam, foot of Gysberg Pass, (–CC), *Bredenkamp 926* (PRE); summit of Garcia Pass, (–CC), *Bredenkamp 927* (PRE); Rooiberg, kloof W of Teeboskop, (–DA), *Oliver 5342* (PRE); Mossel Bay District, Cloete's Pass, (–DD), *Muir 12, 240* (NBG, PRE). 3322 (Oudtshoorn): Zwartberg, behind Ladismith, (–AC), *Levyns 2325* (BOL); George, Langekloof, (–CC), *Ecklon & Zeyher 100/12* (S); Uniondale Division, S slope Mannetjiesberg, (–DB), *Williams 1451* (NBG); Sedgefield District, near Rondevlei, (–DC), *Bayliss BRI.B.1105* (PRE); southern Cape, Ebb and Flow Nature Reserve, (–DC), *Boucher 2012, 2014* (PRE); *Taylor 7987, 7988* (PRE); Kaaiman's River, (–DC), *Wilman s.n.* (PRE); Oudtshoorn, *Jacot-Guillarmod 7610* (GRA). 3323 (Willowmore): Uniondale, (–CA), *Barnes 88* (GRA); Prince Alfred's Pass, Dieprivier, (–CC), *Thompson 3318* (K, MO, PRE); Knysna, Keurboomsrivier Hillsides, (–CD), *Compton 21673* (C, MO); *Theron 2097* (PRE); Bietou River, (–CD), *Theron 2216* (PRE ); Zwellendam, Keurboomsrivier, (–CD), *collector unknown* (S). 3418 (Simonstown): Wineberg Hill, (–AB), *Andraea 597* (PRE); Chapman's Peak, (–AB), *Bredenkamp 959* (PRE); St James Mountain, (–AB), *Davies 33* (PRE); Caput Bonae Spei, (–AB), *Ecklon s.n.* (C); Chapman's Peak Drive, on road to Noordhoek, (–AB), *Germishuizen 4097* (PRE); Bakoven, (–AB), *Hafström s.n.* (S); Muizenberg, (–AB), *Lansdell s.n.* (PRE); Kommetjie, (–AB), *Lavranos 11652* (PRE); Muizenberg, (–AB), *Lynes 1927* (BM); Simonstown, (–AB), *Meebold 15160* (M); between summits of Vlakkeberg and Skoorsteenkop, (–AB), *Pillans s.n.* (BOL, MO); E of Mowbray, (–AB), *Pillans 3779* (BOL, PRE); Constantia Bervliet Farm, (–AB), *Purcell s.n.* (NBG); Wineberg Hill, (–AB), *Salter 9370* (BM); slopes W of Hout Bay, (–AB), *Salter s.n.* (BOL); Glencairne Hill, (–AB), *Schmidt 569* (M); Hout Bay, (–AB), *Wall s.n.* (S); *Wright s.n.* (K); Cape of Good Hope, (–AD), *Alexander-Prior s.n.* (PRE); Cape Peninsula, (–AD), *Behemiae s.n.* (PR); near Cape Town, (–AD), *Bolus s.n.* (BOL); *Grondahl s.n.* (S); Cape Point, (–AD), *Mortensen 200* (C); Cape Peninsula, (–AD), *Oldenland, Herb. Schreb. s.n.* (M); *Osbeck s.n.* (S); *Sieber 74* (BOL, HAL, M, NBG, P, PRE, S, W); Cape of Good Hope Nature Reserve, at Rhebok's Dam, (–AD), *Taylor 5281* (PRE); Cape Flats, Tygerberg, (–BA), *Smuts s.n.* (NBG); foot of Sir Lowry's Pass en route to Villiersdorp, (–BB), *Bredenkamp 963* (PRE); between Gordon's Bay and Kogelbaai, (–BB), *Ihlenfeldt 1652* (PRE); Steenbras Siding, (–BB), *Phillips s.n.* (NBG); Stellenbosch, Van der Stel Triangle, (–BB), *Smith 4637, 4649* (PRE);

Sir Lowry's Pass, (–BB), *Van Rensburg 444* (PRE); Groot Hangklip Mountain, (–BD), *Boucher 761* (PRE); Betty's Bay, Harold Porter NBG, (–BD), *Bredenkamp 951*, *953* (PRE); at Kogelbaai close to Rooiels River, (–BD), *Bredenkamp 955* (PRE); Harold Porter NBG, (–BD), *Ebersohn 136* (NBG); Pringle Bay, (–BD), *Greuter 21517* (PRE). 3419 (Caledon): near Caledon, (–AA), *Penther s.n.* (M, S); Houwhoek near Caledon, (–AA), *Penther 2891* (M, S, W); Kleinmond, Houw Hoek Pass, (–AA), *Werdermann & Oberdieck 691*, *693* (B, PRE); Hermanus, (–AC), *De Beer TRV 16536* (PRE); Bot River, (–AC), *O'Callaghan 273* (PRE); Hermanus, (–AC), *Purcell s.n.* (NBG); *Rogers 26574* (GRA, NBG, PRE); *Van Breda 1664* (PRE); *Walters 2143* (NBG); Fern Kloof, (–AD), *Orchard 312* (C, MO, PRE, S); Mosselrivier, (–AD), *Potts s.n.* (NBG); Stanford, New Granton Farm, (–AD), *Van der Walt 409* (PRE); Vogelgat, (–AD), *Williams 2624* (MO, PRE); Little Hangklip, (–BD), *Levyns 10873* (BOL); Hangklip, (–BD), *Van Rensburg 2148* (PRE); Baardscheersbos, (–DA), *Stokoe s.n.* (NBG). 3420 (Bredasdorp): Swellendam, (–AA), *Burke 45* (K, PRE); Bontebok National Park, (–AB), *Barnard 660* (PRE); *Bredenkamp 943* (PRE); Puspas Valley, Voormansbos, (–AB), *Ecklon & Zeyher 40 (70.10)* (B, BREM, C, S, W); Zwellendam 1 000–4 000 ft, (–AB), *Ecklon & Zeyher s.n.* (GRA); Bontebok National Park, (–AB), *Grobler 454* (NBG, PRE); Swellendam, (–AB), *Zeyher s.n.* (K, P); 13.3 mi. NE of Malgas, (–BA), *Acocks 23379* (PRE); Potberg, (–BC), *Bredenkamp 945* (PRE); *Burgers 1188*, *2270* (PRE); near Cupidoskraal, E side of Potberg, (–BC), *Mauve & Hugo 167* (MO, PRE); Hamerkop Farm, (–BC), *Van Wyk 1920* (PRE, PRU); Cape Infanta, (–BD), *Bredenkamp 944* (PRE); De Hoop, Witwater, (–BD), *Morley 92* (M, PRE); The Poort, Bredasdorp, (–CA), *Acocks 1519* (S); limestone hills near Potberg, (–CA), *Esterhuysen 23319* (BOL); The Poort, (–CA), *Levyns 4443* (BOL); 6 mi. SW of Bredasdorp, (–CA), *Sidey 1812* (MO, PRE, S); Northumberland Point, (–CC), *Acocks 24257* (PRE). 3421 (Riversdale): Zoetmelk's River, (–AB), *Muir 4469* (K, PRE); hills near Riversdale, (–AB), *Muir 4538* (PRE); Brandfontein, (–AB), *Smith 5081* (PRE); 4.5 km S of Vermaaklikheid, (–AC), *Bredenkamp 936* (PRE); Takkiesfontein, (–AD), *Hugo 1241* (PRE); Albertinia District, Ystervarkfontein, (–BA), *Bayliss 5238* (MO); Riversdale District, Albertinia, (–BA), *Muir 683* (BOL, PRE); Albertinia, near cemetery, (–BB), *Bredenkamp 925* (PRE); between Gouritzmond and Stilbaai, (–BC), *Rycroft 3117* (S). 3422 (Mossel Bay): N2 near Klein Brak, (–AA), *Bredenkamp 924* (PRE); between Great and Little Brak Rivers, (–AA), *Burchell 6163* (K); Mossel Bay, Cloete's Pass, (–AA), *Levyns 9644* (BOL); 3 mi. W of Great Brak River crossing national road, (–AA), *Marsh 572* (PRE); Mossel Bay, (–AA), *Rogers 27026* (PRE); *Thompson 3300* (PRE); Great Brak River, 3 km E of Groot Brak River, (–AB), *Thompson 3303* (MO, PRE); south of Pacaltsdorp, George coastal region, inland of Rooiklip headland, (–AB), *Victor 498* (PRE); near Ruigtevlei Siding, (–BB), *Sidey 1696* (MO, PRE, S). 3423 (Knysna): Lake Pleasant Hotel, (–AA), *Acocks 21309* (PRE); Brenton on Lake, (–AA), *Bredenkamp 918* (PRE); Knysna District, (–AA), *Dahlgren & Peterson 168* (M); W of Plettenberg Bay, Cairn Brogil, (–AA), *Hugo 2079* (NBG, PRE); Knysna Heads, (–AA), *Schonland 3398*, *3525* (GRA, PRE); Knysna, (–AA), *Rogers 26987*, *27017* (K, PRE); Lake Pleasant, (–AA), *Story 3109* (PRE); mouth of Bitou River, (–AA), *Theron 2216* (M); Keurboomsrivier, (–AB), *Fourcade 1478* (BOL, GRA, K, PRE); Plettenberg Bay, Formosa, (–AB), *Fourcade 1484* (BOL, K); Plettenberg Bay, (–AB), *Kapp 1* (PRE); E of Bietou River, (–AB), *O'Callaghan 752* (PRE); Plettenberg Bay,

(–AB), *Rogers 15512*, *26983* (K); *Smart 15512* (PRE). Grid ref. unknown: Stikland, *Acocks 1067* (S); Cape, *Andersson s.n.* (S); *Andraea 1227* (NBG); *Boemert*, *Herb. Reg. Monacense s.n.* (M); *Bot. Mus. Univ. Wien s.n.* (WU); *Brehm.*: *Herb. Reg. Monacense s.n.* (M); Link's Herb at B, *Burchell 3835*, *6721* (K); Caput Bonae Spei, ex Herb. Mus. Berol. (UPS); *Cole s.n.* (TCD); Caput Bonae Spei, *Drège 85* (UPS); *Drège s.n.* (MO, P); *Ecklon s.n.* (C); *Ecklon & Zeyher 40* (MO, W); *Ecklon & Zeyher 41* (MO); *Ecklon & Zeyher s.n.* (BREM, MO, WU); Herb. Reg. Monacense, *Erlangh 1017* (M); *Herb. Scholae Lincopensis s.n.* (S); *Herb. J. Peterstein acc. no. 16/1946* (PR); Herb. Princ. Paul, *Dux de Wurte s.n.* (M); *Herb. Schmidel s.n.* (M); *Herb. Sieber 89* (S); *Herb. Swartzii s.n.* (S); *Herb. Bot. Hauniense s,n.* (C); Herb. Praga Karlin, Herb. scholae med., *Praga-Ka* (PR); *Herb. Reg. Monacense s.n.* (M); *Herb. Schreberianum s.n.* (M); *Herb. Thunberg s.n.* (UPS); *Herb. Thunberg s.n.* (UPS); *Joubert s.n.* (S); Caput Bonae Spei, *Jules Verreaux s.n.* (TCD); *Knaf s.n.* (PR); *Le Jolis s.n.* (S); Hortus Monatensis, *Leitz 182b*, *s.n.* (M); Caput Bonae Spei, *Lindley s.n.* (S); Paris Jardin des Plantes, *Meinkauff s.n.* (M); *Mus. Bot. Hauniense s.n.* (C); Cape, *Osbeck s.n.* (S); *Potts BLF 1300* (PRE); *Rogers 4724* (K); *Rutprum s.n.* (S); Caput Bonae Spei, *Schmidel s.n.* (M); *Sieber/Zeyher s.n.* (MO); Caput Bonae Spei, *Sparrman s.n.* (S); *Strey s.n.* (M); Caput Bonae Spei, *Thunberg s.n.* (UPS); *Trinity College s.n.* (TCD); *Von Gedow 473* (GRA); *Ward s.n.* (TCD); Caput Bonae Spei, *Wawra 3* (M); Caput Bonae Spei, *Wells s.n.* (MO); *Wright s.n.* (TCD); *collector unknown s.n.* (S); Table Mountain, *collector unknown s.n.* (S).

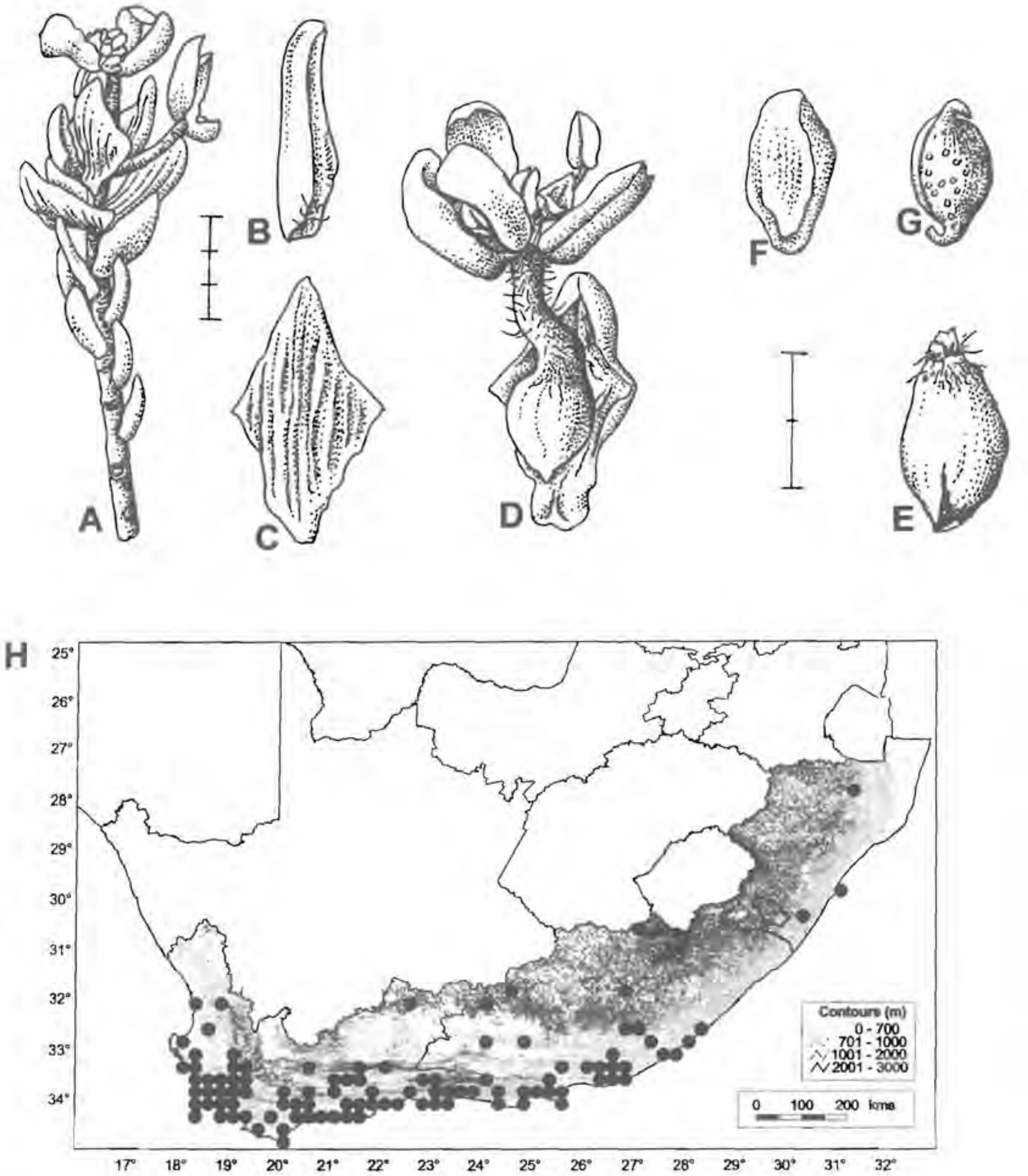

FIGURE 7.15.—*Passerina corymbosa* (*Bredenkamp 944*). A, inflorescence; B, leaf; C, bract; D, flower enveloped by bract; E, fruit enveloped by hypanthium, with fragmentation at neck base; F, achene, enveloped by membranous pericarp; G. achene in side view. Scale bars: A, 4 mm; B–G, 2mm.

H, known distribution of *Passerina* corymbosa.

15. **Passerina obtusifolia** *Thoday*. Bulletin of Miscellaneous Information 4:157 (1924a); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 683 (2000). Type: Western Cape, Worcester Division, between Osplaats and Tunnel Sidings 2 000–3 000 ft., *Rogers 16703* [K!, lecto., designated by Thoday 10: 388 (1924b)].

Erect shrubs with several fairly stout stems, bare at base, branching profusely higher up, (0.3–)0.8–1.8(–2.4) m high. *Stems* ash-grey, indumentum of young stems whitish tomentose, flaking off, becoming scabrid on older branchlets and forming lengthwise patterns with cork, which fissures lengthwise, sclerenchyma fibres protruding between fissures, leaf scars oblate. *Leaves* greyish green, imbricate, spreading at an angle of 45°, plane shape linear, straight or incurved, length × depth 4.0–8.0(–12.0) × 0.9–1.5 mm, adaxial surface concave, comose, abaxial surface convex, coriaceous, glabrous; base sessile; apex obtuse; margins glabrous, involute. *Inflorescences* with multiflowered main and co-florescences; spikes usually extended, 8–16-flowered, arrangement terminal, axis whitish tomentose, proliferating growth common. *Bracts* spreading, narrowly obtrullate, length × depth (4.0–)5.8 × 1.5(–1.7) mm; lamina greyish green, adaxially concave (inside), abaxially convex (outside), coriaceous, glabrous outside, tomentose inside, closely 2-ribbed at margins, midrib extending beyond lamina into a leaf-like point, apex obtuse; wings absent; base cuneate; margins glabrous, involute. *Floral envelope* ± 6.8 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* glabrous at ovary, neck tomentose, ± 1.8 mm long. *Sepals*: with outer sepals cymbiform, adaxially tomentose, abaxially glabrous, inner sepals narrowly oblong, adaxially tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 1.2 mm and those of antisepalous whorl ± 2.2 mm long; anthers 1.1 × 0.5 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.5 × 1.1 mm. *Fruit* an achene with pericarp membranous and dry, 2.3 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at circumference of ovary, resulting in sepals and androecium being shed. Figure 7.16A–F.

## Diagnostic characters and relationships

The growth form of *P. obtusifolia* can easily be confused with that of *P. corymbosa*, but *P. obtusifolia* is distinguished by the spreading, linear, incurved leaves, with obtuse apices. The bracts are narrowly obtrullate, with the midrib extending beyond the lamina into a leaf-like point and the lamina is closely 2-ribbed at the margins. Intermediate forms between *P. obtusifolia* and *P. truncata* subsp. *truncata* are found in the Karoo Desert National Botanical Garden at Worcester. *P. obtusifolia* usually occurs on the northern side of the southern Cape mountain ranges in drier habitats and *P. falcifolia* is confined to the summits of mountains and southwards towards the southern Cape coast. Intermediates between *P. obtusifolia* and *P. falcifolia* have been found on the boundary between the two species, just north of the Prince Albert Pass.

## Etymology

The Latin specific epithet, *obtusifolia*, refers to the obtuse apices of leaves and bracts, which are characteristic of this species.

## Common name

The vernacular name *karoo gonna* is used by the local people at Genadendal.

## Uses

According to the curator at the Museum in Genadendal, *P. obtusifolia* was traditionally used by the local people in the home industry of soap-making. The plants were burnt and the alkaline ashes used to react with the stearic acid in fat at boiling point, thus forming soap. In the Robertson area these plants are used in the wild flower industry. *Bayliss 521* (PRE) is a voucher specimen recorded in cancer research, but the results must have been negative; these plants are not currently known for their medicinal value.

## Distribution and ecology

*Passerina obtusifolia* is endemic to the Northern, Western and Eastern Cape Provinces. It is centred in a belt between 33° and 34°S latitude and from 19° to 27°E longitude, comprising all the Centres within the CFR—it is most common in the Karoo Mountain, Langeberg and Southeast Centres. *P. obtusifolia* is distributed from Worcester in the Western Cape, to Grahamstown in the Eastern Cape. The most northwesterly distribution are the Vanrhyn's Pass and the Hantamberg. The Karoo National Park and the Nuweveld Mountains in the Beaufort West District and the Lootsberg Pass at Middelburg are the most northerly distribution in the Western and Eastern Cape Provinces. *Hilliard & Burtt 14654* and *Acocks 20170* from the Lady Grey District are considered as outliers. Figure 7.16G.

*Passerina obtusifolia* is well adapted to drier karoo habitats and is often found on the north-facing aspect of mountains in the southern Cape. It frequents the boundary of fynbos and karroid vegetation and is common in the Little Karoo, growing at altitudes of (300–)670–1 400(–1 700) m. Although this species occurs at high altitudes on the summit of the Swartberg Pass, it grows below the snow line and does not occur on the highest peaks of mountain ranges in its distribution range. It is common in drier mountainous habitats, growing in shallow rocky soil and between rocks on well-drained slopes. It also grows amongst sandstone boulders of upper mountain slopes and on stony ridges of mountain tops. On the Hantamberg it has been recorded in renosterveld on the flat, rocky, dolerite summit. On Jonaskop it grows in a zone below the fynbos and is absent at the summit. This species is also found amongst rocks in river valleys and dry streambanks. The average height of these plants is 0.8–1.8 m, but stunted forms have been recorded from the arid Bergkwagga National Park, which is one of the most northeasterly localities. *P. obtusifolia* is a very common species and amongst the dominant species within its distribution range.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

EASTERN CAPE.—3027 (Lady Grey): road between Pitlochrie and Lundean's Nek, Glen Gyle, (–DA), *Hilliard & Burtt 14654* (PRE); Barkly East, Moshesh's Ford, (–DC), *Acocks 20170* (M, PRE). 3124 (Hanover): Middelburg, Lootsberg Pass, (–DC), *Greuter 22180* (PRE); Lootsberg, (–DD), *Lavranos 3700* (PRE). 3224 (Graaff-Reinet): Sneeuberg, between Graaff-Reinet and Murraysburg, (–AA), *Oliver 5194* (PRE); Jansenville District, Salt Pan's Neck, (–DC), *Acocks 16000* (K, PRE); Graaff-Reinet, Summit Oudeberg, *no collector 170* (TCD). 3225 (Somerset East): Bergkwagga National Park, (–AD), *Du Toit 155* (PRE); Sterkwater Farm, proposed extension to Bosberg Nature Reserve, (–DA), *Palmer 1094* (PRE). 3323 (Willowmore): 5 mi. N of Willowmore, (–AB), *Acocks 19000* (K, PRE); Willowmore District, Aasvogelberg, (–AC), *Marloth 14128* (PRE); Aasvogelberg, (–AC), *Andraea 979*, *982* (PRE); Slypsteenberg, (–AC), *Levyns 6314* (BOL); Zes Mijlen Farm near Willowmore, (–AD), *Andraea 1030* (PRE); Blydeberg, (–AD), *Andraea 982* (NBG); mountain W of Miller Station, (–BB), *Andraea 1018* (PRE); Baviaanskloof Road between Willowmore and Patensie, (–BC), *Balkwill 456* (K PRE); Baviaanskloof, (–BD), *Levyns 9140*, *9145* (BOL); *Bayliss 7731* (M, MO); upper Kouga; Long Kloof, (–DA), *Bayliss 521* (K, MO, PRE); Baviaanskloof, Nuwekloof, (–DA), *Glen 1568* (C, PRE); between Miskraal and Smitskraal, (–DA), *Hugo 1453* (K, PRE); Kouga Mountains, Smutsberg, Moordenaarskloof, (–DB), *Thompson 2005* (NBG, PRE). 3324 (Steytlerville): Baviaans Kloof, (–CA), *Bayliss 6093* (PRE); Klein Rivier, NE of Smitskraal, (–CB), *Oliver 4555* (PRE); Kleinplaat, (–CB), *Zantovska 120* (PRE); Goedehoop, between Cambria and Smitskraal, (–CD), *Wendelberger 406* (PRE); Kareedouw, Assegaaibos, (–CD), *Britten 1245* (GRA); Hankey, (–DD), *Cowling 926* (GRA). 3325 (Port Elizabeth): Olifantskop Pass, (–BD), *Acocks 21252* (K, PRE); Uitenhage, Addo Road, (–BD), *Long 386* (K, PRE); Groendal Wilderness Catchment Basin, KwaZunga, upper Swartkops, (–CA), *Scharf 1069*, *1522* (PRE ); Port Elizabeth, (–CD), *Paterson 833* (BOL); Uitenhage Mountains, (–CD), *Paterson 883* (PRE); Somerset East District, (–DA), *Van der Walt 250* (PRE); Coega Kop, (–DC), *Dold 2299* (GRA). 3326 (Grahamstown): Riebeeck East, (–AA), *Schrire 1869* (GRA); Alicedale, (–AC), *Jacot-Guillarmod 7464* (PRE); *Cruden 37* (NBG); *Marloth 4273* (PRE); mountains near Howison's Poort, (–AD), *MacOwen 103* (GRA); Botha's Hill, (–BC), *Bredenkamp 904* (PRE); Botha's River, hill above drift en route to Fort Brown, (–BC), *Britten 5523* (PRE); Collingham, (–BC), *Brooker-Leslie s.n.* (GRA); Grahamstown, Bloemhof, (–BC), *Doubell 27* (GRA); Penrock Farm, (–BC), *Dyer 596* (K, PRE); Botha's Ridge, (–BC), *Dyer 960*, *961* (K, PRE); Niemandspoort near Grahamstown, (–BC), *Galpin 178* (PRE); Kariega Park, (–DA), *Burrows 4118* (GRA); Boesman's River Mouth, (–DA), *Burrows 4682* (GRA). 3423 (Knysna): Storm's River Mouth, (–BB), *Munro s.n.* (PRE). 3424 (Humansdorp): Groothoek near Humansdorp, (–BB), *Fourcade 741* (BOL, K, GRA).

NORTHERN CAPE.—3119 (Calvinia): Vanrhyn's Pass, (–AC), *Compton 2884* (BOL, NBG); Hantamsberg, (–BC), *Acocks 18634* (K, PRE); Waterkloof Mountain, (–BC), *Marloth 12785* (PRE); Vanrhynshoek, (–BD), Germishuizen 4024 (PRE).

WESTERN CAPE.—3222 (Beaufort West): Karoo National Park, (–AB), *Shearing 870*, *891* (PRE); Karoo National Park, Torinkies on crest of mountain, (–AD), *Bengis 344* (PRE); Nuweveld, W slopes of Gert Adranskop, (–BA), *Bremer 299* (S); Nuweveld Mountains, (–BD), *Levyns 5538* (BOL). 3319 (Worcester): Orchard Siding, (–BC), *Rogers 16701A*, *16705* (K, PRE); between Osplaas and Tunnel Sidings, (–BC), *Rogers 16703* (K); Hex River, Vendutieskraal, (–BC), *Starke s.n.* (NBG, PRE); Worcester Karoo Garden, (–CB), *Barker 5925* (C, NBG); *Barker 10580* (NBG); *Bredenkamp 971* (PRE); *Compton 18278* (M, NBG); *Cross 58* (MO, NBG); *Dobay 45* (NBG); Breede Rivier, (–CB), *Goldblatt* & *Manning 9589* (NBG); Worcester District, Bosches veld, (–CB), *Levyns 9741* (BOL); Bokkeveld, between Concordia and Eendracht, (–CB), *Michell 326* (PRE); on top of Rondekop Veld Reserve, (–CB), *Olivier 118* (M, PRE); Hex River, (–CB), *Sidey 2312* (MO, NBG, S). Boschjesveld Mountains, (–CB), *Stokoe s.n.* (NBG); Worcester District, (–CB), *Van Breda 131* (PRE); Pokkraal, (–CB), *Van Breda 639* (K); *Walters 384*, *1017* (K, M, NBG, PRE); Langerug, (–CB), *Walters 1* (NBG); *Weltz 743* (NBG); Franschhoek Forest Reserve, (–CC), *Esterhuysen s.n.* (BOL); Jonaskop, (–CD), *Bredenkamp 966–968* (PRE); Hex River Pass, 5 km from De Wet, (–DA), *Bredenkamp 970* (PRE); N slopes above Tierkloof, (–DA), *Oliver 3797* (PRE); 2 mi. N of De Wet, (–DA), *Van Breda 754* (K, PRE); Rabiesberg, (–DA), *Esterhuysen s.n.* (BOL); between Montagu and Eendracht, (–DB), *Compton 18380* (NBG); Hammanshof, Droërivier Mountains, (–DC), *Boucher 2439* (PRE); Jonaskop, (–DC), *Boucher 2244* (PRE); sandstone koppie S of Moordkuil, (–DC), *Levyns 9743* (BOL); Moordkuil, (–DC), *Van Rensburg 442* (PRE); Jonaskop, (–DC), *Walters 1769* (NBG); Kareevlakte, (–DD), *Grobler 540* (K); 8 mi. S of Robertson, (–DD), *Levyns 2813* (BOL); Robertson, (–DD), *Schmidt 41* (PRE); between Agterkliphoogte and Robertson, (–DD), *Simpson 97* (NBG, PRE); Vrolikheid Nature Reserve, (–DD), *Van der Merwe 2420* (K, PRE). 3320 (Montagu): Matjiesfontein, Whitehill, (–BA), *Thoday 214* (BOL, NBG); Touwsberg, (–BD), *Victor 400* (PRE); Keisiesberg, (–CA), *Lewis 1796* (NBG); Montagu District, Baden, (–CA), *Lewis 1797* (NBG, PRE); Montagu, Ouberg Pass, (–CA), *McMurtry 335* (PRE); Dobbelaarskloof, (–CB), *Esterhuysen 23446* (BOL); *Levyns 8029* (BOL); *Lewis 1795* (NBG); Montagu, Rabiesberg, (–CC), *Compton 5725* (NBG); Montagu, (–CC), *Compton 18449* (NBG); Langeberg S of Montagu, (–CC), *Levyns 6514* (BOL); Keurkloof in Kogmanskloof, (–CC), *Raitt s.n.* (PRE); E of Anysberg, (–DA), *Van Zyl 3366* (NBG, PRE); Touwsberg, (–DB), *Oliver 10318* (NBG); Barrydale, (–DC), *Hutchinson 1101* (BM, K, PRE); Warmwaterberg near springs, (–DD), *Boucher 1559a* (NBG, PRE); Grootvaderbosch State Forest above Witbooisrivier, (–DD), *McDonald* & *Morley 1005* (BM, NBG, PRE, TCD); Montagu Baths, *Page 97* (PRE). 3321 (Ladismith): Ladismith, (–AC), Fourie s.n. (NBG); Prince Albert District, summit Swartberg Pass, (–AC), *Stokoe s.n.* (NBG, PRE); Towerkop, (–AC), *Wurts 1210*, *1211* (NBG); Klein Swartberg, (–AD), *Bond 1820* (NBG); Rooiberg, (–AD), *Compton 3835* (BOL NBG); Seweweekspoort, (–AD), *Compton 7438* (NBG); Huis River Mountains, (–AD), *Compton 7498* (NBG); Waterkloof, (–AD), *Hutchinson 1104* (PRE); S entrance to Seweweekspoort, (–AD), *Levyns 2349* (BOL); foot of Swartberg, lower slopes in Seweweekspoort, (–AD), *Levyns 2414* (BOL);

Towerkop, (–AD), *Maguire 1210* (NBG); Seweweekspoort, (–AD), *Phillips 1503* (NBG); Seweweekspoort, (–AD), *Taylor 9356* (K, MO, PRE); Prince Albert District, Swartberg Pass, (–BD), *Stokoe s.n.* (NBG); Swartberg Mountains, Kliphuisvlei, *Taylor 7562* (K, PRE); *Thompson 2151* (NBG, PRE); Noukloof Nature Reserve, (–CA), *Laidler 372* (NBG, PRE); Ladismith District, (–CB), *Adamson 5124* (PRE); 10 km from Ladismith, Hartebeesfontein, (–CB), *Bredenkamp 929, 930* (PRE); Oudtshoorn, Gamka Mountain Reserve, (–CB), *Cattell & Cattell 167* (NBG); Van Wyksdorp, Rooiberg, (–CB), *Hoekstra 73* (NBG); *Levyns 6626* (BOL); *Marshall 130, 131* (NBG); *Thompson 3374* (PRE); foot of Garcia Pass, farm Muiskraal, (–CC), *Bredenkamp 928* (PRE); Riversdale, Langeberge, Springfontein, Kliphoogte, (–CC), *Fellingham 169* (NBG, PRE); Karoo between Muiskraal and Springfontein, (–CC), *Levyns 2303* (BOL); Calitzdorp, (–DA), *Bayliss 1684* (PRE); Gamka Mountain, (–DA), *Boshoff 156* (NBG); Rooiberg Pass, (–DA), *Oliver 3679* (K, PRE); *Thompson 1427* (NBG); Gamka Mountain Reserve, (–DB), *Allardice 1726* (NBG); Waterkloof near Ladismith, (–DC), *Hutchinson 1104* (K); Ladismith, Rooiberg, *Levyns 6627* (BOL). 3322 (Oudtshoorn): Prince Albert, (–AA), *Marloth 12724* (PRE); Swartberg Pass, (–AC), *Acocks 1007* (S); *Bean 1385* (BOL, MO, NBG); *Bolus 11630* (BM, BOL); *Boucher 2008* (PRE); *Esterhuysen 8978* (BOL); *Gillett 1986* (NBG); *Stokoe 6335, 8677, 8977* (BOL); *Stokoe s.n.* (NBG, PRE); *Vlok 1235* (PRE); *Wall 30, s.n.* (S); Swartberg Pass, (–AD), *Brink 924* (GRA); Prince Albert District, Kriedouw Mountains, (–AD), *Marloth 11283* (PRE); Swartberg Mountains, Die Aap, (–AD), *Marshall 244* (NBG, PRE); Oudtshoorn District, (–CA), *Britten 1633* (GRA, PRE); De Rust, P.K. le Roux's farm 'Die Krans', (–CB), *Dahlstrand 1490* (C, MO, NBG, PRE); foot of Robinson Pass, from Oudtshoorn to Mossel Bay, (–CC), *Bredenkamp 922* (PRE); Perdepoort adjacent to Doorn River, en route to Leydsdorp, (–CD), *Bredenkamp 919* (PRE); 4 mi. NW of Camfer's Station, (–CD), *Acocks 22862* (K, PRE); Kammanassie Mountains, (–DA), *Matthews 1153* (NBG); Kammanassie Mountains, (–DB), *Bredenkamp 1549, 1554* (PRE); Roode Els Kloof Farm, (–DB), *Matthews 284* (PRE); Mannetjiesberg, (–DB), *Williams 1451* (PRE); N side of Montagu Pass, (–DD), *Marloth 6862* (PRE). 3323 (Willowmore): between Uniondale and Avontuur, (–CA), *Marloth 10964* (PRE); upper Kouga, Longkloof, (–CB), *Bayliss 6060* (PRE); Uniondale, Kouga near Misgund, (–CD), *Compton 7427* (NBG). 3419 (Caledon): 18.4 km W of Greyton, (–AB), *Acocks 24427* (K, PRE). 3420 (Bredasdorp): Hill on E side of the Poort, (–CA), *Acocks 1549* (S). 3421 (Riversdale): Zandkraal, *Muir 4485* (BOL, PRE). Grid ref. unknown: Farm Hounslow, near Piggot Bridge, *Bayliss 8908* (M, MO); *Ecklon & Zeyher 98* (BOL); *Ecklon & Zeyher s.n.* (WU); Laingsburg district, Karoo Garden, Whitehill, *Esterhuysen 1998* (BOL); Zuurberg at Georgida, *Fourcade 4624, 4625* (BOL); Cradock Road, roadside in Hellpoort, *Jacot-Guillarmod s.n.* (GRA); Montagu Baths, *Levyns 15495* (BOL); Cogman's Kloof, *Michell 71* (PRE); above Cape Town, *Rogers 17222* (K); Caledon District, Somerset, Sneeuwkop, *Stokoe s.n.* (NBG).

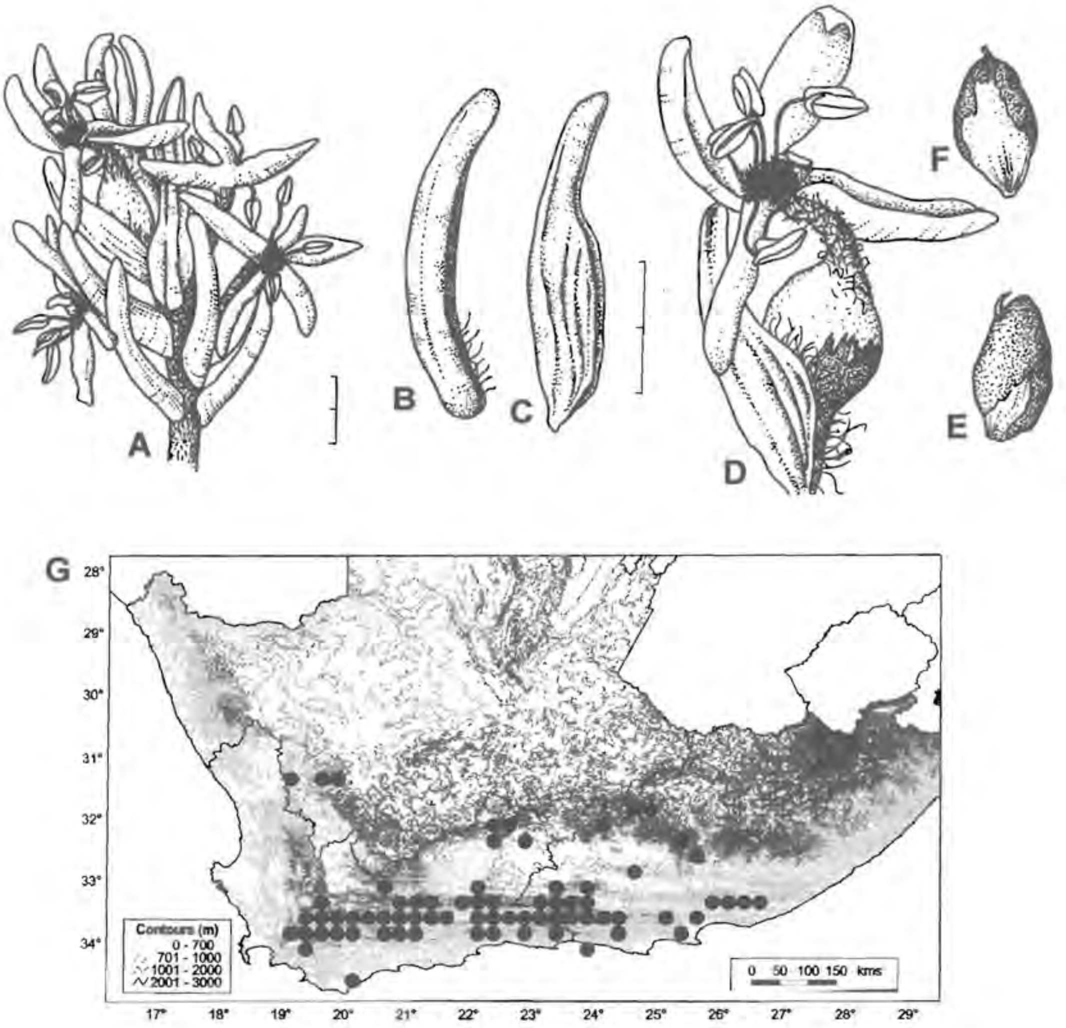

FIGURE 7.16.—*Passerina obtusifolia* (*Bredenkamp 919*). A, flowering inflorescence; B, leaf; C, bract; D, flower clasped by bract, fragmenting at circumference of ovary; E, achene in lateral view, with basal fragment of membranous pericarp; F, achene in ventral view, with remnant of membranous pericarp. Scale bars: 2 mm. G, known distribution of *Passerina obtusifolia*.

16. **Passerina paludosa** *Thoday*. Bulletin of Miscellaneous Information. Kew 4: 161 (1924a); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 683 (2000). Types: Western Cape, Simonstown, Cape Flats, Riet Valley, in and near shallow vleis, November 1922, *Thoday 100* [K!, lecto., designated by Thoday 10: 388 (1924b); C!, NBG!, PRE!].

Much branched shrubs or small tree, up to 2.0 m high. *Stems* fawn, indumentum of young stems closely white-tomentose, forming lengthwise patterns with cork on older branches, which gradually become glabrous, leaf scars oblate, comose at upper rim. *Leaves* erect, nearly straight, greyish green, imbricate, overlapping ± 25%, appressed; plane shape narrowly lanceolate to lanceolate, longitudinaly folded and somewhat keeled, length × depth (3.0–)5.5–6.8(–10) × 0.8–1.4 mm, adaxial surface concave, tomentose, abaxial surface glabrous; base sessile; apex acute, sometimes incurved, bearing a persistent tuft of white, erect hairs; margins setose. *Inflorescences* with multiflowered main and co-florescences; spikes usually extended, 10–12-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* greyish green, appressed, narrowly obtrullate with leaf-like point, length × depth (5.2–)7.0 × 1.8(–2.0) mm; lamina folded lengthwise and keeled, adaxially concave (inside), abaxially slightly convex (outside), basally setose inside, glabrous outside, coriaceous, ± 2-ribbed; wings membranous with obscure venation, glabrous; base cuneate; apex acute; margins white setose. *Floral envelope* ± 7.2 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* shortly tomentose at ovary, neck strigose, ± 2.6 mm long. *Sepals*: outer sepals cymbiform, ad- and abaxially glabrous, apex setose; inner sepals oblong, ad- and abaxially glabrous, apex setose with margins tomentose. *Androecium* with filaments of antipetalous whorl ± 1.2 mm and those of antisepalous whorl ± 2.4 mm long; anthers ovoid, 0.7 × 0.5 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.3 × 1.0 mm. *Fruit* an achene with pericarp membranous and dry, 2.4 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in sepals and androecium being shed. Figure 7.17A–D.

### Diagnostic characters and relationships

*Passerina paludosa* is a stout shrub up to 2 m high, occurring mostly in marshy ground on lowland flats. It is characterized by erect, nearly straight, greyish green, imbricate, appressed leaves, which are ± lanceolate. The bracts are narrowly obtrullate, with the midrib and leaf-like point stout and the apex acute. This species is distinguished from *P. filiformis* subsp. *filiformis* which has filiform leaves and widely obovate bracts, which narrow abruptly into a filiform point.

### Etymology

The specific epithet *paludosa* refers to the habitat of this species, namely marshy lowland flats; from the Latin *paludosus* (= marshy, swampy or boggy).

### Distribution and ecology

*Passerina paludosa* is endemic to the Southwestern Centre within the CFR. Herbarium specimens dated from 1921 to 1995 show that this species used to be distributed from sandy places along the Malmesbury Road (*Acocks 2482*), along marshy areas of the Cape Flats and the Stellenbosch District to the Palmiet River at Elgin, the most easterly locality. As *P. paludosa* was severely affected by urbanization and invasion by alien vegetation in the Cape Peninsula, it is currently confined to small marshy areas east of Muizenberg.

According to Smuts (1996) the only three extant populations known, are at the Rondevlei Nature Reserve, Zeekoevlei and along the Strandfontein Road. Label information on *Peterson 1263*, collected in 1982, states that the population at a housing estate site SE of Zeekoevlei consisted of ± 400 plants, but Smuts (1966) reported only 60 living plants. At the same time the population at Rondevlei consisted of 35 plants and the one along the Strandfontein Road of possibly a few hundred. Currently both the Zeekoevlei and Strandfontein sites are in danger of urban development and are being threatened by invasive alien vegetation, primarily Port Jackson (*Acacia saligna* (Labill.) Wendl.) and rooikrans (*A. cyclops* A.Cunn. ex G.Don). Conservation measures proposed by Smuts (1996) include an environmental impact study at the Zeekoevlei site prior to any development and a plea for urgent attention by conservation authorities to ensure the conservation of the Strandfontein population. Figure 7.17E.

The Rondevlei Nature Reserve boasts more than 250 plant species of which many are rare and endangered. Species associated with *P. paludosa* include *Chondropetalum nudum* Rottb., *Juncus krausii* Hochst. and *Leucadendron levisanus* (L.) Berg. In recent years the management at the reserve concentrated on restoring and managing its biodiversity. Alien vegetation has been cleared, plant species that occurred there historically have been re-introduced and *P. paludosa* has been successfully propagated by cuttings to expand the population. As aridification is an important effect of urbanization and as alien vegetation impacts on the natural drainage system of an area, the whole wetland east of Muizenberg can be conserved only if it is included in the Rondevlei Nature Reserve (Smuts 1996).

Recently two new populations of plants, that appear to be *P. paludosa*, were collected at the farm Springfontein near Stanford [3419AD, *Louw 7083* (NBG, PRE)], and in seasonally wet clays at Heidehof, 5 km NW of Pearly Beach [3419CB, *Helme 2376* (NBG, PRE)]. These specimens were not included in the distribution of *P. paludosa* as further population studies need to be done. Taking urbanization and invasion by alien vegetation into account the Red List status of *P. paludosa* was also not changed.

*Conservation status*: Critically Endangered, [CR B1ab(i,ii,iii,iv); C1] (IUCN Species Survival Commission 2000).

## Specimens examined

WESTERN CAPE.—3318 (Cape Town): Stellenbosch District, Cape Flats, along Klipfontein Road, (–DC), *Esterhuysen 29962* (BOL, MO); Stellenbosch Flats, rare, *Duthie 1517* (BOL). 3418 (Simonstown): Muizenberg, marshy plot S of Sandvlei, (–AB), *Milton 2* (BOL); Rondevlei Nature Reserve, population between peninsula road and reserve, seasonal wetland, (–BA), *Bredenkamp 1035* (PRE); wetland on N bank of vlei, (–BA), *Jangle 156* (PRE); Cape Flats, (–BA), *Moss 5644* (BM); in and near Riet Valley, (–BA), *Thoday 100*, (C, NBG, PRE); 300 m SE of Zeekoevlei, c. 400 plants, housing estate site, (–BB), *Peterson 1263* (BOL). 3419 (Caledon): Palmiet River, Elgin, (–AA), *Stokoe 8226* (BOL). Grid ref. unknown: Malmesbury Road, sandy places near 27th milestone, *Acocks 2482* (S).

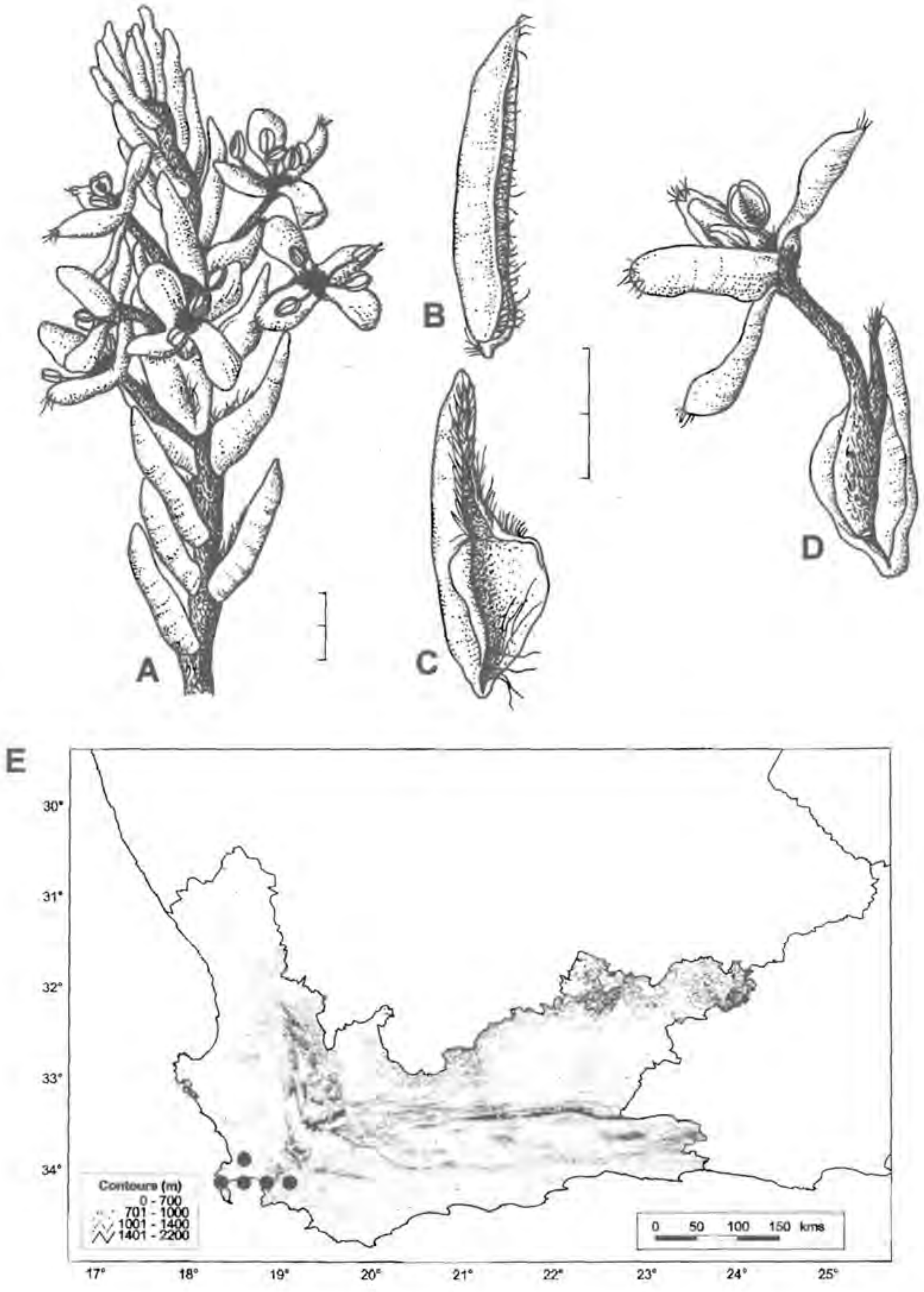

FIGURE 7.17.—*Passerina paludosa* (*Jangle 156*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract. Scale bars: 2 mm.
E, known distribution of *Passerina paludosa*.

17. **Passerina montivaga** *Bredenk. & A.E.van Wyk* , sp. nov., a *P. filiforme* L. habitu robustiore et luxuriantiore distinguenda. *Folia* cymbiformia, secus nervum medium plicata, lanceolata, ad apicem rotundatum decrescentia, basi expansa. *Bracteae* cymbiformes, ovatae ad obovatae, extra glabrae, intra basaliter setosae, in carinam longam, fere cylindricam, adaxialiter sulcatam, leviter incurvam gradatim decrescentes, basi cuneatae, coriaceae, sed lateris vel alis chartaceis, plus minusve tricostatis, marginibus trichomatibus conspicuis crassis serialibus secus dimidium distalem obsitis.

TYPUS.—KwaZulu-Natal, 2930 (Pietermaritzburg): Hills above Pinetown, 2 400 ft, (–DD), 3 December 1891, *J.M.Wood in PRE 49409* (PRE!, holo.; MO!, iso.).

*Passerina filiformis* L.: 559 (1753) pro parte, excluding type; Thunb.: 75 (1794): Wikstr. 39: 324 (1818); Thunb.: 374 (1825a); Meisn. 14: 562 (1857); C.H.Wright: 10 (1915); Thoday 4:159 (1924a); Bond & Goldblatt: 432 (1984); Hilliard & B.L.Burtt: 182 (1987); Goldblatt & Manning: 683 (2000).

*Passerina sp. nov. 4* Bredenk. & A.E.van Wyk 129: 70 (2000); 31,1: 56 (2001a); 31,2: 217 (2001b).

Low, spreading shrub 1(–2) m high; a vigorous resprouter. *Stems* initially greyish tomentose, cork fissuring lengthwise into fine, dark-grey, tomentose strips, older branchlets glabrous, with conspicuous leaf scars. *Leaves* greyish green, coriaceous, smooth, sessile, spreading from stem at angle of ± 45°; lamina cymbiform, folded along sturdy main vein, adaxial surface tomentose, abaxial surface glabrous, plane shape lanceolate, often slightly falcate, length × depth 5.6–7(–8) × 0.7–1 mm, tapering towards rounded apex, expanded at base; margin involute, ciliate. *Inflorescences* subterminal, 10–20-flowered, composed of proliferating spikes, common. *Bracts* cymbiform, outside glabrous, inside basally setose; lamina coriaceous, ovate to obovate, narrowing gradually into sturdy, leaf-like point of extended main vein; length × depth ± 6.3 × 1.6 mm; base cuneate; wings chartaceous, ± 3-ribbed, obscurely veined, greyish green; margins conspicuously lined with strong white trichomes along distal half, often reaching up to apex. *Floral envelope* ± 6.6 mm long, yellow-pink during pollination; distal half of ovary and neck tomentose; neck ± 2.3 mm long; adaxial surface of outer and inner sepals glabrous, apex setose abaxially; outer sepals cymbiform, inner sepals obovate and ± 2.1 × 1.3 mm. *Androecium* with filaments of antipetalous whorl ± 0.8 mm, and those of antisepalous whorl ± 1.7 mm long; anthers ± 0.8 × 0.3 mm. *Ovary* ± 2.2 × 0.7 mm. *Fruit* enveloped by persistent, loosely arranged hypanthium fragmented at neck base; pericarp membranous and dry. Figure 7.18A–G.

### Nomenclatural notes

Thoday (1924a) noted that plants named *P. filiformis* in present day KwaZulu-Natal, were more robust and luxuriant than those from the Western Cape. *Wood in PRE 49409* from Pinetown has been chosen as holotype of *P. montivaga* as it is a good representation of the new taxon; it was also determined and cited by Thoday (1924a).

### Diagnostic characters and relationships

*Passerina montivaga* is easily distinguished from *P. filiformis* by its more robust and luxuriant habit. For some distance below the inflorescences, the foliage leaves are expanded at the base. Bracts are ovate to obovate, narrowing gradually into a sturdy, leaf-like point, with margins along their distal half conspicuously fringed by strong white trichomes. *P. montivaga* can also be distinguished from *P. falcifolia* by the apical beard on the young leaves and outer sepals and by the adaxial surface of the bracts, which is basally setose, with glabrous wings.

### Etymology

The specific epithet is a compound of the Latin *montanus* (= pertaining to mountains) and *vagus* (= in several directions), referring to the distribution of this species from Mossel Bay and Oudtshoorn in the Western Cape to the Eastern Cape and northwards along the Great Escarpment.

### Common names

Von Breitenbach *et al.* (2001) give the names 'brown gonna', *bruingonna* and *unwele oluncane* for *P. filiformis* in the wide sense, but these names are most appropriate for *P. montivaga* because of its wide distribution.

### Distribution and ecology

*Passerina montivaga* has a wide distribution, from Mossel Bay and Oudtshoorn in the Western Cape northwards mainly along the Great Escarpment to KwaZulu-Natal, Swaziland, Mpumalanga, the Northern Province, Mozambique and Zimbabwe. The most southwesterly distribution of this species is in the southern Cape, a region transitional between winter and summer-rainfall. However, over most of its range the species is subject to summer-rainfall. Because of its wide distribution, especially along the Great Escarpment, *P. montivaga* is adapted to a variety of habitats, with relatively high rainfall. It is often found along forest margins in the ecotonal zone between Afromontane forest and grassland. It has been recorded from rocky mountain peaks and slopes, river valleys, gorges, and among riverside rocks. In coastal regions, it grows on hills and often borders small tributaries of streams flowing to the sea. Figure 7.18H.

Story (1952) reported that *P. montivaga* (=*P. filiformis*) dominated the western half of a small plateau north of the Mount McDonald beacon in the Keiskammahoek District. The plants were not browsed by stock although the plateau was heavily grazed. He regarded the species as useless and advised that it should be eradicated by hand, as it was not dense enough to burn without additional fuel. This fynbos species, distributed along the Great Escarpment, has not been reported as undesirable, and is currently not regarded as invasive, although it might be a dominant species in restricted areas.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

## Specimens examined

ZIMBABWE.—1932: Chimanimani Mountains, Bundi Gorge, below hut, (–DD), *Goodier 637* (BM, M, PRE); Chimanimani, Melsetter, (–DD), *Goodier & Phipps 270* (MO).

MOZAMBIQUE.—1934: Manica and Sofala, *Pedro & Pedrogao 7310* (BOL).

MPUMALANGA.—2530 (Lydenburg): Lowveld Botanical Garden, (–BD), *Buitendag 712* (NBG, PRE); Badplaas, Buffelspruit, (–DC), *Botha 1445* (PRE).

SWAZILAND.—2631 (Mbabane): Black Mbuluzi Valley, (–AA), *Compton 26157* (NBG, PRE); Hlambanyati Valley, (–AC), *Compton 25157* (NBG); Mantenga Falls, (–AC), *Compton 29473* (NBG); Gobolo, (–AC), *Dlamini s.n.* (NBG, PRE); Usutu Dam, (–AC), *Dlamini s.n.* (NBG, PRE).

KWAZULU-NATAL.—2731 (Louwsburg): Vryheid District, Zungeni Peak, (–CD), *Acocks 11549* (PRE); Hlobane 20 mi. from Vryheid, (–CD), *Strey 9321* (PRE, S). 2830 (Dundee): Krantzkop District, The Kop, (–DD), *Edwards 820* (PRE). 2831 (Nkandla): Upper Umhlatuzi Dam, *Vincent & Wearne 4* (PRE); Eshowe, (–CD), *Meebold 15156* (M); Mtunzini District, Ngoye, (–DC), *Huntley 612* (MO, PRE). 2929 (Underberg): Umkomasi Forest Station, Nzinga River Valley, farm 'Cyprus', (–BC), *Hilliard & Burtt 14463* (PRE); upper tributaries S of Mkomazi, (–CB), *Hilliard & Burtt 15671* (N, PRE, S). 2930 (Pietermaritzburg): Table Mountain, forest margin close to descent into Amatulu, (–CB), *Killick 238* (PRE); Umgeni Valley, (–DA), *Cheadle & Wells 668* (M, PRE); Camperdown District, Nagle Dam, (–DA), *Wells 1809* (MO); Inanda, (–DB), *Wood 1182* (BOL); hills above Pinetown, (–DD), *Wood s.n.* (MO, PRE). 2931 (Stanger): Isipingo near Durban, (–CC), *Forbes & Obermeyer 58* (PRE); Bluff at Durban, (–CC), *Meebold 15157* (M). 3027 (Lady Grey): Barkley East District, road between Pitlochrie and Lundean's Neck, Glen Gyle, (–DA), *Hilliard & Burtt 14654* (K). 3029 (Mataticle): Mt Currie Nature Reserve, (–AD), *Van Wyk BSA 2586* (PRE, PRU); Kokstad District, (–CB), *Mogg 5206* (PRE); Weza, Ngele Nature Reserve, KwaShiwili, (–DA), *Sikhakhane 524* (PRE); Mt Ingeli, (–DA), *Tyson 1287* (MO, NBG). 3030 (Port Shepstone): Emersdale, Dumisa Station Alexandra (–AC), *Rudatis 1204* (BM, PR, S); Oribi Falls, (–CA), *Mogg 13350* (K, PRE); Oribi Gorge, The Rocks, (–CA), *Mantell & Vassilatos 32* (PRE); Port Shepstone, farm Highlands, (–CB), *Strey 11363, 11364* (PRE); Oribi Gorge Hotel, (–CB), *Bredenkamp 1016, 1017* (PRE); Umtamvuna Nature Reserve, Beacon Hill, (–CC), *Abbott 43* (PRE); Umtamvuna Gorge, (–CC), *Germishuizen 1705* (PRE); Paddock District, (–CC), *Sidey 3862* (PRE, S); Port Edward, Beacon Hill, (–CC), *Van Wyk 5332* (PRE, PRU); Uvongo, littoral cliffs, (–CD), *Mogg 13397* (PRE); Uvongo Reserve, Skyline farm, 110 mi. S of Durban, (–CD), *Mogg 38026* (PRE); Mgongo, (–CD), *Strey 9284* (PRE); Margate, (–CD), *Ward 8832* (N, PRE); Uvongo N, Ngongongo K, off road to Gamalahke, (–CD), *Van Wyk 2622* (PRE, PRU, M).

EASTERN CAPE.—3128 (Umtata): hill above Mhlahlane Forest Station, (–BC), *Hilliard & Burtt 18772A* (K, S). 3129 (Port St Johns): Lusikisiki District, Ngogwana Falls, (–BC), *Galpin 11016* (PRE). 3130 (Port Shepstone): Umtamvuna Nature Reserve, Pont Trail, (–AA), *Abbott 308* (PRE); Umtamvuna Bridge, E side of Bridge, (–AA), *Bredenkamp 1012, 1015* (PRE); Umtamvuna

Bridge, hills near sea, (–AA), *Strey 7112* (PRE); Umtamvuna River Bridge, (–AA), *Van Wyk & Bredenkamp 1* (PRE, PRU); Port Edward, (–AA), *Ward 10669* (PRE); Mkambati Game Reserve, Waterfall, (–AC), *Bredenkamp 1327, 1359, 1360* (PRE); Mkambati Game Reserve, Horseshoe Waterfalls, (–AC), *Germishuizen 9089* (PRE). 3227 (Stutterheim): Amatole Mountains, Lenye Plateau, (–CA), *Phillipson 1200* (MO, PRE); Keiskammahoek District, Mt McDonald Beacon, overlooking Amatola Basin, (–CA), *Story 3765* (GRA, PRE). 3228 (Butterworth): Kentani, Qolora River Bank, (–AD), *Pegler 1273* (BOL, GRA, NBG, PRE). 3326 (Grahamstown): Howison's Poort, (–AD), *MacOwen 16388* (BM); Howison's Poort, (–BC) *MacOwen s.n.* (MO). 3424 (Humansdorp): Diep River Valley near Humansdorp, (–BB), *Bolus 2440* (BOL, K).

WESTERN CAPE.—3321 (Ladismith): Mossel Bay Division, Voorattaquaskloof, (–DD), *Killick 3469* (PRE). 3322 (Oudtshoorn): Mossel Bay Division, valley of Ruitersbos, (–CC), *Bremer 317* (PRE, S); Oudtshoorn, Hoogekraal, Sedgefield area, (–DD), *Hugo 2019* (PRE); Homtini Pass, (–DD), *Roberts 66* (S). 3422 (Mossel Bay): E of Herold's Bay, George coastal region, inland of Oubaai, (–AB), *Victor 556* (PRE); George Division, Victoria Bay, (–BA), *Lewis s.n., 4064* (NBG); on road to Knysna from George, (–BB), *Gillett 4537* (BOL, PRE); Hoogekraal, 34 mi. E of George, (–BB), *Hutchinson 1298* (PRE); between George and Knysna, Garden Route, (–BB), *Roberts s.n.* (S). 3423 (Knysna): Redlands, (–AA), *Keet s.n.* (NBG, PRE); Knysna, Barrington, (–AA), *Morris 441* (NBG); Plettenberg Bay, (–AB), *Fourcade 4809* (BOL); W of Plettenberg Bay, between Marathon and Bosfontein, (–AB), *Hugo 2086* (NBG, PRE); Oyster Bay, (–BA), *Joffe 576* (TCD, PRE). Grid ref. unknown: Bey Plaats, *Fourcade 3473* (NBG); Tusizwa, *Penther 1919* (M, S); Tvungu River, *Thode 4657* (NBG); Pondoland, Umkwani River, *Tyson 2621* (NBG); Bothas, *Wood 8938* (MO).

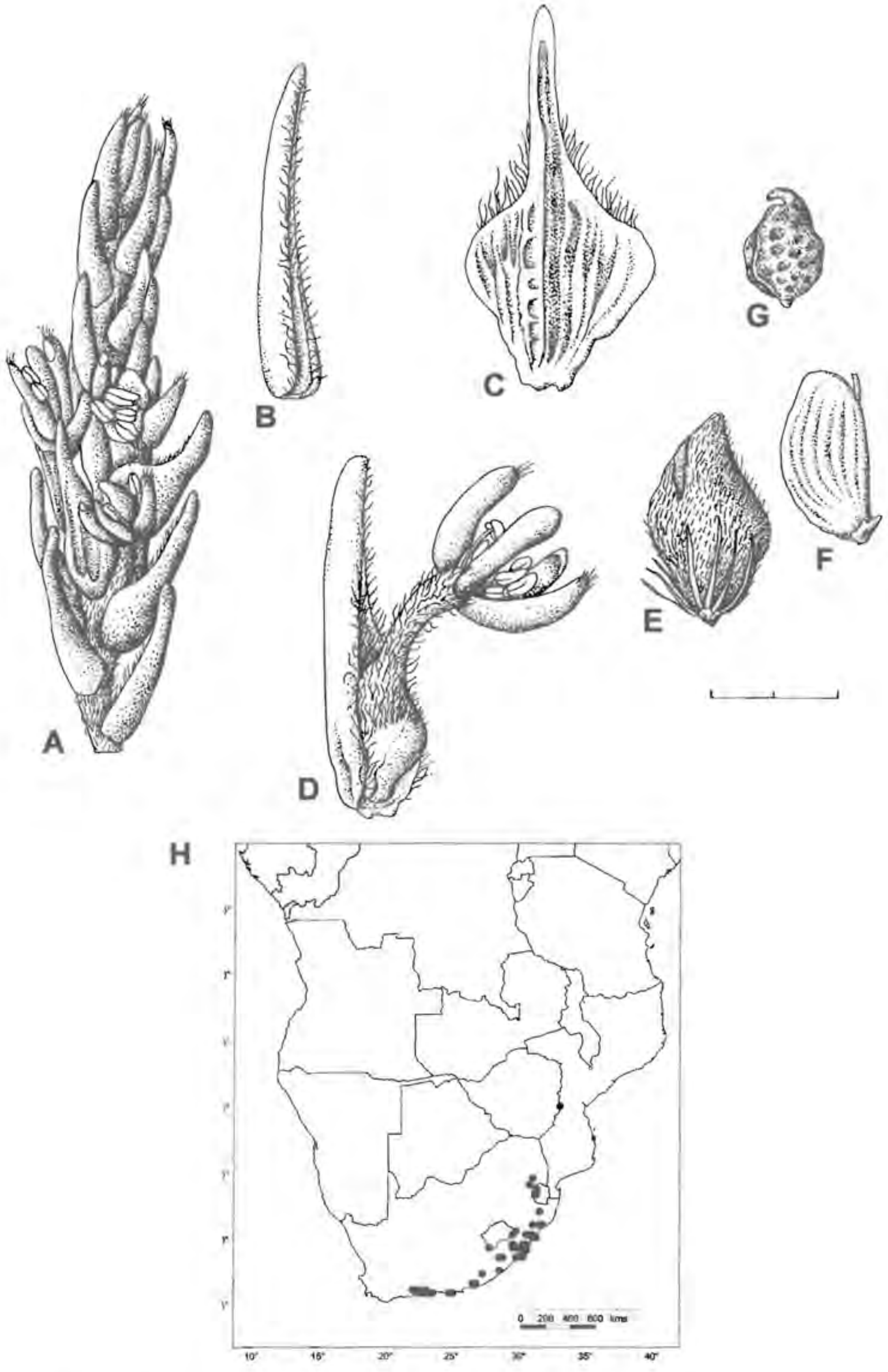

FIGURE 7.18.—*Passerina montivaga* (*Bredenkamp 1327*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract; E, fruit enveloped by hypanthium, fragmented at neck base; F, achene, enveloped by membranous pericarp; G, achene in side view. Scale bars: 2 mm. H, known distribution of *Passerina montivaga*.

18. **Passerina filiformis** *L.* in Species plantarum: 559 (1753); Thunb.: 75 (1794): J.C.Wendl.: 18 (1798); Wikstr. 39: 324 (1818); Thunb.: 374 (1825a); Meisn. 14: 562 (1857); C.H.Wright: 10 (1915); Thoday 4:159 (1924a); Palmer & Pitman: 1587 (1972); Coates Palgrave: 648 (1977); Bond & Goldblatt: 432 (1984); Hilliard & B.L.Burtt: 182 (1987); A.E.van Wyk & P.van Wyk (1997); Goldblatt & Manning: 683 (2000). Type: *Passerina filiformis*, *Linnean Herbarium 504.1* [LINN, lecto.!, designated by Thoday 10: 388 (1924b)].

*P. cupressina* J.C.Wendl. nom. nud. Meisn.: 404 (1840); Meisn. 14: 563 (1857); Thoday 4:159 (1924a). *P. cupressoides* Steud.: 273 (1841).

*P. pectinata* Lodd.: 18 (1816) nom. nud. Wikstr. 39: 347 (1818); Meisn.: 404 (1840); Meisn. 14: 562 (1857); Thoday 4:159 (1924a).

Large rounded shrubs up to 2 m high, often lax in the shade. *Stems* initially greyish tomentose, cork finely grey-brown tessellate, becoming glabrous, with conspicuous leaf scars and hair-like, whitish fibres protruding between bark fissures. *Leaves* dark green to greyish green, often drying brown, coriaceous, smooth, sessile, sometimes glutious, closely adhering to stem or spreading from stem at an angle of ± 30°; lamina narrow, almost terete, adaxial groove tomentose, abaxial surface convex, glabrous, plane shape acerose or linear, transversely elliptic or cordiform in cross section, length × depth (4.0–)5.5–8.0(–10.0) × (0.4–)0.6–1.0 mm, tapering towards rounded apex, slightly widening or widening towards base; margin involute. *Inflorescences* subterminal, 10–20-flowered, composed of proliferating spikes. *Bracts* cymbiform, outside glabrous, inside setose from base to central part, ovate-acuminate to widely obovate, gradually narrowing to point or narrowing abruptly into filiform point, length × depth ± 4.6–7.3 × 1.5–2.0 mm; base cuneate to widely cuneate; main vein strongly developed, often keeled, shortly extended or extending to form a leaf-like point; lamina coriaceous or chartaceous; wings glabrous, membranous with distinct venation, margins glabrous or ciliate, often with a few trichomes at apex adjacent to filiform point. *Flowers* glutious or not. *Floral envelope* ± 6.0–6.5 mm long, yellow-pink during pollination, scantilly tomentose or tomentose at ovary, neck scantilly tomentose or tomentose, 1.5–1.7 mm long; outer and inner sepals concave, obovate and with adaxial surface glabrous, apex abaxially setose; inner sepals ± 2.2–2.5 × 1.4–1.5 mm. *Androecium* with filaments of antipetalous whorl ± 1.1–1.2 mm, and those of antisepalous whorl ± 2.2 mm long; anthers ± 0.8 × 0.3 mm. *Ovary* ± 2.3–2.5 × 0.5–0.6 mm. *Fruit* enveloped by persistent, loosely arranged hypanthium fragmenting at neck base; pericarp membranous and dry.

## Nomenclatural notes

Two of the four *Passerina* specimens in the Linnean Herbarium are named *P. filifomis* in the handwriting of Linnaeus; these specimens are numbered 504.1 and 504.2 in Savage (1945). Number 504.2 is without a doubt *P. paleacea* Wikstr. Thoday (1924a) maintained that number 504.1 is a Clifford specimen and probably the one Linneaus saw when he wrote the first edition of *Species plantarum* (1753). Savage (1945) added the inscription [? ex herb. Cliff.], indicating doubt as to the origin of this specimen. The present author has seen this specimen and agrees with Thoday (1924a) that it perfectly matches the concept of *P. filiformis* as it is known in the Cape Peninsula. The phrase "Passerina foliis linearibus" in the *Species plantarum* (1753) has clearly been copied by Linnaeus from *Hortus Cliffortianus* (1737) and from Van Royen (1740). The leaves of the illustration in *Hortus Cliffortianus* are ± lanceolate and the bracts are very similar to those of *P. filiformis* subsp. *glutinosa* (Thoday) Bredenk. & A.E.van Wyk stat. nov., which has acerose or filiform leaves. The specimen labelled *Passerina filiformis* L. in Clifford's Herbarium is sterile, lacks characteristic bracts or flowers, and could possibly be *P. corymbosa* Eckl. ex C.H.Wright (= *P. vulgaris* Thoday). *P. corymbosa* is the dominant *Passerina* species in the southern and southwestern Cape and is constantly confused with *P. filiformis*. Specimen 504.1 in the Linnean Herbarium, named *P. filifomis* by Linnaeus, is here designated as the lectotype. *Thymelaea aethiopica*, in Plukenet (1700: 180), is cited in synonymy of *P. filiformis* by Linnaeus (1753). The illustrated synonym from Breyne (1678) most probably belongs to the genus *Phylica* L. (Rhamnaceae) and that of Burman (1739) is clearly a member of *Struthiola* L. (Thymelaeaceae).

**Etymology**

The Latin specific epithet *filiformis* (= thread-like) obviously refers to the narrow leaves of this species.

**Common names**

The vernacular name 'sparrow-wort' was suggested by Miller (1768) for all *Passerina* species, indicating *P. filiformis* as 'sparrow-wort with linear convex leaves'. Wendland (1798) used the German equivalent *fadenförmige Vogelkopf*. Marloth (1925) mentioned the names *kannabas* and *kaalgaar*. The following Afrikaans names appear in Smith (1966) and some of them also in Palmer & Pitman (1972) and Coates Palgrave (1977): *bakbossie*, *bakkersbossie*, *bruingonna*, *fyntaaibos*, *gannabas*, *gonnabas*, *kaalgaarbos*, *kaalgaring*, *kabelgaring*, *kannabas*, *koordehaar*, *taaibos*, *windmakersbessie*, *windmakersbossie*.

**Key to subspecies**

1a Branchlets and inflorescences dry, mostly not glutious; bracts widely obovate, narrowing abruptly into filiform point.................................18a. subsp. *filiformis*

1b Branchlets and inflorescences glutious; bracts ovate acuminate, gradually narrowing into a point....................................................... 18b. subsp. *glutinosa*

18a. subsp. **filiformis**

*Leaves* dark-green to greyish green, spreading from stem at angle of ± 30°; lamina almost terete, cordiform in cross section, length × depth (4–)5.5–8(–10) × 0.6–1 mm, slightly widening towards base. *Inflorescences* not glutious. *Bracts* widely obovate, narrowing abruptly into filiform point; length × depth ± 7.3 × 2.0 mm; base widely cuneate; main vein strongly developed, often keeled, extending to form a leaf-like point; lamina chartaceous; margins glabrous, often with a few trichomes at apex adjacent to filiform point. *Flowers* not glutious. *Floral envelope*

± 6.0 mm long; hypanthium surrounding ovary, and neck tomentose; neck 1.7 mm long; outer sepals concave, obovate, inner sepals obovate. Figure 7.19A–C.

### Diagnostic characters and relationships

Subsp. *filiformis* is morphologically distinguished by the almost terete, adaxially grooved, acerose or linear leaves and the cymbiform, widely obovate floral bracts, which abruptly narrow to a filiform point. Diagnostic characters of *P. corymbosa* include linear to narrowly lanceolate leaves and diamond-shaped bracts. Some specimens of subsp. *filiformis* with incurved, tapering leaves, exserted receptacle tubes and veined bracts could be mistaken for *P. falcifolia*. The apical beard on the young leaves and outer sepals and the glabrous inner sides of the bracts are reliable diagnostic characters for subsp. *filiformis*.

### Common name

According to Van Wyk & Gericke (2000) the name *bakkerbos* commemorates an era in the Cape when the officially licensed bakers used this plant to heat their ovens. The plants used at that time were clearly subsp. *filiformis*.

### Uses

When ignited, plants of subsp. *filiformis* disappear in a blaze of hot flame owing to a waxy secretion on the leaves (Smith 1966). The plants were formerly used for heating up stoves. Today it is quite scarce around Cape Town, probably because of the impact of collecting on this once abundant resource. At maturity these plants are quite ornamental and they have been cultivated in Britain and Europe since the time of Linnaeus. Plants of subsp. *filiformis* are vigorous resprouters, they are well adapted to the Cape climate and would be suitable for reclamation plantings in areas where invasive alien vegetation has been cleared. The bark is very tough and has been used by indigenous peoples as twine (Marloth 1925). According to Laidler (1928) a decoction of this plant has been used by the Khoekhoe for the treatment of shooting pains.

### Distribution and ecology

*Passerina filiformis* subsp. *filiformis* is endemic to the Northwestern, Southeastern and Langeberg Centres within the CFR. It is found in the Cape Peninsula, and is distributed from Piquetberg, across the Hex River Mountains, to Attaquaskloof in the southwestern Cape. It grows in rocky areas, mostly on south-facing mountain slopes, as well as on sandy plains, like the Rietvallei and Stellenbosch Flats. Figure 7.19D.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

WESTERN CAPE.—3218 (Clanwilliam): Piquetberg, (–AD), *Penther s.n., 1912* (S, WU); Piquetberg near Sauer, (–DC), *Barker 8095*, *5795*, (MO, NBG). 3318 (Cape Town): between Darling and Vredenburg, (–AA), *Hutchinson 258* (PRE); Kloofnek, slopes above old tram, (–CD), *Acocks 890* (S); Table Mountain, Cairn Face, (–CD), *Andraea 1165* (NBG, PRE); Cape Town, (–CD), *Bolus 2925* (BOL, K); Signal Hill, (–CD), *Bredenkamp 1039* (PRE); Cape Town, (–CD), *Burchell 66* (K); Table Mountain, (–CD), *Ecklon s.n.* (PR); *Esterhuysen 26437*, *34096*, (BOL, MO, M, S); India Window Route, (–CD), *McKinnon 32* (NBG); Kloofnek, (–CD), *Moss 5643* (BM); Table Mountain, (–CD), *Prior s.n.* (K); *Rob & Fries 3393*, *3396*, *3397*, *3398*, *3399* (UPS, S); Kirstenbosch, (–CD), *Schmidt 568* (M); Lions Head, (–CD), *Wall 1060* (S); Signal Hill, close to signal station, (–CD), *Wolley-Dod*, *3103* (K); Cape Town, (–CD), *Worsdell s.n.* (K); Paarlberg, (–DB), *Drège s.n.* (K); Rietvallei Flats, (–DC), *Mund & Maire s.n.* (K); Stellenbosch Flats, (–DD), *Garthside 17* (K). 3319 (Worcester): Tulbagh Kloof, (–AC), *Grant 1* (C); Hex River Pass, (–BD), *Rogers 16701B* (PRE). 3321 (Ladismith): Attaquas Kloof, (–DD), *Gill s.n.* (K). 3418 (Simonstown): granite gravel beside Llandudno Road, (–AB), *Acocks 5174* (S); Hout Bay, (–AB), *Compton 11762* (NBG); Llandudno, (–AB), *Compton 14827* (NBG); Table Mountain, (–AB), *Esterhuysen 35680* (BOL); Simon's Bay, (–AB), *Wright s.n.* (MO). 3420 (Bredasdorp): De Hoop, (–AD), *Van der Merwe 1101* (PRE). Grid ref. unknown: *Acocks 5754* (S); *Anferweg 850* (PR); Hortus Botanicus Frankfurt, *Buchenau s.n.* (BREM); *Burchell 276* (K); Great False River, Riversdale, *Burchell 6544* (K); ex Horto Leindenb., *Burmeister s.n.* (SBT); *Gerrard 1478* (BM, TCD, K); *Hardy s.n.* (K, S); ex *Herb. Linairiaro* (PR); *Herb. Regium Monacense s.n.* (M); ex *Herb. Rofski* (PR); *Herb. Zuccarinii s.n.* (M); *Krebs 282* (MO); Prague, *Kutzelman's Herbarium s.n.* (PR); *Lehman 1891* (C); *Medical Soc. Univ. s.n.* (K); *Moss T10* (BM); *Museum Bot. Hauniense s.n.* (C);

*Niven & Laubert s.n.* (S); *Pappe s.n.* (NBG); *Sparrman s.n.* (S); *Talbot s.n.* (K); *Thom 553* (K); Somerset, *Thom 577* (K); *Trinity College s.n.* (TCD); C.B.S., *without collector 692* (K); Cap. *Wie Leidelbast benubst* (UPS).

Cultivated, *s.n.* (BM); cultivated, *Hort. Herb. Pallas s.n.* (BM); cultivated, *s.n.* (PR); cultivated, *Hort. Prague s.n.* (PR); cultivated, *Vinaf s.n.* (PR).

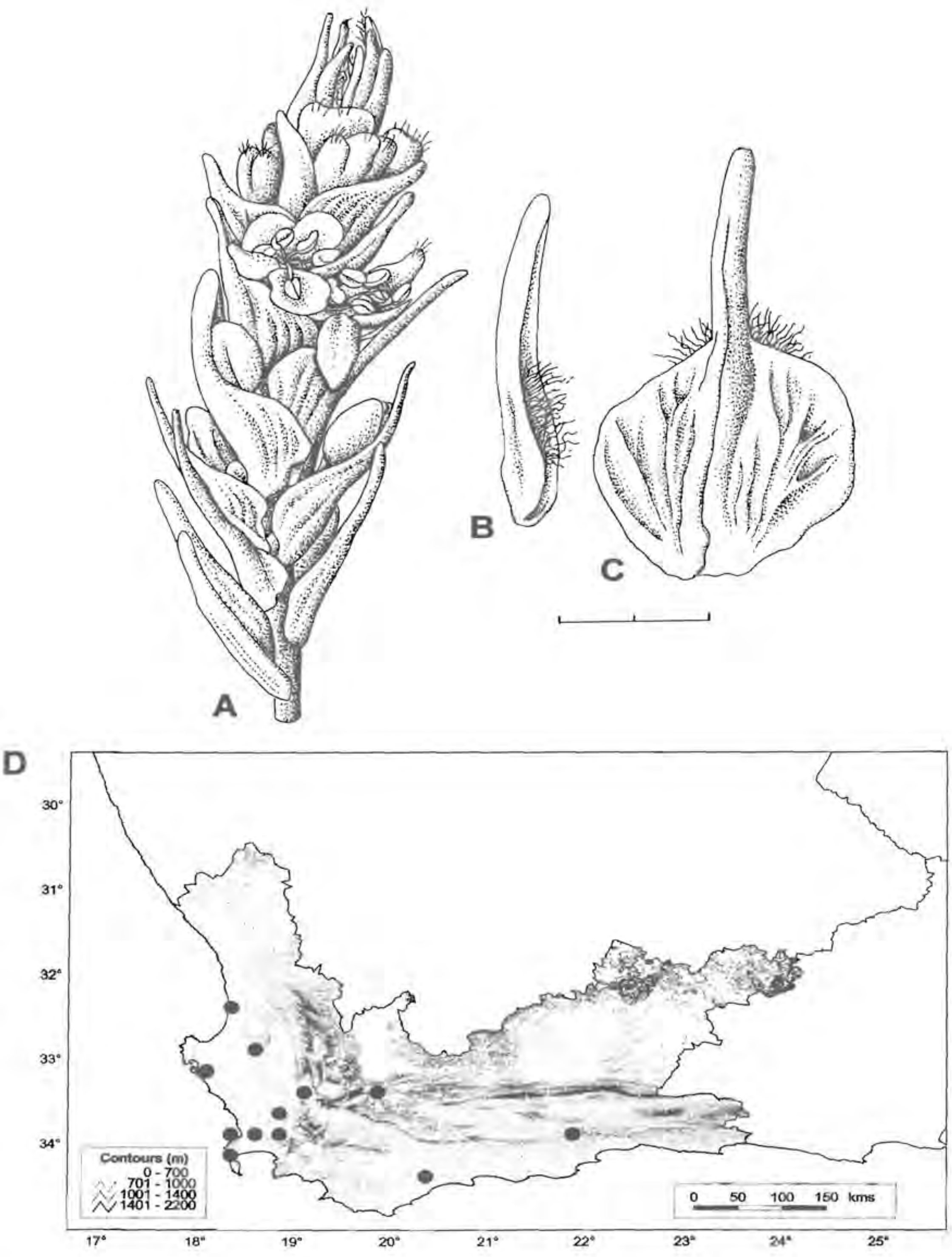

FIGURE 7.19.—*Passerina filiformis* subsp. *filiformis*, A–C (*Bredenkamp 1039*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract. Scale bar: 2 mm.

D, known distribution of *Passerina filiformis* subsp. *filiformis*.

18b. subsp. **glutinosa** (*Thoday*) *Bredenk.* & *A.E.van Wyk* , stat. nov. TYPUS.—Malmesbury Division: round Langeenheid Station, *Thoday 215* (NBG, lecto.!, here designated; BOL!).

*Passerina filiformis* L. var. *glutinosa* Thoday 4: 160 (1924a). Type: as above.

*Leaves* dark green, drying brown, glutious, closely adhering to stem or spreading at angle of ± 30°; lamina narrow, acerose or linear, transversely elliptic in cross section; length × depth ± 7.0 × 0.4 mm, tapering towards rounded apex, widening towards base. *Inflorescences* glutious, somewhat longer than in typical subspecies. *Bracts* ovate-acuminate, gradually narrowing to point; length × depth ± 4.6 × 1.5 mm; base cuneate; main vein strongly developed; lamina coriaceous; wings membranous with distinct venation; margins often ciliate. *Flowers* glutious. *Floral envelope* ± 6.5 mm long; ovary scantilly tomentose, neck scantilly tomentose, 1.5 mm long; outer and inner sepals concave, obovate. Figure 7.20A–C.

### Nomenclatural notes

*Thoday 215* in NBG was chosen as lectotype because of the longer inflorescences and the conspicuously glutious, narrow leaves. Duplicates of the syntype of var. *glutinosa*, *Schlechter 5125*, were seen from BM, C, K, MO, PRE and S. Although these specimens agree closely with the concept of var. *glutinosa* (Thoday 1924), they are somewhat atypical as the glutious character is not evident in the dried material.

### Etymology

The Latin name *glutinosa* (= viscous) obviously refers to the branchlets and inflorescences that are glutious in this subspecies.

### Distribution and ecology

Subsp. *glutinosa* is endemic to the Northwestern and Southwestern Centres within the CFR. It occurs in the Strandveld (Acocks 1988), from Doring Bay in the north to St Helena Bay in the south. The vegetation around Doring Bay is described as Strandveld Succulent Karoo by Hoffman (1998). The area is characterized by deep, calcareous, coastal Quaternary sands and generally low rainfall. St Helena Bay is situated in the Sand Plain Fynbos (Rebelo 1998) and this part of the range is characterized by a Mediterranean climate with summer drought and deep acid sands. Sand Plain Fynbos is a highly endangered vegetation type as a result of urbanization and the impact of invasive alien plant species (Rebelo 1998). Figure 7.20D.

*Conservation status*: Near Threatened, [NT] (IUCN Species Survival Commission 2000).

### Specimens examined

WESTERN CAPE.—3118 (Vanrhynsdorp): Vredendal Division, 7 m E by S of Doring Bay, (–CD), *Acocks 24062* (PRE); Doring Bay, (–CD), *Thompson* 41 (S); Doring Bay, (–DA), *Thompson 41* (NBG). 3217 (Vredenburg): Vredenburg, (–DD), *Compton 15888* (NBG). 3218 (Clanwilliam): Diepkloof S of Verlorevlei, (–AD), *Boucher 2833* (PRE); 6 m W by N of Graafwater, (–BA), *Acocks 19671* (K, M, NBG, PRE); Alexandershoek, (–BC), *Schlechter 5125* (BM, C, K, MO, PRE, S); Steenberg Cove, (–CC), *Taylor 1542* (NBG, PRE); Saldanhabaai, Langeenheid Station, (–CC), *Thoday 215* (BOL, NBG); St Helena Bay, 9 km from Velddrif, (–CC), *Thompson 801* (NBG, PRE).

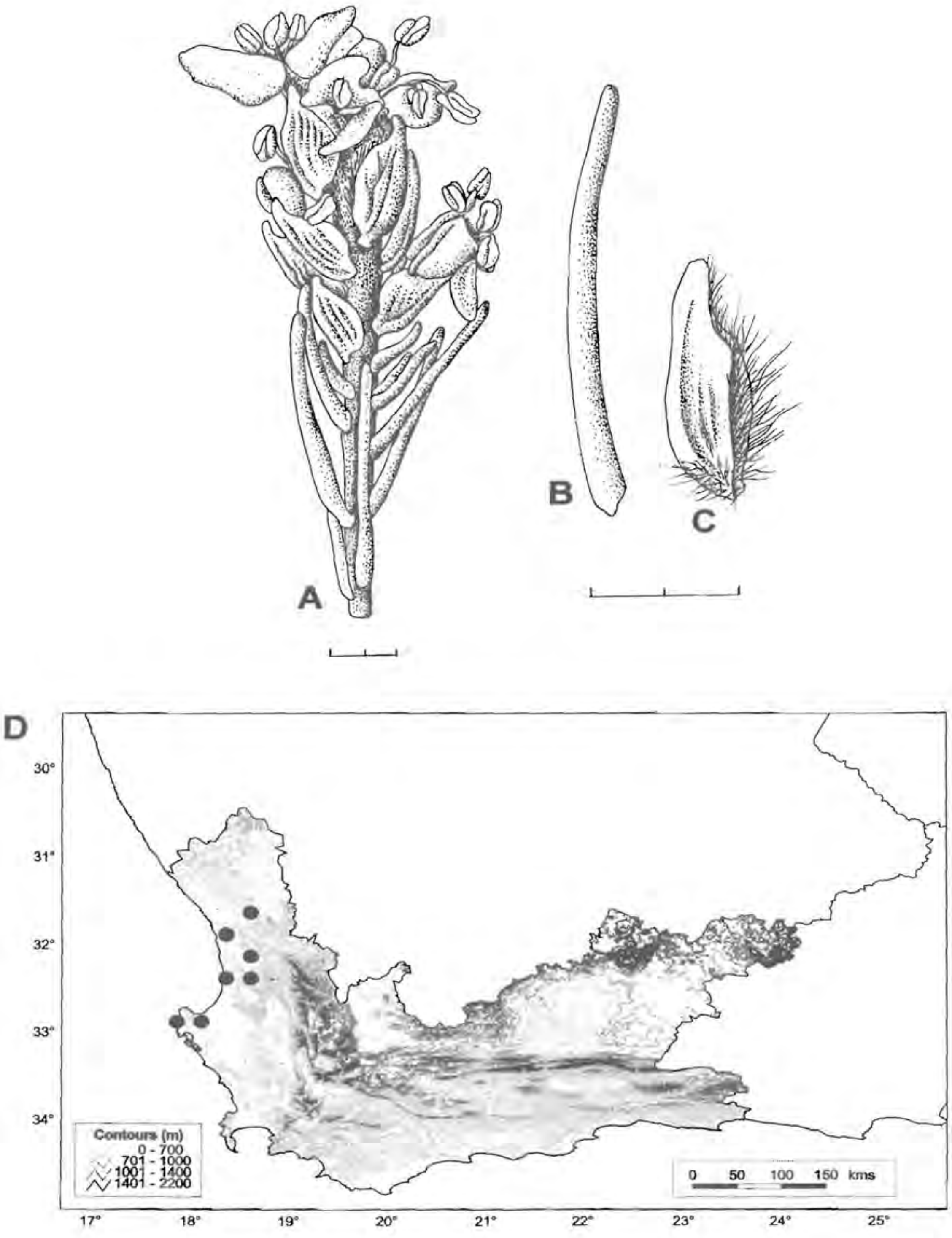

FIGURE 7.20.—*P. filiformis* subsp. *glutinosa*, A–C (*Schlechter 5125*). A, flowering inflorescence; B, leaf; C, bract. Scale bar: 2 mm.
D, Known distribution of *Passerina filiformis* subsp. *glutinosa*.

19. **Passerina falcifolia** (*Meisn.*) *C.H.Wright*. Flora capensis 5,2: 10 (1915); Thoday 4:158 (1924a); Palmer & Pitman: 1585 (1972); Coates Palgrave: 648 (1977); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 683 (2000). Type: Eastern Cape, Uitenhage, Vanstaadesberg [now Van Staden's Mountains], 1 000–2 000 ft, *Drège s.n.* (K!, lecto., designated by Thoday 10: 388 (1924b)].

*Passerina filiformis* L. var. *divaricata* Wikstr. 39: 325 (1818); Thoday 4:158 (1924a). Type: Western Cape: Caput Bonae Spei [Cape Peninsula], *Sparrman s.n.*, *Herb. Thunberg 9573* (UPS, holo.!), *Herb. Swartzii* (S, iso.!).

*Passerina filiformis* L. var. *falcifolia* Meisn.: 399 (1840); Drège: 118, 124 (1843); Meisn. 14: 562 (1857); C.H.Wright: 10 (1915); Thoday 4:158 (1924a). Type: same as for *P. falcifolia*.

Much-branched tall shrubs or small ornamental trees, (1.0–)1.2–2.0(–3.04) m high, branchlets often arcuate, pendulous. *Stems* grey-brown, indumentum of young stems closely whitish tomentose, forming lengthwise patterns, with cork on older branches, which gradually become glabrous, fissuring lengthwise, yellowish brown lenticulae present; leaf scars oblate. *Leaves* greyish green, drying greyish brown, falcate, linear to narrowly lanceolate, longitudinaly folded, triangular in section, length × depth 3.9–5.6 × 0.6 mm, adaxial surface concave, tomentose, abaxial surface glabrous; base sessile; apex obtuse or tapered; margins glabrous, involute; younger leaves inclined, diverging at an angle of ± 60°, imbricate, overlapping up to 50%, older leaves horizontally spreading, not imbricate. *Inflorescences* with multiflowered main and co-florescences; spikes usually extended, lax, often arcuate, up to 16-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* mottled grey-green, rose-tinted during flowering time, ascending, imbricate, widely ovate, narrowing into a leaf-like, falcate point, length × depth (5.3–)5.8 × 1.7(–2.0) mm; older bracts folded lengthwise along midrib and keeled, younger bracts adaxially concave (inside), abaxially slightly convex (outside), villous inside, glabrous outside, coriaceous; wings chartaceous, distinctly ± 4-ribbed and reticulately veined; base cuneate; apex obtuse or tapered; margins ciliate in distal half. *Floral envelope* ± 8.4 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* scantily tomentose at ovary, neck exserted, often arcuate, tomentose, ± 3.0 mm long. *Sepals*: outer sepals concave, obovate, adaxially scantily tomentose, abaxially glabrous; inner sepals obovate, adaxially tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 1.4 mm and those of antisepalous whorl ± 2.1 mm long; anthers ovoid, 1.0 × 0.4 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.5 × 0.7 mm. *Fruit* an achene with pericarp membranous and dry, 2.5 × 1.4 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in sepals and androecium being shed. Figure 7.21A–F.

### Nomenclatural notes

Wright (1915) overlooked the combination *P. filiformis* L. var. *divaricata* Wikstr. (1818), also indicated by Thoday (1924a), which is the earliest name for the taxon. However, this name based on *Sparrman s.n.* (Herb. Thunberg 9573) falls into synonymy under *P. falcifolia*, as the name of a taxon does not have priority outside the rank in which it was published (Greuter *et al.* 2000).

### Diagnostic characters and relationships

*Passerina falcifolia* can be distinguished by the mottled grey-green falcate leaves, which are inclined or horizontally spreading. The widely ovate bracts are villous inside and narrow into a leaf-like, falcate point, with chartaceous wings that are distinctly ± 4-ribbed and reticulately veined. The most conspicuous floral character is the slender, often arcuate, tomentose hypanthium neck, exserted from the clasping bract. This species can be confused with *P. filiformis* subsp. *filiformis* which has widely obovate bracts, narrowing abruptly into a filiform point. The bracts are basally to centrally setose on the inside and the wings are glabrous. *P. montivaga* is another close species, but can be distinguished by bracts that are basally setose on the inside, with glabrous wings.

## Etymology

The specific epithet *falcifolia* is derived from the Latin *falcatus* (= curved like a sickle), referring to the falcate or sickle-shaped leaves of these plants.

## Common names

*Passerina falcifolia* is also known as the 'Outeniqua gonna' or the *Outeniekwagonna*, referring to the Outeniqua Mountains where it occurs (Coates Palgrave 1977). Palmer & Pitman (1972) use the vernacular name 'forest gonna', as these plants are commonly seen along roadsides on mountain passes of the southern Cape forests. Von Breitenbach *et al.* (2001) use the names *Outeniekwa-gonna*, *gonnabas*, *gonnabos*, *kannabas* and 'Outeniqua gonna, gonna bush'.

## Uses

*Passerina falcifolia* is used for fuel or for making cord (Palmer & Pitman 1972). According to label information on *Dahlstrand 1905* (PRE), the species is cultivated by florists. Plants grow into small ornamental trees and could be used more widely in horticulture. According to *Grobbelaar 63* (PRE), *P. falcifolia* is a host to members of the insect genus *Eremnus*.

## Distribution and ecology

*Passerina falcifolia* is associated with forests and Mountain Fynbos (Rebelo 1998) in the southern Cape and the southern parts of the Eastern Cape. It is a near-endemic to the CFR and occurs in the Karoo Mountain, Southwestern and Southeastern Centres, as well as the Zuurberg, Blaauwkrantz and Alexandria Forests of the Eastern Cape. It most commonly occurs in a belt between the coast and the 33°S latitude and from 22° to 26°E longitude. The two specimens, *Brown 25975* and *Rogers 28858*, collected near Caledon in October 1924, are regarded as outliers, possibly indicating a wider previous distribution of the species into areas with woody vegetation in the Western Cape. *P. falcifolia* occurs from Meiringspoort, in the Oudtshoorn area, to Ruytersbosch in the Mossel Bay area, and along the Outeniqua, Tsitsikamma and Great Winterhoek Mountains to the Grahamstown area. Figure 7.21G.

*Passerina falcifolia* is found on mountain plateaus and southeast-facing slopes on Table Mountain Sandstone in shallow, sandy loam soil. Plants commonly occur along forest margins, in open patches, or disturbed areas along roadsides. This species is also found in coastal regions and riverine fynbos. *P. falcifolia* grows at a range of altitudes, from sea level up to 1 100 m.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

**Specimens examined**

EASTERN CAPE.—3225 (Somerset East): Zuurberg, (–DA), *Compton 20274* (NBG). 3323 (Willowmore): 12.5 mi. from Keurboomsrivier to Storms River, (–CD), *Thompson 880* (K, PRE); Joubertina, Groot River, (–DA), *Manson 147* (PRE); Ratel's Bosch, (–DC), *Fourcade 74* (BOL, K); Nature's Valley, Grootwes River Mouth, (–DC), *Parsons 172* (PRE); Bloukrantz Hoek, (–DC), *Schrire 2083* (GRA); Uniondale District, Tsitsikama Forest, (–DD), *Capener CF/2* (PRE). 3324 (Steytlerville): Slagboom Mountain, (–AD), *Britten 5812* (GRA, PRE); opposite Tsitsikama Lodge, near Sanddrif turn-off, (–CD), *Bredenkamp 915* (PRE); Cockscomb, (–DB), *Abel s.n.* (NBG); Uitenhage, Swartkops River, (–DB), *Zeyher 277* (BOL, K, NBG, TCD); Baviaanskloof near Cambria, (–DD), *Van Wyk 390* (K). 3325 (Port Elizabeth): Grootwinterhoekberge, Strydomsberg, (–CA), *Noel s.n.* (GRA); Uitenhage District, Groendal Wilderness, Eland's River Catchment Basin, (–CA), *Scharf 1023* (PRE); Deysel's Kraal Farm, (–CA), *Scharf 1578, 2001, 2005* (NBG, PRE); KwaZunga Catchment Basin, Os Plaat Farm, (–CA), *Scharf 2002* (PRE); Kromkloof Catchment Basin, Strydomsberg, Farm Waainek, (–CA), *Scharf 2033* (GRA, PRE); Coega Catchment Basin, (–CB), *Scharf 1689* (K, NBG, PRE); Groendal Wilderness Reserve, Bauerskraal Farm, (–CB), *Scharf 1985* (PRE); near Uitenhage, Van Staden's Mountains, stony places, 1 000–3 000 ft, (–CC), *Drège s.n.* (K); Van Staden's Mountains, Longmore Forest Station, (–CC), *Hugo 1405* (K, NBG, PRE); Longmore Bosstasie, (–CC), *Olivier 593* (K, PRE); Van Staden's Mountains, (–CC), *Thompson 1856* (PRE); Van Staden's Mountains, (–CC), *Zeyher 3778* (NBG); stony channels of Swartkops River, (–CD), *Zeyher 277* (K). 3326 (Grahamstown): Grahamstown, Port Elizabeth Road, (–BD), *Britten 5812* (PRE); Blaauwkrantz Pass, (–BD), *Story 3559* (K, M, PRE); Boknes

Strand, 7 km SW of Kenton-on-Sea, near Bakana's River, (–DA), *Burrows 2464* (PRE). 3423 (Knysna): Humansdorp District, Storms River, (–BB), *Marloth 13044* (PRE). 3424 (Humansdorp): Kruisfontein Mountains, (–BA), *Cowling 1419* (GRA); Groot River Forest, (–BB), *Barker 6036* (S); Humansdorp, Stan's River Mouth, (–BB), *Rycroft 3000* (S); Humansdorp District, (–BB), *Thode 993* (K, MO, PRE).

WESTERN CAPE.—3322 (Oudtshoorn): Meiringspoort, (–BC), *Ueckermann 7793* (PRE); Mossel Bay, Outeniqua Mountains, Ruiterbosch, (–CC), *Britten 130* (PRE); Kouma River, Outeniqua Pass, (–CC), *Campbell 13541* (NBG); S foot of Robinson Pass, (–CC), *Salter 6352* (BM, BOL, K); between Ruytersbosch and Robinson Pass, (–CC), *Van Niekerk 95* (NBG); Montagu Pass, near George, (–CD), *Bayliss BRI b295* (PRE); Prince Alfred Pass, (–CD), *Bredenkamp 920* (PRE); Robinson Pass, (–CD), *Bredenkamp 921* (PRE); Wolf-drift, Malgaten River, (–CD), *Burchell 6109* (K, PRE); Montagu Pass, (–CD), *Compton 7584* (C), Montagu Pass, Saasveld Forest Station, (–CD), *Dahlstrand 1285* (C); George on road to Knysna, (–CD), *Gillett 4536* (K); Montagu Pass, (–CD), *Humbert 9908* (PRE); Montagu Pass, (–CD), *Levyns 5040* (BOL); George, (–CD), *Marloth 6244* (PRE); George, (–CD), *Mund s.n.* (BM, NBG); Montagu Pass, (–DC), *Compton 7422, 7584* (NBG); Wilderness, Hoekwil, (–DC), *Wahl 42* (NBG); Hoogekraal, Sedgefield, (–DD), *Hugo 2019* (K); Karatara, (–DD), *Keet 1152* (PRE); 20 mi. NW of Knysna beyond Homtini Pass, (–DD), *Marsh 594* (K, PRE). 3323 (Willowmore): Gouna Staatsbos, (–CC), *Bredenkamp 917* (PRE); Knysna, Gouna Road, (–CC), *Levyns 7842* (BOL). 3419 (Caledon): near Caledon, (–AB), *Brown 28858* (PRE). 3422 (Mossel Bay): on road to Knysna from George, (–BB), *Gillett 4536* (BOL, PRE). 3423 (Knysna): Groot Rivier, (–AA), *Barker 6036* (NBG); Knysna, (–AA), *Grobbelaar 63* (PRE); Blaauwkrantz, (–AA), *Martin s.n.* (GRA); Paardekop, (–AA), *Morris 396* (NBG); near Coldstream, (–AA), *Rodin 1305* (BOL, K, MO, PRE); Knysna, (–AA), *Rogers 27004* (BM, NBG, PRE); Knysna, Blaaukrantz, (–AA), *Tyson 1449* (K, NBG, PRE); Groot Rivier, (–AA), *Wurts 2121* (NBG); George, (–AA), *Zeyher 38* (BOL); Knysna, (–AA), *collector unknown s.n.* (S); bordering forest at Plettenberg Bay and Knysna, (–AB), *Bowie 5* (BM); Plettenberg Bay, (–AB), *Rogers 28983* (GRA, NBG). Grid ref. unknown: Cultivated, *Dahlstrand 1905* (MO, PRE); *Ecklon & Zeyher 38* or *91* (MO); Humansdorp District, Rietvlei, *Esterhuysen 6634* (BOL); *Herb. Thunberg s.n.* (UPS); Montagu Pass, *Lam & Meeuse 4660* (MO); Paris Jardin des Plantes, *Meinkauff s.n.* (M); Caput Bonae Spei, Herb. Gasstromii, *Sparrman s.n.* (S); ex Herb. Swartzii, *Sparrman s.n.* (S); Herb. Wikstromii, *Sparrman s.n.* (S); Herb. Regium Monacense, *Sparrman s.n.* (M); *Wallich s.n.* (K); Cape, *Zeyher s.n.* (S).

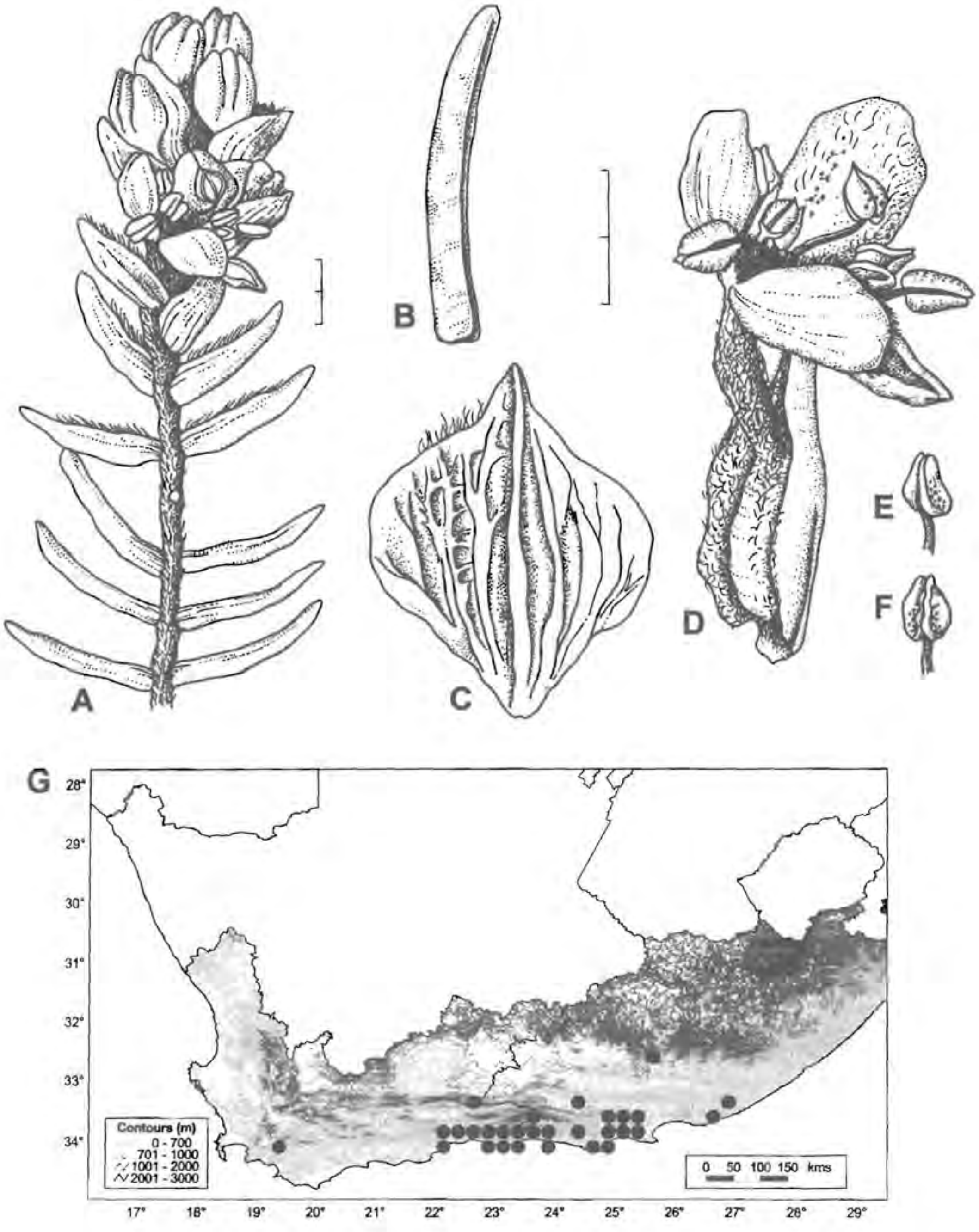

FIGURE 7.21.—*Passerina falcifolia* (*Bredenkamp 917*). A, flowering inflorescence; B, leaf; C, bract; D, flower clasped by bract. E, anther, dorsal view; F, anther ventral view. Scale bars: 2 mm.

G, known distribution of *Passerina falcifolia*.

20. **Passerina rubra** *C.H.Wright*. Flora capensis 5,2: 12 (1924a); Thoday 4:156 (1924a); Bond & Goldblatt: 433 (1984); Goldblatt & Manning: 684 (2000). Type: Western Cape, Ladismith, Muiskraal, near Garcia Pass, 1 200 ft, 3 October 1897, *Galpin 4492* [K!, lecto., designated by Thoday 10: 388 (1924b); GRA!, PRE!].

*Passerina filiformis* L. var. *squarrosa* Meisn. 14: 562 (1857); Thoday 4:156 (1924a). Type: Eastern Cape, prope Cradockstad et Port-Elisabeth [near Cradock Town and Port Elizabeth], October, *Zeyher 3779* (S!, lecto., here designated; BM!, MEL!, NBG!, W!).

Much branched, erect shrubs, with rigid branchlets and inflorescences or smaller, extensively branched, rounded shrublets under arid, calcareous habitat conditions, (0.2–)0.3–0.75(–1.1) m high. *Stems*: older ones grey-brown, indurate, and sclerenchyma fibres exposed; young stems reddish brown, indumentum whitish tomentose, forming lengthwise patterns with cork on older branches, which gradually become glabrous, cork fissuring lengthwise; internodes longer than leaves during prolific lengthening of branchlets or shorter under arid conditions. *Leaves* greyish green, ascending, appressed, decussate and rigid, or under arid conditions, imbricate (overlapping 5–30%), appressed or ascending, diverging at an angle of up to 30°; lamina narrowly lanceolate or oblong, longitudinaly folded, triangular in section, length × depth 2.4–4.3 × 0.7 mm, adaxial surface concave, tomentose, abaxial surface glabrous; base sessile; apex obtuse; margins glabrous, involute. *Inflorescences* with conspicuous, multiflowered main and co-florescences; spikes robust, rigid, extended, narrowly ellipsoid, with rows of enlarged, decussate, pointed bracts, 20–30-flowered, arrangement subterminal, axis white-tomentose, proliferating growth common. *Bracts* grey-green, rose-tinted during flowering time, ascending, imbricate, widely ovate, midrib shortly extended into a point, length × depth (4.3–)5.1 × 1.8(–2.0) mm; older bracts folded lengthwise along midrib, younger bracts adaxially concave (inside), abaxially slightly convex (outside), villous inside, glabrous outside, coriaceous; wings widely ovate, chartaceous, ± 5-ribbed, reticulately veined; base cuneate; apex acute; margins ciliate in distal half. *Floral envelope* ± 8.4 mm long, papyraceous and yellow-pink during pollination, dehydrated after shedding of pollen, turning red to brown. *Hypanthium* glabrous at ovary, neck exserted, sparsely pubescent, ± 2.0 mm long. *Sepals*: outer sepals cymbiform, ad- and abaxially glabrous, inner sepals obovate, adaxially scantilly tomentose, abaxially glabrous. *Androecium* with filaments of antipetalous whorl ± 0.7 mm and those of antisepalous whorl ± 1.7 mm long; anthers ovoid, 0.9 × 0.3 mm, subbasifixed, 2-thecous and 4-locular. *Ovary* 2.7 × 1.1 mm. *Fruit* an achene with pericarp membranous and dry, 2.1 × 1.2 mm, enveloped by persistent, loosely arranged hypanthium, breaking up at neck base due to dehydration and torsification of tissue, resulting in the sepals and androecium being shed. Figure 7.22A–G.

### Nomenclatural notes

As the starting date for a Latin diagnosis is 1 January 1935 (Greuter *et al.* 2000), *P. rubra* is a valid name, although it was published with a full description, but without a Latin diagnosis, by Wright (1915). The combination *P. filiformis* L. var. *squarrosa* (Meisner 1857), was overlooked by Wright (1915), but mentioned in synonymy by Thoday (1924a). In the present revision all the type material cited by both Wright (1915) and Meisner (1857) was studied. *Galpin 4492* (K) was selected as the lectotype of *P. rubra* by Thoday (1924b) and *Zeyher 3779* in S was selected as lectotype for *P. filiformis* var. *squarrosa* as it is internationally available in many herbaria.

### Diagnostic characters and relationships

The distribution of *P. rubra* partly coincides with that of *P. corymbosa*, *P. montivaga* and *P. falcifolia*. *P. rubra* is a smaller shrub (average height 0.3–0.75 m), often occurring in calcareous soil. It can be distinguished from the other three species which are taller (average heights 1–2 m), and especially from *P. falcifolia*, which is a tall shrub or a small tree (up to 3.04 m), often associated with indigenous forests. *P. rubra* can also be separated by the inflorescences which have extended, robust spikes, with up to 30 fertile, enlarged bracts. The bracts are typified by the midrib which is shortly extended into a point and by the wings which are adaxially tomentose, widely ovate, chartaceous, ± 5-ribbed and reticulately veined. Flowers are distinguished by the exserted hypanthium neck, which is ± 2.0 mm long and glabrous to sparsely pubescent.

### Etymology

The specific epithet *rubra* has been derived from the Latin *ruber* (= red), referring to the conspicuous, multiflowered inflorescences of these plants, which have 20–30 flowers arranged in four rows and turning red after wind pollination.

### Uses

*Passerina rubra* is a pioneer which often occurs along to roadsides or in disturbed places, e.g. close to the salt works in the vicinity of Port Elizabeth. It is also found on calcareous soils between Port Elizabeth and Cradock. In the Coega area, earmarked for industrial development, *P. rubra* might be a useful plant for combatting erosion.

### Distribution and ecology

*Passerina rubra* is near-endemic to the CFR, occurring in the Langeberg, Karoo Mountain and Southeastern Centres, as well as southern parts of the Eastern Cape. It most commonly occurs in a belt between the coast and the 33°S latitude and from 20° to 26°E longitude. *P. rubra* is distributed from the Bontebok National Park in the Swellendam District, eastwards to Gowie's Kloof near Grahamstown (Figure 7.22H). This species is somewhat variable. It was initially thought that plants in the Western Cape were more rigid, with longer internodes and appressed leaves, which did not overlap, whereas those in the Eastern Cape tended to be rounded shrublets, with imbricate, ascending leaves. After many specimens, from all parts of the range had been studied, no geographical or morphological discontinuity between the two forms could be shown, and it was decided that the morphological differences were probably due to plasticity. Plants growing in more arid conditions and calcareous soil, typical of the Port Elizabeth and Cradock areas, tend to be rounded much-branched shrublets, with short internodes and imbricate, ascending leaves. Under more favourable conditions in sandy loam, the plants are taller, less branched, internodes are longer and the appressed leaves do not overlap.

*Passerina rubra* is common in the Steytlerville, Humansdorp, Port Elizabeth and Grahamstown areas of the Eastern Cape and less frequent in the Western Cape. The area between Cradock and Port Elizabeth is renowned for the ancient dunes and flats, abounding in limestone. Acocks (1988) described the vegetation occurring on the limestone as False Fynbos (A70), also known as Mountain Fynbos or Grassy Fynbos (Rebelo 1998). *P. rubra* seems to be well adapted to the calcareous soils on which it occurs. These plants are often pioneers in disturbed areas and along roadsides, as in the Colchester, Coega and the Markman industrial areas of Port Elizabeth. At the Groendal Catchment Basin, this species occurs in grassland on sandstone and it is also found on semikarroid, dry, rocky hillsides in the Baviaanskloof area. At the Bontebok National Park it is found in flat areas between fynbos species. *P. rubra* grows at altitudes of 70–700 m.

*Conservation status*: Least Concern (LC) (IUCN Species Survival Commission 2000).

### Specimens examined

WESTERN CAPE.—3321 (Ladismith): Muiskraal, near Garcia Pass, (–CC), *Galpin 4492* (GRA, K, PRE). 3322 (Oudtshoorn): near George, (–CD), *Bayliss 6861* (K, MO, S); Langkloof, Keurboomsrivier, (–CD), *Fourcade 1646* (BOL). 3420 (Bredasdorp): Swellendam district, Bontebok National Park, (–AB), *Acocks 22365* (PRE); *Barnard 699* (PRE); E of Swellendam, (–AB), *Johnson 102* (M, NBG); Bontebok National Park, (–AB), *Liebenberg 6574* (PRE); Breede River, N of National Road Bridge, (–AB), *Taylor 3413* (NBG, PRE); Langeberg, Clock Peaks, (–AB), *Wurtz 208* (NBG); near Heidelberg, (–BB), *Barker 5565* (NBG); Potberg, above Diepkloof, (–BC), *Burgers 1464* (PRE). 3422 (Mossel Bay): Sedgefield District, hills above Rondevlei, (–BB), *Bayliss 6856* (M, MO). 3423 (Knysna): near Knysna, (–AB), *Edwards 17260* (BM).

EASTERN CAPE.—3324 (Steytlerville): en route to Cradock, (–BC), *Bayliss BRI.B.1088* (PRE); Baviaanskloof, (–CA), *Bayliss 546* (K, M, MO, NBG); Kareedouw, Vaalkraal, (–CC), *Schrire 2037* (GRA); Zuuranys en route to Kareedouw, (–CD), *Bredenkamp 914* (PRE); Humansdorp, Papiesfontein, (–DD), *Cowling 1223* (GRA); Humansdorp, on road to Hankey, (–DD), *Fourcade 5747* (NBG); Gamtoos Bridge, (–DD), *Van Jaarsveld & Sardien 10998* (PRE). 3325 (Port Elizabeth): Addo Elephant National Park, Zuurkop, (–BD), *Archibald 5259* (K, PRE); *Barnard 526* (PRE); Zuurkop, Bruinveld, (–BD), *Botha 5656* (GRA); Paterson en route to Mimosa, Vista Farm, (–BD), *Retief 12* (PRE); hills between Coega River and Zondagsrivier, (–CB), *Ecklon 598* (S); between Swartkops- and Zondagsrivier, (–CB), *Zeyher 156* (BM, BOL, K, NBG, TCD); Van Stadensberg, Lady's Slipper, (–CD), *Dold 1063* (GRA); Bethelsdorp, (–CD), *Paterson 270* (GRA); Swartkops Catchment, Groendal Forest Reserve, Great Winterhoek Mountains, (–CD), *Scharf 1961* (K, PRE); Port Elizabeth, flats SW of Greenbushes, (–CD), *Thompson 1874* (PRE); on Motherwell, Addo road, Tregathlyn Estate, (–DA), *Palmer 3932* (GRA); Addo, Farm Windmolen, (–DA), *Schrire 1968*, *1969* (GRA); Colchester, on limestone, (–DB), *Bredenkamp 905* (PRE); NE of Coega, (–DC), *Acocks 21424* (K, M, PRE); Port Elizabeth, hillsides, (–DC), *Bolus 1905* (BOL); 2 km E of Coega, (–DC), *Bredenkamp 906* (PRE); Markman industrial area, (–DC), *Dahlstrand 2836*, *2849*, *2850*, *3251* (C, GRA, MO, NBG, PRE); Aloes, (–DC), *Drège 3006* (GRA, PRE); Swartkopsrivier, (–DC), *Long 809* (PRE); Redhouse, (–DC), *Long 1061* (GRA, PRE); Emerald Hill, (–DC), *Lynes 1737* (BM); Redhouse, (–DC), *Paterson TRV 25754* (PRE); slopes around Port Elizabeth, (–DC), *Tyson 2178* (K, NBG); *West 358* (GRA); near Cradock Town and Port Elizabeth, *Zeyher 3779* (BM, MEL, NBG, S W). 3326 (Grahamstown): Albany, Grahamstown, (–AD), *Bayliss 5164* (MO); Cradock Road, Albany, (–AD), Bayliss 8850 (M, MO); army base, (–AD), *Bredenkamp 900* (PRE); military camp, (–AD), *Brink 232* (GRA, K, PRE); mountains near Howison's Poort, (–AD), *MacOwen 103* (K, GRA, S); Albany, (–AD), *Williamson s.n.* (TCD); near Grahamstown, (–BC), *Bolton s.n.* (DUB); Grahamstown near drive-in, (–BC), *Hoole 10* (GRA, PRE); Grahamstown, (–BC), *Shumane P58* (GRA); Gowie's Kloof, (–BC), *Sidey 1219* (S); *Story 3162* (PRE); Alexandria, (–CB), *Archibald 3833* (GRA); Hougham Park, (–CB), *Archibald 4558* (K, PRE). 3424 (Humansdorp): Essenbosch Hills, (–BB), *Fourcade 4417* (BOL); 7 mi. from Humansdorp Kloof, on road to Hankey, (–BB), *Fourcade 5747* (BOL); between Kabeljous and Mondplaas, (–BB), *Fourcade 5940* (BOL, PRE); Seekoei River, (–BB), *Montgomery 18* (NBG); 8.8 mi. from Humansdorp to Cape St Francis, (–BB), *Thompson 903* (NBG, PRE); Humansdorp District, Bokkeveld Shale, (–BB), *Youthed 663* (GRA); Kareedouw, Suuranys Mountains, (–CC), *Schrire 2038* (GRA). Grid ref. unknown: Cape District, *Bowie 3* (BM); *Masson s.n.* (BM).

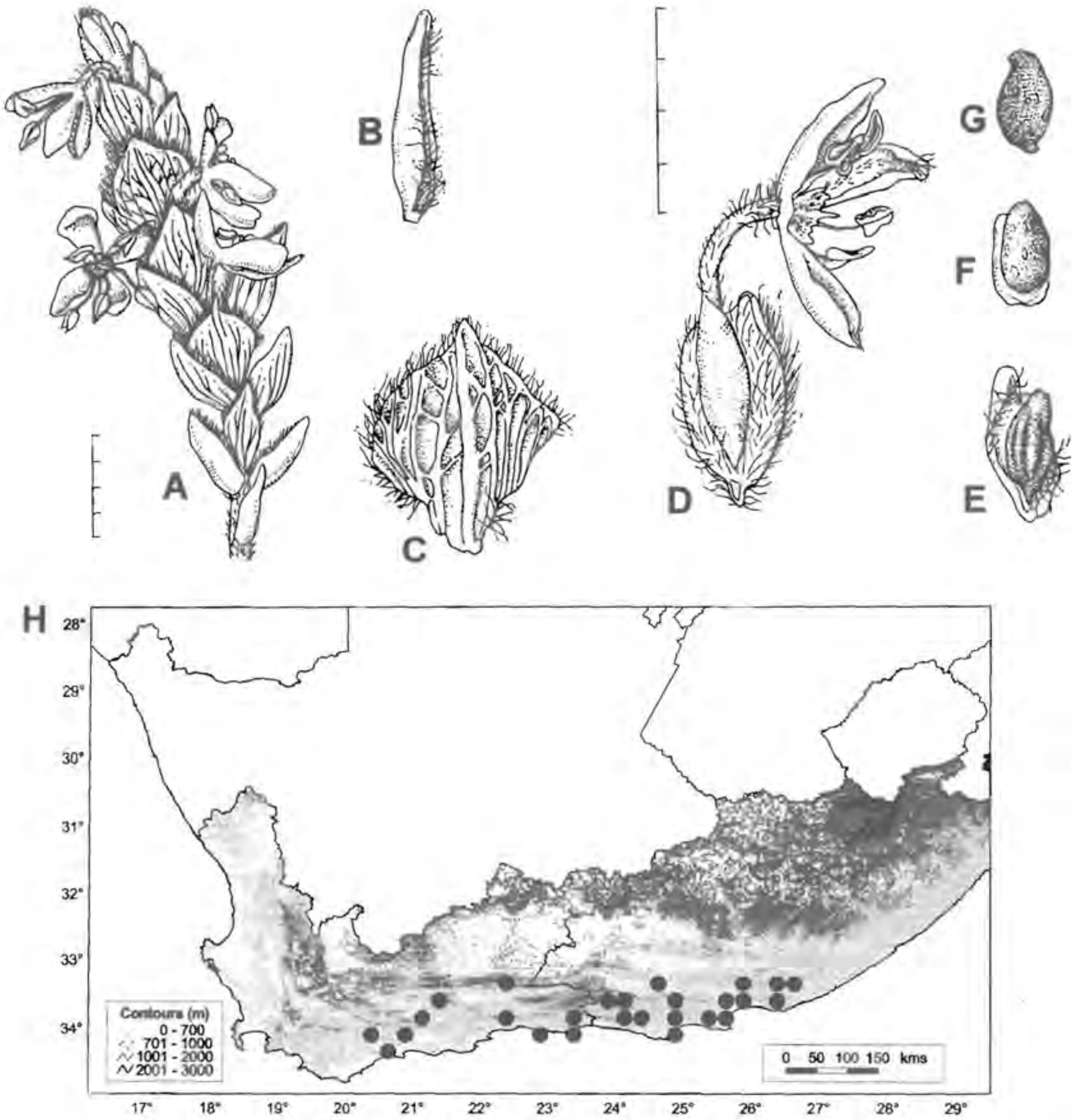

FIGURE 7.22.—*Passerina rubra* (*Bredenkamp 914*). A, inflorescence with apex growing out, returning to vegetative growth (proliferating growth); B, leaf; C, bract; D, flower clasped by bract; E, fruit clasped in tomentum of bract, enveloped by hypanthium, fragmented at neck base; F, achene, enveloped by membranous pericarp; G. Achene in side view. Scale bars: 4 mm.

H, known distribution of *Passerina rubra*.

## 7.4 Doubtful name

*Passerina hamulata* Gdgr.: 418 (1913). Hab.: Cap, in dunis arenosis prope Wynberg [Western Cape, Simonstown, sand dunes near Wineberg], *Bolus s.n.*—Notes: *Passerina paleacea*, *Bolus 2926*, complies with this distribution, but the name *P. hamulata* is not written on this specimen, therefore *P. hamulata* was not placed in synonymy under *P. paleacea*.

## 7.5 Excluded names

Sources of information:

- *Passerina* databases at National Botanical Institute
- Literature cited in the list
- Royal Botanic Gardens, Kew. Index Kewensis on Compact Disc (1997).

*Lachnaea conglomerata* L.: 560 (1753); 374 (1784); Willd.: 434 (1799); Wikstr. 39: 323 (1818); Thunb: 374 (1825a); Meisn. 14: 562 (1857); Cafferty & Beyers: 171, 172 (1999); Brummitt: 805 (2000) nom. rejic. = **Phylica stipularis** L. (Rhamnaceae) in Cafferty & Beyers: 171 (1999).

*Passerina ammodendron* Kar. & Kir.: 444 (1842) =**Stellera lessertii** C.A.Mey. in Meisn. 14: 550 (1857). Iran.

*Passerina annua* Auch. ex Meisn. 14: 552 (1857) =**Thymelaea aucheri** Meisn. 14: 552 (1857); K.Tan: 235 (1980). Syria, Lebanon, W Iran.

*Passerina annua* Wikstr. 39: 320 (1818) = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980) [= *Thymelaea arvensis* Lam. in Meisn. 14: 551 (1857) (= *Stellera passerina* L.)]. Widespread: C and S Europe, SW Asia, C Russia.

*Passerina anthylloides* L.f.: 226 (1782) = **Gnidia virescens** Wikstr. in Meisn. 14: 592 (1857). South Africa: Cape Peninsula.

*Passerina anthylloides* Thunb.: 75 (1794) = **Gnidia virescens** Wikstr. in Meisn. 14: 592 (1857). South Africa: Cape Peninsula.

*Passerina aragonensis* Rouy: 123 (1910). Pyrenees.

*Passerina argentata* Pau: 67 (1922) = **Thymelaea argentata** (Lam.) Pau in K.Tan: 212 (1980). Spain and N Africa.

*Passerina arvensis* Ball: 653 (1878) = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980) [= *Thymelaea arvensis* Lam. in Meisn. 14: 551 (1857) (= *Stellera passerina* L.)]. Widespread: C and S Europe, SW Asia, C Russia.

*Passerina axillaris* Thunb.: 106 (1792), =**Pimelea virgata** Vahl in Meisn. 14: 516 (1857). New Zealand.

*Passerina baccifera* Mihi? nom. nud., *Eckl. & Zeyh. s.n.* (BOL!, P!, W!) = **P. ericoides** L.

*Passerina baccata*, *Pappe s.n.* (NBG!, SAM!) err. typogr. = **P. ericoides** L.

*Passerina bartlingiana* Meisn. True identity unknown.

*Passerina broteriana* (Cout.) Sampaio: 104 (1913) = **Thymelaea broteriana** Cout.: 145 (1909); K.Tan: 227 (1980). Endemic to N and C Portugal.

*Passerina bruniades* Eckl. & Zeyh. ex Meisn. 14: 579 (1857) =**Lachnaea penicillata** Meisn. 14: 579 (1857); J.B.P.Beyers: 96 (2001). South Africa: Western Cape Province.

*Passerina brunioides* Eckl. & Zeyh. in Meisn. 14: 563, 579 (1857) = *Passerina bruniades* Eckl. & Zeyh. ex Meisn.

*Passerina calocephala* Meisn.: 393 (1840) = **Gnidia calocephala** (C.A.Mey.) Gilg: 226–228 (1894a). South Africa: KwaZulu-Natal and Eastern Cape Provinces.

*Passerina calycina* Lam. & DC.: 360 (1805) = **Thymelaea calycina** (Lapeyr.) Meisn. 14: 555 (1857); K.Tan: 226 (1980). C Pyrenees, rare.

*Passerina campanulata* E.Mey. ex Meisn.: 407 (1840) = **Lachnaea grandiflora** (L.f.) Baill. in J.B.P.Beyers: 45 (2001). South Africa: Western Cape Province.

*Passerina canescens* Schousb.: 190 (1800) = **Thymelaea lanuginosa** (Lam.) Ceballos & Vicioso in K.Tan: 211 (1980) [= *Thymelaea canescens* (Schousb.) Endl. in Meisn. 14: 556 (1857)]. S Spain, Marocco and Gibraltar.

*Passerina cantabrica* Pourr. ex Willk. & Lange: 299 (1862) =**Thymelaea coridifolia** (Lam.) Endl. in K.Tan: 226 (1980). Endemic to N Spain.

*Passerina capitata* L.: 88 (1760) =**Lachnaea capitata** (L.) Crantz in J.B.P.Beyers: 66 (2001). South Africa: Western Cape Province.

*Passerina cephalophora* Thunb.: 75 (1794) = **Lachnaea eriocepahala** L. in J.B.P.Beyers: 98 (2001). South Africa: Western Cape Province.

*Passerina chamaedaphne* Bunge: 58 (1833) =**Wikstroemia canescens** Meisn. 14: 547 (1857). Nepal.

*Passerina chamaejasme* Fisch. ex Meisn. 14: 549 (1857) = **Stellera chamaejasme** L. in Meisn. 14: 549 (1857). Siberia.

*Passerina chamaejasme* Schangin: in Meisn. 14: 549 (1857) = **Stellera altaica** Thieb. in Meisn. 14: 549 (1857). Siberia.

*Passerina ciliata* L.: 559 (1753) = **Gnidia penicillata** Licht. ex Meisn. in B.Peterson: 476 (1959). South Africa: Western Cape Province.

*Passerina ciliata* Thunb.: 75 (1794) = *Lachnaea ciliata* (L.) Crantz in J.B.P.Beyers: 109 (2001), excluded species.

*Passerina concinna* Walp.: 583 (1849) = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980) [= *Thymelaea arvensis* Lam. in Meisn. 14: 551 (1857) (= *Stellera passerina* L.)]. Widespread: C and S Europe, SW Asia, C Russia.

*Passerina conglomerata* (L.) Thunb.: 75 (1794); Wikstr. 39: 322 (1818) = **Phylica stipularis** L. (Rhamnaceae) in Cafferty & Beyers: 171 (1999).

*Passerina coridifolia* Wikstr. 39: 334 (1818) = **Thymelaea coridifolia** (Lam.) Endl. in K.Tan: 226 (1980). Endemic to N Spain.

*Passerina cornucopiae* = **Pimelea cornucopiae** Vahl in B.Hansen & P.Wagner: 352 (1998). Australia.

*Passerina corsica* J.Gay ex Litard. in Briq.: 6 (1938) = **Thymelaea tartonraira** All. subsp. **thomasii** (Duby) Briq. in K.Tan: 220 (1980) [= *Thymelaea tartonraira* All var. *calvescens* Gren. & Godr. in Meisn. 14: 556 (1857)]. Circum-Mediterranean.

*Passerina costata* Griff.: 367 (1854) =**Diarthron vesiculosum** C.A.Mey. in Meisn. 14: 558 (1857). Persia.

*Passerina diarthronoides* Griff.: 365 (1854) = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980) [= *Thymelaea arvensis* Lam. in Meisn. 14: 551 (1857) (= *Stellera passerina* L.)]. Widespread: C and S Europe, SW Asia, C Russia.

*Passerina dichotoma* Steud.: 273 (1841) =**Stellera chamaejasme** L. in Meisn. 14: 549 (1857). Siberia.

*Passerina dioica* Ramond: 139 (1800) =**Thymelaea dioica** (Gouan) All. in K.Tan: 222 (1980). W Pyrenees to SW Alps.

*Passerina dodecandra* L.: 10 (1755) =**Struthiola dodecandra** (L.) Druce in Levyns: 599 (1950). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina elliptica* Boiss.: 556, t. 158 (1842) = **Thymelaea pubescens** (L.) Meisn. subsp. **elliptica** (Boiss.) K.Tan: 231 (1980) [= *T. elliptica* (Boiss.) Endl.: 66 (1847)]. Endemic to S. Spain.

*Passerina empetrifolia* Lapeyr.: 212 (1813) = **Thymelaea dioica** (Gouan) All. subsp. **dioica** in K.Tan: 222 (1980). W Pyrenees to SW Alps.

*P. filiformis* var. *ereifoifolia* Eckl. & Zeyh. 39 (G!), err. typogr. = **P. ericoides** L.

*Passerina eriocephala* Thunb.: 75 (1794) =**Lachnaea globulifera** Meisn. 14: 576 (1857); J.B.P.Beyers: 107 (2001). South Africa: Western Cape Province.

*Passerina filiformis* Mill. 8: no. 1 (1768) =**Struthiola sp.**

*Passerina ganpi* Sieb. ex Miq. 2: 77, no. 696 (1870); Meisn. 14: 564 (1857) = **Stellera? ganpi** Meisn. 14: 550 (1857). Japan.

*Passerina geminiflora* Ram. in K.Tan: 222 (1980) = **Thymelaea dioica** (Gouan) All. subsp. **dioica** in K.Tan: 222 (1980). W Pyrenees to SW Alps.

*Passerina globosa* Lam. 2: 431 (1792) =**Lachnaea alpina** Meisn. 14: 578 (1857); J.B.P.Beyers: 59 (2001). South Africa: Western Cape Province.

*Passerina gnidia* L.f.: 226 (1782) = **Pimelea gnidia** Banks et Sol. New Zealand.

*Passerina gnidia* Forst.: 28 no. 170 (1786); Meisn. 14: 516 (1857) = **Pimelea gnidia** Banks et Sol. in Meisn. 14: 516 (1857). New Zealand.

*Passerina granatensis* Pau: 7 (1904) = **Thymelaea dioica** (Gouan) All. subsp. **granatensis** (Pau) Malag in K.Tan: 222 (1980). SE Spain, C and W Pyrenees.

*Passerina grandiflora* L.f.: 226 (1782) = **Lachnaea grandiflora** (L.f.) Baill. in J.B.P.Beyers: 45 (2001). South Africa: Western Cape Province.

*Passerina gymnostachya* Meisn.: 397 (1840). = **Gnidia gymnostachya** (C.A.Mey.) Gilg in E.Phillips: 63 (1944). South Africa: North-West, Gauteng, Mpumalanga, Free State, KwaZulu-Natal and Eastern Cape Provinces, also in Lesotho.

*Passerina hirsuta* Asso in Meisn. 555 (1857) =**Thymelaea tinctoria** (Pourr.) Endl. subsp. **tinctoria** in K.Tan: 223 (1980). Portugal (?), NE and E Spain and S France.

*Passerina hirsuta* Brot. in K.Tan: 227 (1980) = **Thymelaea broteriana** Cout.: 145 (1909); K.Tan: 227 (1980). Endemic to N and C Portugal.

*Passerina hirsuta* L.: 559 (1753) = **Thymelaea hirsuta** Endl. in K.Tan: 209 (1980). Circum-Mediterranean, Europe, SW Asia and N Africa.

*Passerina imbricata* Burm.f.: 12 (1768). True identity unknown.

*Passerina imbricata* Sennen: 69 (1924). True identity unknown. Spain.

*Passerina incana* Pourr. ex Willk. & Lange 1: 300 (1862) = **Thymelaea velutina** (Pourr. ex Camb.) Endl. in K.Tan: 221(1980). Endemic to the Balearics.

*Passerina inconspicua* Meisn.: 397 (1840) = **Gnidia inconspicua** Meisn. in Arnold & De Wet: 516 (1993) [=*Arthrosolen inconspicuus* Meisn. 560 (1857)]. South Africa: Western Cape Province.

*Passerina incurva* Wendl. ex Bartl.: 404 (1840). True identity unknown.

*Passerina involucrata* Spreng. ex Meisn. 14: 595 (1857) = **Gnidia capitata** L.f. in B.Peterson: 627 (1958) [= *Lasiosiphon linifolius* Decne. var. *glabrata* Meisn. 14: 595 (1857)]. South Africa: Northern Province, North-West, Gauteng, Mpumalanga, Free State, KwaZulu-Natal and Eastern Cape Provinces, also Botswana, Swaziland and Lesotho.

*Passerina involucrata* Thunb. 13: 106 (1792) = **Pimelia linifolia** Sm. in B.Hansen & P.Wagner : 352 (1998). Australia.

*Passerina japonica* Sieb. & Zucc.: 76 (1846) = **Wikstroemia japonica** Miq.: 184 (1863). Japan.

*Passerina javanica* Thunb.: 19 (1825b). True identity unknown. Java.

*Passerina juniperifolia* Lapeyr.: 213 (1813) = **Thymelaea tinctoria** (Pourret) Endl. subsp. **nivalis** (Ramond) K.Tan [= *Thymelaea nivalis* (Ram.) Meisn. 14: 555 (1857)] K.Tan: 224 (1980). Endemic to C and W Pyrenees.

*Passerina kalifolia* Pourr. ex Willk. & Lange: 301 (1862) = **Thymelaea lanuginosa** (Lam.) Ceballos & Vicioso in K.Tan: 211 (1980) [= *Thymelaea canescens* (Schousb.) Endl. in Meisn. 14: 556 (1857)]. S Spain, Marocco and Gibraltar.

*Passerina laevigata* L.2: 15 (1756) = **Gnidia oppositifolia** L. in Meisn. 14: 586 (1857). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina laniflora* C.H.Wright: 11 (1915) = **Lachnea laniflora** (C.H.Wright) Bond in J.B.P.Beyers: 81 (2001). South Africa: Western Cape Province.

*Passerina lanuginosa* Pau: 67 (1922) = **Thymelaea lanuginosa** (Lam.) Ceballos & Vicioso in K.Tan: 211 (1980). Marocco, S Spain, Gibraltar.

*Passerina lateriflora* Hort. ex Wikstr. 39: 347 (1818) = **Gnidia spicata** (L.f.) Gilg in E.Phillips: 63 (1944). South Africa: Western Cape Province.

*Passerina laxa* L.f.: 226 (1782) = **Gnidia laxa** (L.f.) Gilg: 226 (1894a). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina lessertii* Wikstr. 39: 341 (1818) = **Stellera Lessertii** C.A.Mey. in Meisn. 14: 550 (1857). Persia.

*Passerina linariaefolia* Pourr. ex Wikstr. 39: 333 (1818) = **Thymelaea pubescens** (L.) Meisn. subsp. **thesioides** (Lam.) K.Tan: 231 (1980). Spain.

*Passerina linearifolia* Wikstr. 39: 343 (1818) = **Gnidia linoides** Wikstr. var. **major** Meisn. 14: 583 (1857).

*Passerina linearis* Wendl. ex Bartl.: 404 (1840). Species non descriptae, Meisn. 14: 563 (1857).

*Passerina linoides* Thunb.: 75 (1794) = **Gnidia linoides** Wikstr. in Meisn. 14: 582 (1857). South Africa: Western Cape Province.

*Passerina longiflora* Thunb.: 189 (1800) = **Pimelea longifolia** Banks et Sol. in Meisn. 14: 516 (1857). New Zealand.

*Passerina longifolia* Thunb. 22: 32 (1797) = **Pimelia longifolia** Banks et Sol. in

Meisn. 14: 516 (1857). New Zealand.

*Passerina matnak* J.F.Gmel.: 1597 (1792), sphalm. = *Passerina metkan* J.F.Gmel.: 634 (1791), sphalm.

*Passerina metnam* Forssk.: 81 (1775) = **Thymelaea hirsuta** Endl. in K.Tan: 209 (1980). Circum-Mediterranean, Europe, SW Asia and N Africa.

*Passerina metnan* Forssk. in Meisn. 14: 564 (1857) = **Thymelaea hirsuta** Endl. in K.Tan: 209 (1980). Circum-Mediterranean, Europe, SW Asia and N Africa.

*Passerina microphylla* Coss. & Dur.: 744 (1856) 744 =**Thymelaea microphylla** Meisn. 14: 556 (1857); K.Tan: 214 (1980). N Africa.

*Passerina nervosa* Thunb.: 75 (1794) = **Lachnaea nervosa** (Thunb.) Meisn. in J.B.P.Beyers: 69 (2001). South Africa: Western Cape Province.

*Passerina nervosa* Wikstr. 39: 328 (1818) =**Lachnaea striata** (Poir.) Meisn. 14: 577 (1857); J.B.P.Beyers: 77 (2001). South Africa: Western Cape Province.

*Passerina nitida* (Vahl) Desf.: 331, t. 94 (1798) = **Thymelaea argentata** (Lam.) Pau in K.Tan: 212 (1980) [= *Thymelaea nitida* Endl. in Meisn. 14: 554 (1857)]. Spain and N Africa.

*Passerina nivalis* Ram.: 131, t. 9 (1800) = **Thymelaea tinctoria** (Pourret) Endl. subsp. **nivalis** (Ramond) K.Tan: 224 (1980). Endemic to C and W Pyrenees.

*Passerina orientalis* Willd.: 431 (1799) = **Thymelaea tinctoria** (Gouan) All. subsp. **dioica** [*Thymelaea orientalis* Meisn. 14: 557 (1857)] in K.Tan: 222 (1980). W Pyrenees to SW Alps.

*Passerina passerina* Huth.: 135 (1898) = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980) [= *Thymelaea arvensis* Lam. in Meisn. 14: 551 (1857) (= *Stellera passerina* L.)]. Widespread: C and S Europe, SW Asia, C Russia.

*Passerina pentandra* Thunb.: 76 (1794) =**Lonchostoma obtusiflorum** Wikstr. in Meisn. 14: 564 (1857).

*Passerina persica* Boiss.: 85 (1846) =**Stellera lessertii** C.A.Mey. in Meisn. 14: 550 (1857). Persia.

*Passerina pilosa* G.Forst. in Meisn. 14: 564 (1857); B.Hansen & P.Wagner: 352 (1988) = **Pimelea tomentosa** (J.R. & G.Forst.) Druce in B.Hansen & P.Wagner: 352 (1998). New Zealand.

*Passerina* pilosa L.f.: 226 (1782) = **Pimelea tomentosa** (J.R. & G.Forst.) Druce in B.Hansen & P.Wagner: 352 (1998) (= Pimelea virgata Vahl). New Zealand.

*Passerina planifolia* Burm.f.: 12 (1768) =**Lachnaea alpina** Meisn. 14: 578 (1857);

J.B.P.Beyers: 59 (2001). South Africa: Western Cape Province.

*Passerina polycephala* E. Mey ex Meisn.: 390 (1840) = **Gnidia polycephala** (C.A.Mey.) Gilg: 227 (1894a). Namibia, Botswana and South Africa: North-West, Gauteng, Mpumalanga, Free State, Eastern Cape and Northern Cape Provinces.

*Passerina polygalaefolia* Lapeyr.: 214 (1813) = **Thymelaea hirsuta** Endl. in K.Tan: 209 (1980). Circum-Mediterranean, Europe, SW Asia and N Africa.

*Passerina prostrata* Forst.: 28 (1786) = **Pimelea prostrata** (J.R. & G.Forst.) Willd. in B.Hansen & P.Wagner: 352 (1998). New Zealand.

*Passerina prostrata* L.f.: 227 (1782) = **Pimelea prostrata** (J.R. & G.Forst.) Willd. in B.Hansen & P.Wagner: 352 (1998). New Zealand.

*Passerina pubescens* Guss.: 451 (1843) = **Thymelaea mesopotamica** (Jeffrey) Peterson in K.Tan: 239 (1980) [= *Thymelaea arvensis* Lam. var. *pubescens* (Guss.) Meisn. 14: 552 (1857)]. SE Anatolia, Iraq, W Iran, Kuwait.

*Passerina pubescens* (L.) Wikstr. 39: 332 (1818) = **Thymelaea pubescens** (L.) Meisn. subsp. **pubescens** in K.Tan: 231 (1980). Pyrenees, S and E Spain.

*Passerina pubescens* (L.) Loscos var. *virgata* Pau: 33 (1925) = **Thymelaea pubescens** (L.) Meisn. subsp. **thesioides** (Lam.) K.Tan: 231 (1980). Spain.

*Passerina purpurea* Wikstr. 39: 323 (1818) = **Lachnaea eriocephala** L. in J.B.P.Beyers: 99 (2001). South Africa: Western Cape Province.

*Passerina racemosa* Wikstr. 39: 320 (1818) = **Stellera altaica** Thieb. in Meisn. 14: 549 (1857). Subalpine region, the Caucasus.

*Passerina rosmarinifoliae* fide Meisn.: 400 (1840) = **Phylica sp.**, *Herb. Lamarck* (P, microfiche 574).

*Passerina ruizii* (Loscos.) Font-Quer in K.Tan: 225 (1980) = **Thymelaea ruizii** [Loscos] Casav. in K.Tan: 225 (1980). High ranges, Sierra de Cabrera in NE Portugal to C Pyrenees.

*Passerina salina* Munby = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980); seen from (C), specimen without collector and number.

*Passerina salsa* Hunley, *Debeaux s.n.* (PR), cf. *P. annua* (Salisb.) Wikstr. var. *salsa* Munby in K.Tan: 238 (1980) = **Thymelaea salsa** Murb. in K.Tan: 238 (1980). S Spain, Marocco and Algeria.

*Passerina salsolaefolia* Poir.: 41 (1804) = **Phylica sp.** in Meisn.: 400 (1840); *Herb. Lamarck* (P, microfiche 574).

*Passerina sanamunda* (All.) Bub.: 135 (1897) = **Thymelaea sanamunda** All. in Meisn. 14: 553 (1857); K.Tan: 233 (1980). Spain, S France and Italian Riviera.

*Passerina segobriensis* Pau: 25 (1887) = **Thymelaea argentata** (Lam.) Pau in K.Tan: 212 (1980) [= *Thymelaea nitida* Endl. in Meisn. 14: 554 (1857)]. Spain and N Africa.

*Passerina sericea* L.: 15 (1755) =**Gnidia sericea** L. in Meisn. 14: 583 (1857). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina setosa* Thunb.: 75 (1794) = **Gnidia setosa** Wikstr. in Meisn. 14: 590 (1857). Eastern Cape.

*Passerina spicata* L.f.: 226 (1782) = **Gnidia spicata** (L.f.) Gilg in E.Phillips: 63 (1944). South Africa: Western Cape Province.

*Passerina stachyoides* Schrenk in Meisn. 14: 550 (1857) = **Stellera stachyoides** Schrenk in Meisn. 14: 550 (1857). Siberia.

*Passerina stellera* Ram. ex Lam. & DC.: 361 (1805) = **Thymelaea passerina** (L.) Coss. & Germ. in K.Tan: 236 (1980) [= *Thymelaea arvensis* Lam. in Meisn. 14: 551 (1857)]. Widespread: C and S Europe, SW Asia, C Russia.

*Passerina stelleri* Wikstr. 39: 321 (1818) = **Stellera chamaejasme** L. in Meisn. 14: 549 (1857). Siberia.

*Passerina striata* Poir.: 44, t. 291, f. 2 (1804) = **Lachnaea striata** (Poir) Meisn.: 415–416 (1840); J.B.P.Beyers: 77 (2001). South Africa: Western Cape Province.

*Passerina stricta* Thunb.: 75 (1794) = **Gnidia wikstroemiana** Meisn. 14: 582 (1857). South Africa: Northern Cape and Free State Provinces.

*Passerina subspicata* Meisn.: 395 (1840) = **Wikstroemia subspicata** Meisn. 14: 547 (1857).

*Passerina tartonraira* Schrad.: 89 (1810) = **Thymelaea Tartonraira** All. in Meisn. 14: 556 (1857); K.Tan: 215 (1980). Circum-Mediterranean.

*Passerina tenuiflora* Willd.: 426 (1809) = **Gnidia laxa** (L.f.) Gilg: 226 (1894a). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina tetragona* Steud.: 274 (1841) = **Struthiola dodecandra** (L.) Druce in Levyns: 599 (1950). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina thesioides* Wikstr. 39: 333 (1818) = **Thymelaea pubescens** (L.) Meisn. subsp. **thesioides** (Lam.) K.Tan [= *Thymelaea thesioides* (Lam.) Endl. in Meisn. 14: 553 (1857)] in K.Tan : 231 (1980). Spain.

*Passerina thomasii* Duby: 406 (1828) = **Thymelaea tartonraira** All. subsp. **thomasii** (Duby) Briq. [= *Thymelaea tartonraira* All var. *calvescens* Gren. & Godr. in Meisn.

14: 556 (1857)] in K.Tan: 220 (1980). Circum-Mediterranean.

*Passerina thunbergii* Wikstr. 39: 343 (1818) = **Gnidia sericea** L. in Meisn. 14: 583 (1857). South Africa: Eastern Cape and Western Cape Provinces.

*Passerina thymelaea* (Lam.) DC. in Lam. & DC.: 366 (1815) = **Thymelaea sanamunda** All. in Meisn. 14: 553 (1857); K.Tan: 233 (1980). Spain, S France and Italian Riviera.

*Passerina tinctoria* Pourr. in Meisn. 14: 565 (1857) = **Thymelaea tinctoria** (Pourr.) Endl. subsp. **tinctoria** in K.Tan: 223 (1980). Portugal (?), NE and E Spain and S France.

*Passerina tinctoria* var. *angustifolia* Boiss.: 556 (1842) = **Thymelaea calycina** Meisn. 14: 555 (1857); K.Tan: 226 (1980). C Pyrenees, rare.

*Passerina tingitana* Salzm. ex Meisn. 14: 554 (1857) = **Thymelaea villosa** (L.) Endl. in K.Tan: 229 (1980). S Portugal, Spain, Gibraltar, Marocco.

*Passerina tomentosa* Wikstr. 39: 332 (1818) = **Thymelaea tartonraira** All. in Meisn. 14: 556 (1857); K.Tan: 215 (1980). Circum-Mediterranean.

*Passerina uniflora* Drège ex Meisn. 14: 574 (1857) = **Gnidia penicillata** Licht. ex Meisn. in B.Peterson: 476 (1959), [=*Cryptadenia ciliata* (Thunb.) Meisn. in J.B.P.Beyers: 45 (2001), exluded species].

*Passerina uniflora* L.: 560 (1753) = **Lachnaea uniflora** (L.) Crantz in J.B.P.Beyers: 43 (2001). South Africa: Western Cape Province.

*Passerina uniflora* L. var. *angustifolia* Burm.f.: 12 (1768). = **Lachnaea uniflora** (L.) Crantz in J.B.P.Beyers: 43 (2001). South Africa: Western Cape Province.

*Passerina uniflora* L. var. *purpurea* Berg.: 128 (1767). = **Lachnaea uniflora** (L.) Crantz in J.B.P.Beyers: 43 (2001). South Africa: Western Cape Province.

*Passerina uniflora* L. var. *alba* Berg.: 129 (1767) = **Lachnaea grandiflora** (L.f.) Baill. in J.B.P.Beyers: 45 (2001). South Africa: Western Cape Province.

*Passerina uniflora* L. var. *latifolia* Burm.f.: 12 (1768). = **Lachnaea grandiflora** (L.f.) Baill. in J.B.P.Beyers: 45 (2001). South Africa: Western Cape Province.

*Passerina velutina* Boiss.: 81 (1838) = **Thymelaea pubescens** (L.) Meisn. subsp. **elliptica** (Boiss.) K.Tan: 231 (1980). Endemic to S Spain.

*Passerina velutina* [Pourr.] Cambess.: 183 (1827) = **Thymelaea velutina** (Pourr. ex Camb.) Endl. in K.Tan: 221(1980). Endemic to the Balearics.

*Passerina vesiculosa* Fisch. & C.A.Mey.: 170 (1839) = **Diarthron vesciculosum** C.A. Mey. in Meisn. 14: 558 (1857). Persia.

*Passerina villosa* Thunb.: 106 (1792) = **Pimelea arenaria** Cunn. in Meisn. 14: 517 (1857). New Zealand.

*Passerina villosa* Wikstr. 39: 332 (1318) = **Thymelaea villosa** (L.) Endl. in Meisn. 14: 554 (1857); K.Tan: 229 (1980). S Portugal and Spain, Gibraltar, Morocco.

*Passerina virescens* Coss. & Dur. ex Meisn. 14: 554 (1857) = **Thymelaea virescens** Meisn. 14: 554 (1857); K.Tan: 212 (1980). NW Africa.

*Passerina virgata* Desf.: 331, t. 95 (1798) = **Thymelaea virgata** (Desf.) Endl. in K.Tan: 228 (1980); subsp. **virgata** from NW Africa and S Spain & subsp. **broussonetii** from NW Africa.

TABLE 7.1.—A summary of taxa in the most comprehensive works on *Passerina* from Linnaeus (1753) to the present study

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
| P. filiformis *L.* | P. filiformis *L.* | P. filiformis *L.* | P. filiformis *L.* | P. filiformis *L.* | P. filiformis *L.* | P. filiformis *L.* | P. filiformis *L.*<br>(= P. *cupressina* J.C.Wendl. nom. nud.)<br>(= *P. pectinata* Lodd. nom. nud.)<br><br>*subsp.* filiformis<br>*subsp.* glutinosa (*Thoday*) *Bredenk.* & *A.E.van Wyk* |
| | | | P. filiformis L.<br>α vulgaris *Meisn.* | P. filiformis L.<br>α vulgaris *Meisn.* | P. corymbosa *Eckl.* ex C.H.Wright | P. vulgaris *Thoday*<br>(= *P. filiformis* L. var. *vulgaris* Meisn. )<br>(= *P. corymbosa* Eckl. ex Meisn) | P. corymbosa *Eckl.* ex *C.H.Wright*<br>(= *P. filiformis* L. var. *vulgaris* Meisn.)<br>(=*P. vulgaris* (Meisn.) Thoday) |

| Linnaeus (1753) | Wikström (1818) | Thunberg (1825a) | Meisner (1840) | Meisner (1857) | Wright (1915) | Thoday (1924a) | Present study |
|---|---|---|---|---|---|---|---|
| | P. filiformis *L.*<br>β divaricata *Wikstr.* | | P. filiformis *L.*<br>β falcifolia *Meisn.* | P. filiformis *L.*<br>β falcifolia *Meisn.* | P. falcifolia *C.H.Wright* | P. falcifolia *C.H.Wright*<br>(= *P. filiformis* L. var. *divaricata* Wikstr.)<br>(= *P. filiformis* L. var. *falcifolia* Meisn.) | P. falcifolia (*Meisn.*) *C.H.Wright*<br>(= *P. filiformis* L. var. *divaricata* Wikstr.)<br>(= *P. filiformis* L. var. *falcifolia* Meisn.) |
| | | | P. filiformis L.<br>γ comosa *Meisn.* | P. filiformis L.<br>γ comosa *Meisn.* | P. comosa *C.H.Wright* | P. comosa *C.H.Wright* | P. comosa (*Meisn.*) *C.H.Wright*<br>(= *P. filiformis* L. var. *comosa* Meisn.)<br>(= *P. falciformis* Drège) |
| | | | | P. filiformis L.<br>δ squarrosa *Meisn.* | P. rubra *C.H.Wright* | P. rubra *C.H.Wright*<br>(= *P. filiformis* L. var. *squarrosa* Meisn.) | P. rubra *C.H.Wright*<br>(= *P. filiformis* L. var. *squarrosa* Meisn.) |

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
| P. hirsuta *L.* | P. hirsuta *L.*<br>(= *P. metnan* Forsk.) | | | Thymelaea hirsuta *Endl.*<br>(= *P. hirsuta* L.)<br>(= *P. metnan* Forsk.) | | | |
| P. ciliata *L.* | P. ciliata *L.* | P. ciliata *Thunb.*<br>(= *P. ciliata* L.) | | Cryptadenia ciliata *Meisn.*<br>(= *P. ciliata* Thunb.)<br>Gnidia? ciliata *Meisn.*<br>(= *P. ciliata* L.) | | | |
| P. uniflora *L.* | P. uniflora *L.* | P. uniflora *L.* | | Cryptadenia uniflora *Meisn.*<br>(= *P. uniflora* L.) | | | |
| Lachnaea conglomerata *L.* | P. conglomerata *Thunb.*<br>(= *L. conglomerata* L.)<br>(= *P. glomerata* Thunb.) | P. glomerata *Thunb.*<br>(= *L. conglomerata* L.)<br>(= *P. ericoides* L.) | | *L. conglomerata* L. | | P. glomerata *Thunb.*<br>(= *L. conglomerata* L.) | *L. conglomerata* L. nomen rejiciendum |

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
|  | P. paleacea *Wikstr.*<br>(= *Lachnaea paleacea* fide Wikstr.) |  | P. paleacea *Wikstr.* | P. paleacea *Wikstr.*<br>(= *Lachnaea paleacea* fide Wikstr.) | P. paleacea *Wikstr.*<br>(= *Lachnaea paleacea* fide Wikstr.) | P. paleacea *Wikstr.*<br>(= *Lachnaea paleacea* Wikstr.)<br>(= *P. glomerata* fide Thunb.) | P. paleacea *Wikstr.*<br>(=*Lachnaea paleacea* fide Wikstr.)<br>(= *P. glomerata* sensu Thunb.)<br>(= *P. ericoides* sensu Thunb.) |
|  | P. ericoides *L.* |  | P. ericoides *L.* ? | P. ericoides *L.*<br>(= *P. glomerata* Thunb.)<br>(= *Lachnaea conglomerata* L.) | P. ericoides *L.*<br>(= *P. glomerata* Thunb.)<br>(= *Lachnaea conglomerata* L.) | P. ericoides *L.*<br>(= *Chymococca empetroides* Meisn.)<br>(= *P. filiformis* var. *crassifolia* Eckl. & Zeyh. fide Meisn.) | P. ericoides *L.*<br>(= *Chymococca empetroides* Meisn.)<br>(= *P. filiformis* L. var. *crassifolia* Eckl. & Zeyh. fide Meisn.)<br>(= *P. glomerata* sensu Meisn.) |

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
|  | P. rigida *Wikstr.* |  | P. rigida *Wikstr.* | P. rigida *Wikstr.* | P. rigida *Wikstr.* | P. rigida *Wikstr.* | P. rigida *Wikstr.*<br>(= *P. eriophora* Gand.)<br>(= *P. ericoides* sensu Meisn.) |
|  |  |  | P. rigida *Wikstr.*<br>α comosa *Meisn.* | P. rigida *Wikstr.*<br>α comosa *Meisn.* | P. rigida *Wikstr.*<br>*var.* δ comosa *Meisn.* | P. pendula *Eckl. & Zeyh.* ex *Meisn.*<br>(= *P. rigida* var. *comosa* Meisn. pro parte) | P. pendula *Eckl. & Zeyh.* ex *Thoday.*<br>(= *P. rigida* Wikstr. var. *comosa* Meisn.) |
|  |  |  | P. rigida *Wikstr.*<br>β tetragona *Meisn.* | P. rigida *Wikstr.*<br>β tetragona *Meisn.* | P. rigida *Wikstr.*<br>*var.* γ tetragona *Meisn.* | P. burchellii *Thoday*<br>(= *P. rigida* var. *comosa* Meisn. pro parte).<br>(= *P. tetragona* Burch.) | P. burchellii *Thoday*<br>(= *P. tetragona* fide Thoday) |
|  |  |  | P. rigida *Wikstr.*<br>γ truncata *Meisn.* | P. rigida *Wikstr.*<br>γ truncata Meisn. | P. rigida *Wikstr.*<br>β truncata *Meisn.* | P. glomerata *Thunb.*<br>(= *P. rigida*Wikstr. | P. truncata (*Meisn.*) *Bredenk. & A.E.van Wyk*<br>(= *P. rigida* Wikstr. |

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
| | | | | | | var. *truncata* Meisn.)<br>(= *P.* rigida Wikstr. var. *tetragona* Meisn. pro parte) | var. *truncata* Meisn.)<br>(= *P. rigida* Wikstr. var. *tetragona* Meisn.)<br>(= *P. glomerata* sphalm. quoad *L. conglomerata* L. sensu Thunb.)<br>(= *Lachnaea glomerata* sphalm. quoad *L. conglomerata* L. sensu Thunb.)<br>(= *P. ericoides* sensu Thunb.)<br>(= *P. glomerata* sensu Thoday)<br><br>*subsp.* truncata<br>*subsp.* monticola Bredenk. & A.E.van Wyk |

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
|  |  |  | P. pectinata *nom. nud.* | P. filiformis *L.* (=*P. pectinata* nom. nud.) |  | P. filiformis *L.* (= *P. pectinata* nom. nud.) | P. filiformis *L.* (= *P. pectinata* nom. nud.) |
|  |  |  | P. cupressina *J.C.Wendl.* ex *Bartl.* nom. nud. Capensis nobis ignotae. | P. cupressina *J.C.Wendl.* ex *Bartl.* nom. nud. |  | P. filiformis L. (= *P. cupressina J.C.Wendl.* nom. nud.) | P. filiformis L. (= *P. cupressina J.C.Wendl.* nom. nud.) |
|  |  |  |  | Chymococca empetroides *Meisn.* | Chymococca empetroides *Meisn.* | P. ericoides *L.* (= *Chymococca empetroides* Meisn.) | P. ericoides *L.* (= *Chymococca empetroides* Meisn.) |
|  |  |  |  |  | P. galpini *C.H.Wright* | P. galpini *C.H. Wright* | P. galpinii *C.H. Wright* |
|  |  |  |  |  | P. laniflora *C.H.Wright* | P. laniflora *C.H.Wright*: type specimen is a *Lachnaea.* | Lachnaea laniflora *(C.H.Wright) Bond* (= *P. laniflora* C.H.Wright) = |
|  |  |  |  |  | P. eriophora *Gand.* | P. rigida *Wikstr.* (= *P. eriophora* Gand.) | P. rigida *Wikstr.* (= *P. eriophora* Gand.) |

| **Linnaeus (1753)** | **Wikström (1818)** | **Thunberg (1825a)** | **Meisner (1840)** | **Meisner (1857)** | **Wright (1915)** | **Thoday (1924a)** | **Present study** |
|---|---|---|---|---|---|---|---|
| | | | | | P. hamulata *Gand.* | P. hamulata *Gand.*<br>Probably P. paleacea | P. hamulata *Gand.*<br>Nom. dub. |
| | | | | | | P. montana *Thoday* (= *P. ericoides* C.H.Wright non L. pro parte) | P. montana *Thoday* (= *P. ericoides* sensu Meisn.)<br>(= *P. rigida* Wikstr. var. *tetragona* Meisn. pro parte) |
| | | | | | | P. obtusifolia *Thoday* | P. obtusifolia *Thoday* |
| | | | | | | P. paludosa *Thoday* | P. paludosa *Thoday* |
| | | | | | | | P. drakensbergensis *Hilliard & B.L.Burtt.* |
| | | | | | | | P. quadrifaria *Bredenk. & A.E.van Wyk* |

| Linnaeus (1753) | Wikström (1818) | Thunberg (1825a) | Meisner (1840) | Meisner (1857) | Wright (1915) | Thoday (1924a) | Present study |
|---|---|---|---|---|---|---|---|
| | | | | | | | P. nivicola *Bredenk. & A.E.van Wyk* |
| | | | | | | | P. esterhuyseniae *Bredenk. & A.E.van Wyk* |
| | | | | | | | P. montivaga *Bredenk. & A.E.van Wyk* |

*The complete list of excluded species described by Meisner (1857: 563) was not included in Table 7.1 as most names are dealt with under 'Excluded names'.

## 7.6 INDEX TO SCIENTIFIC NAMES IN THE TAXONOMIC TREATMENT (CHAPTER 7)

## SEE ALSO INDEX TO EXCLUDED NAMES ON PAGE 309

Accepted names in *Passerina* are in bold roman type and synonyms in italics.

# CHAPTER 8

## GENERAL DISCUSSION

This monograph of *Passerina* is presented as a contribution towards the 'Flora of southern Africa'. Of the 16 species recognized by Arnold & De Wet (1993) one was reduced to synonymy. Four species and four subspecies were newly described.

In *Passerina* the highest number of species per grid (nine) occurs in each of the grids 3321 (Ladismith), 3322 (Oudtshoorn) and 3419 (Caledon). The highest diversity of species (six) occurs in the False Bay area, from Seekoeivlei, including the Cape Flats, to De Mond at the Palmiet River (3418B). Currently the Western Cape is regarded as the centre of diversity for *Passerina*, from where certain species extend west, north and east (Chapters 4.3 and 4.5).

Although Thoday (1921) did a preliminary anatomical study on leaves of two Cape species of *Passerina*, his revision of the genus (Thoday 1924) was based on macromorphological characters mainly derived from herbarium specimens. The present monographic study incorporated extensive fieldwork, during which the ecology, populations, habitat and growth form of the taxa were recorded. Data on fruiting and flowering time, flower colour, pollination, possible relationships with insects, rodents and birds, regeneration strategy and dispersal of fruits were also documented. In addition, material from 22 herbaria was studied for macromorphological, distributional and nomenclatural data.

The palynological study (Chapter 4.1) showed that the morphology of the pollen grains in *Passerina* is adapted for wind dispersal. The pollen wall structure in the genus is regarded as the climax of a continuum of variation, as all the subunits (typical of crotonoid pollen) had fused completely to form a continuous secondary reticulum, unique to *Passerina*. On this basis *Passerina* is easily distinguished from the other southern African genera in the Thymelaeaceae. Taxonomically the secondary reticulum of the pollen wall was used as motivation to elevate the subtribe Passerininae to the tribe Passerineae. However, no pollen morphological characters were identified that could be used at the species level.

The leaf anatomy turned out to be quite complex. One aspect was the identity of the abaxial epidermal cells with so-called 'gelatinised' or mucilaginous inner periclinal cell walls, especially as these epidermal cells have frequently been interpreted erroneously as a biserial epidermis (Chapter 4.2). The present study has shown that the periclinal as well as anticlinal walls of epidermal cells in *Passerina* are conspicuously mucilaginous, positively confirming the authenticity of mucilaginous cell walls, especially in epidermal tissue. The development of mucilagination of epidermal cell walls is probably an advanced state, especially, in *Passerina* where this phenomenon is considered an adaptation to survive the dry warm summers typical of the mainly Mediterranean climate of the Cape Floristic Region. The character is present in all species of *Passerina*, irrespective of their environment. Mucilaginous epidermal cell walls are also well known in other families and genera in the Cape Floristic Region and in the Mediterranean flora.

In *Passerina* the decussate or sometimes imbricate leaf arrangement is probably of vital importance to the physiology of the plant as water droplets can drain from the convex abaxial surface of an inversely ericoid leaf, running onto the concave adaxial surface of the leaf below. Leaf arrangement is also of taxonomic importance at the species level, e.g. *P. falcifolia* is characterised by falcate leaves separated by longer internodes whereas the leaves of *P. quadrifaria* are completely imbricate.

The leaf epidermal study of *Passerina* (Chapter 4.3) proved to be a source of new taxonomic characters at both generic and specific levels. The structure and function of the epidermis should be considered in context with the inversely dorsiventral leaves in *Passerina*. Two groups of species, called Groups A and B, could be distinguished on the basis of the arrangement and shape of epidermal cells as well as cuticular ornamentation.

### Systematic value of the leaf epidermis

*Generic level*

- leaves epistomatic;

- adaxial epidermis concave, villous, cuticle relatively thin, cells uniserial and relatively small;
- abaxial epidermis convex, cuticle relatively thick and epidermal cells relatively large.

*Species level*

- stomata sunken (stomatal apparatus anomocytic);
- size, shape and arrangement of epidermal cells;
- thickness of abaxial cuticle;
- cuticular ornamentation;
- epicuticular waxes.

Leaf anatomical evidence (Chapter 4.4) proved extremely useful in the classification of *Passerina*. Four leaf structural types and 10 states are associated with specific habitats and geographical distribution, suggesting 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*.

**Systematic value of the leaf anatomy**

*Family level*

- presence of extraxylary sclerenchyma in vascular bundle.

*Generic level*

- palisade parenchyma developing abaxially;
- mesophyll inverted;
- leaves inversely dorsiventral.

*Species level*

- leaf outline;

- leaf width;
- shape of main vascular bundle;
- bundle sheath completely enveloping main vascular bundle or forming an adaxial cap;
- number of secondary vascular bundles;
- shape of palisade parenchyma;
- number of layers of palisade parenchyma;
- number of palisade parenchyma cells per unit length (50 μm);
- type of spongy parenchyma;
- presence of abaxial hypodermal sclerenchyma fibres;
- development of an abaxial hypodermal sclerenchymatous sheath;
- leaf structural type—orientation and structure of main vascular bundle in relation to epidermis and mesophyll.

The present research on the flowers in *Passerina* (Chapter 4.5) has produced new morphological and anatomical evidence. This study has succeeded in resolving the floral morphology in *Passerina*. As the flower in *Passerina* is considered a phylogenetically advanced structure, the genus is also regarded advanced within the Thymelaeoideae. This study also contributes towards a better understanding of the taxonomic relationships of the Thymelaeaceae. From 1996–1999 several botanists, making use of modern techniques, placed the Thymelaeaceae in various subclasses and superorders (Chapter 4.5). Although palynological evidence indicates that the very distinctive pollen in Thymelaeaceae is similar to that of most Euphorbiaceae, the present palynological study of *Passerina* (Chapter 4.1) supports Dahlgren (1980) in placing the Thymelaeales in the Malviflorae (= Dilleniiflorae).

In Chapter 4.5 it is also hypothesized that the plane of circumcission of the hypanthium tube (in *Gnidia*, *Struthiola* and *Lachnaea*) possibly indicates a difference in tissue composition between the basal and upper portions of the hypanthium and that this articulation could be of morphological importance in the Thymelaeaceae. The basal portion of the floral tube below the plane of circumcission possibly indicates the inclusion of receptacle tissue in the hypanthium, while the upper portion consists of calyx and androecium tissue only (accepting the apetalous state). An alternative interpretation 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, could still be further investigated.

In *Passerina,* the structure of the integuments surrounding the ovule provides taxonomically useful evidence. The study has 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. It is also clear that the mechanical part of the seed coat is derived from the palisade-like outer epidermis of the inner integument, hence it is an exotegmen. Corner (1976) distinguishes the Euphorbiales–Malvales–Thymelaeales–Tiliales (Malvalean complex) on the basis of the exotegmic palisade. He dismisses the derivation of the Malvalean complex from the Dilleniales (endotestal seeds) or Violales and looks towards the Myristicaceae (Magnoliales–Ranales) for the origin of the Malvalean seed.

Recent evidence from molecular phylogeny should be interpreted in context with evidence from other botanical fields. Magallón *et al.* (1999) have especially attempted to compare these groups to the existing systems. APG (1998) places the Thymelaeaceae in the subgroup Eurosids II and order Malvales, while all the other authors place it in the Expanded Malvales. The Malvalean relationship of the Thymelaeaceae seems to be strongly supported by molecular phylogeny as well as by floral morphology, anatomy, embryology and palynology. The Euphorbiales–Malvales–Thymelaeales relationship indicated by embryology and palynology is, however, not supported by the molecular data.

**Systematic value of floral morphology and anatomy**

*Family level*

- exotegmic palisade [basis of Corner's (1976) Euphorbiales–Malvales–Thymelaeales–Tiliales complex];
- distinctive obturator.

*Subfamily level*

The Thymelaeoideae is distinguished on the basis of:

- calyx tube (hypanthium in the present study);
- diplostemonous androecium;
- pseudomonomerous ovary (Domke 1934; Heinig 1951).

*Tribal level*

The Passerineae is distinguished on the basis of:

- secondary reticulum unique to the pollen wall in *Passerina*.

*Genus level*

- exserted, extrorse anthers;
- anemophilous habit.

*Species level*

- polytelic inflorescences—spikes;
- polytelic inflorescences—multiflowered main and co-florescences;
- morphology of bracts;
- fruit—fleshy or dry;
- floral envelope (hypanthium and sepals) colour during pollination;
- floral envelope texture;
- floral envelope length;
- ovary size;
- antipetalous filament length;
- antisepalous filament length;
- anther size.

The present cladistic study (Chapter 6) highlighted the necessity of using different analyses and procedures. The results generated by the HENNIG 86 analysis were strongly supported by those of the PAUP analysis, to the extent that the cladogram length and the CI and RI values were almost identical.

Based on leaf and floral morphological and anatomical characters (Chapters 4.3–4.5), the cladistic study supports *Passerina* as a monophyletic group (bootstrap values of different analyses ranging from 84–91%). Although *P. filiformis* and *P. paludosa* are paraphyletic species in certain analyses, there are indications that these two species are basal to other species in the genus. Based on distribution and array of plesiomorphic characters, these species are regarded as morphologically close to the hypothetical ancestor of the genus.

The taxonomic and phylogenetic values of the character set were evaluated. The following possible plesiomorphic character states were identified:

- leaf structural types A and B;
- single flowers and multiflowered spikes;
- obovate, chartaceous and winged floral bracts;
- relatively long hypanthium neck;
- long internodes;
- spreading leaves.

Several synapomorphies were identified. Of these, certain characters provided invaluable phylogenetic information and are of considerable taxonomic importance:

- differentiated floral bracts that are coriaceous and adaxially villous;
- hypanthium that is glabrous in the lower portion and hairy in the upper portion;
- absence of wings in differentiated floral bracts;
- subcapitulate spikes;
- multiflowered spikes with more than 16 flowers;
- fleshy fruit;
- carinate leaves with an abaxial, paradermal sclerenchyma sheath and the main vascular bundle sunk into the V-shaped palisade parenchyma (leaf structural type D).

Taking all the above-mentioned into account, the cladistic analysis in *Passerina*, based on leaf and floral morphological and anatomical characters, is regarded as a contribution towards a better understanding of the taxonomic and phylogenetic status of characters, as well as towards the delimitation of infrageneric taxa.

The conservation status of the different species was assigned as follows: 16 species and three subspecies—Least Concern; two species and one subspecies—Near Threatened; one species—Vulnerable; one species—Critically Endangered (IUCN Species Survival Commission 2000). The species classified as Vulnerable has a small population size. The Critically Endagered species grows on the Cape Flats where it is exposed to the invasion of alien vegetation and aridification, an important effect of urbanization.

Objectives of this study that were largely accomplished:

- the pollen morphological study yielded taxonomically useful characters, especially at the tribal level;
- studies on the morphology and anatomy of the leaves, inflorescences and flowers contributed largely towards identification of significant taxonomic characters and an improved understanding of the taxonomy of *Passerina*;
- the phytogeography of *Passerina* indicates the Western Cape as the centre of diversity for *Passerina*, from where certain species extend to the west, north and east;
- the infrageneric phylogenetic analysis is regarded as a contribution towards a better understanding of the taxonomic and phylogenetic status of characters, as well as towards the delimitation the species in the genus;
- this monograph of *Passerina* is suitable for publication as a contribution towards the 'Flora of southern Africa'.

# CHAPTER 9

# CONCLUSIONS

- *Passerina* is a monophyletic genus that probably evolved in accordance with environmental pressures associated with the predominantly winter-rainfall area of the Western Cape. The most important climatic features driving evolutionary change probably are windy conditions in spring and drought in summer.
- Currently *Passerina* comprises 20 species and four subspecies. No sections are upheld. A key to the species, illustrations and distribution maps of each species are provided.
- The conservation status of the different species was assessed (IUCN Species Survival Commission 2000) and the categories were assigned as follows: 16 species and three subspecies—Least Concern; two species and one subspecies—Near Threatened; one species—Vulnerable; one species—Critically Endangered.
- In *Passerina* the highest number of species per grid (nine) occurs in each of the grids 3321 (Ladismith), 3322 (Oudtshoorn) and 3419 (Caledon). The highest diversity of species (six) occurs in the False Bay area, from Seekoeivlei, including the Cape Flats, to De Mond at the Palmiet River (3418B). The Western Cape is regarded as the centre of diversity for *Passerina*, from where certain species extend to the west, north and east.
- The unique secondary reticulum in the pollen wall of *Passerina* probably evolved in conjunction with the anemophilous habit, induced by dry windy climatal conditions.
- Mucilaginous epidermal cells probably evolved because of summer drought.
- The anatomical leaf structural types (Chapter 4.4) probably evolved because of increasing dry conditions, with expanding speciation further away from the centre of diversity of the genus in the Western Cape.
- *Passerina* probably adapted to environmental conditions at a generic level, as it is the only southern African genus in the Thymelaeaceae with an anemophilous habit. It is also distinguished from other southern African genera by the exserted, extrorse anthers and inverse-dorsiventral leaves.

- Fleshy berries evolved from dry fruits, probably as a result of the selective pressure of bird dispersal and maritime conditions (*Passerina* is the only southern African genus in the Thymelaeaceae with fleshy berries).
- *Passerina* is probably not closely related to other genera in the Thymelaeaceae and can be regarded as phylogenetically advanced. Although many of the following advanced morphological and anatomical character states are present in other genera of the Thymelaeoideae, they 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; complete absence of petals or petaloid scales; asymmetric development of 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.
- A cladistic analysis based on leaf and floral morphological and anatomical characters contributes towards a better understanding of the phylogenetic status of various characters, as well as towards the delimitation and affinities of the species in the genus.
- The multidisciplinary approach that was followed, indicated that the Malvalean relationship of the Thymelaeaceae is strongly supported by molecular phylogeny, as well as by floral morphology, anatomy, embryology and palynology. The traditional Euphorbiales–Malvales–Thymelaeales relationship indicated by embryology and palynology is, however, not supported by available molecular data.

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> Isaiah 50: 4 and 5. The Sovereign Lord has given me an instructive tongue. The Sovereign Lord has opened my ears. He wakens me morning by morning, wakens my ear to listen like one being taught.

# SUMMARY

## A MONOGRAPH OF THE GENUS *PASSERINA* L. (THYMELAEACEAE)

by

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May 2002

The primary objective of this study was to provide a taxonomic revision of the genus *Passerina*, here treated as comprising 20 species and four subspecies. Most species are concentrated in the Cape Floristic Region. Certain species occur along the Great Escarpment, with outliers in East Africa. The present monographic study included extensive fieldwork, more than 5 000 specimens from 22 herbaria were studied and the conservation status of the different species was assessed.

Pollen grains in *Passerina* are adapted to wind pollination. The pollen wall is characterized by a continuous secondary reticulum, distinguishing *Passerina* from the characteristic crotonoid pattern of the pollen wall in all other southern African genera in the Thymelaeaceae. This character was used to elevate the subtribe Passerininae to the tribe Passerineae.

The structure of the abaxial leaf epidermal cells with mucilaginous inner periclinal cell walls, was clarified in the present study. The authenticity of mucilaginous periclinal as well as anticlinal walls of epidermal cells in *Passerina* has also been confirmed. This phenomenon is considered an adaptation to survive the dry warm summers typical of the Cape Floristic Region.

The epidermal study in *Passerina* proved to be a source of new characters at both genus and species levels. The structure and possible function of the epidermis should be considered in context with the inversely dorsiventral leaves in *Passerina*. Two groups of species, Groups A and B, were distinguished on the basis of the arrangement and shape of epidermal cells as well as cuticular ornamentation.

Leaf anatomical evidence was extremely useful in the infrageneric classification of *Passerina*. Four anatomical leaf structural types and ten states were identified and correlated with specific habitats and geographical distributions. The leaf structural types and states also illustrate a xeromorphic gradient. On this basis all infrageneric taxa in *Passerina* could be identified.

Floral morphological and anatomical evidence assisted in resolving the floral structure in *Passerina* and also proved taxonomically useful at species level. The structure of the integuments surrounding the ovule also provided taxonomically useful evidence. The mechanical part of the seed coat is derived from the palisade-like outer epidermis of the inner integument, hence it is an exotegmen. The Euphorbiales–Malvales–Thymelaeales–Tiliales (Malvalean complex) is distinguished on the basis of the exotegmic palisade. A Malvalean relationship for the Thymelaeaceae is strongly supported by molecular phylogeny, as well as by floral morphology, anatomy, embryology and palynology.

A cladistic study based on leaf and floral morphological and anatomical characters supports *Passerina* as a monophyletic group. The taxonomic and phylogenetic values of the character set were also evaluated, indicating the most significant plesiomorphic and synapomorphic characters. Based on the distribution and array of plesiomorphic characters, *P. filiformis* and *P. paludosa* are regarded as morphologically close to the hypothetical ancestor of the genus.

# OPSOMMING

## 'N MONOGRAFIE VAN DIE GENUS *PASSERINA* L. (THYMELAEACEAE)

deur
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Die hoofdoelwit van hierdie ondersoek was die daarstel van 'n taksonomiese hersiening van die genus *Passerina*, wat tans uit 20 spesies en vier subspesies bestaan. Die meeste spesies is in die Kaapse Floristiese Gebied gekonsentreer. Sommige spesies word op die Groot Eskarp aangetref, met uitskieters in Oos-Afrika. Die huidige monografiese studie is op uitgebreide veldwerk sowel as die studie van meer as 5 000 eksemplare uit 22 herbariums gebaseer en die bewaringstatus van al die verskillende spesies is vasgestel.

Stuifmeelkorrels by *Passerina* is aangepas by windbestuiwing. Die stuifmeelwand word gekenmerk deur 'n aaneenlopende sekondêre retikulum, wat *Passerina* onderskei van die tipiese krotonoïede patroon van die stuifmeelwand, kenmerkend van al die ander Suider-Afrikaanse genusse van die Thymelaeaceae. Hierdie kenmerk is gebruik om die subtribus Passerininae na die tribus Passerineae te verhef.

Die huidige studie het die struktuur van die abaksiale epidermisselle van die blaar, wat slymagtige binneste periklinale wande het, bevestig. Die bestaan van slymagtige periklinale sowel as antiklinale wande by die epidermisselle van *Passerina* is verder ook bevestig. Hierdie verskynsel word beskou as aanpassing om die droë, warm somers van die Kaapse Floristiese Gebied te oorleef.

Die epidermale studie van *Passerina* word as 'n bron van nuwe kenmerke op beide genus- en spesievlak beskou. Die struktuur en moontlike funksie van die epidermis moet in konteks met die omgekeerd dorsiventrale blare van *Passerina* gesien word. Twee groepe spesies, naamlik Groepe A en B, is op grond van die rangskikking en vorm van die epidermisselle, sowel as die ornamentasie van die kutikula, onderskei.

Blaar-anatomiese getuienis is uiters suksesvol by die infrageneriese klassifikasie van *Passerina* aangewend. Vier anatomiese blaar-strukturele tipes en tien state is vasgestel en is met spesifieke habitats en geografiese verspreidings gekorreleer. Die blaar-strukturele tipes en state dui ook 'n xeromorfiese gradiënt aan. Op grond hiervan kon al die infrageneriese taksons in *Passerina* geïdentifiseer word.

Bewyse gebaseer op die blommorfologie en -anatomie het grootliks gehelp om die blomstruktuur van *Passerina* te bepaal en was ook taksonomies waardevol om die spesies te onderskei. Die struktuur van die integumente wat die saadknop omring is ook 'n bron van taksonomies nuttige kenmerke. Die meganies verharde deel van die saadhuid ontstaan uit die palissade-agtige buitenste epidermis van die binneste integument en word daarom as 'n eksotegmen geklassifiseer. Die Euphorbiales–Malvales–Thymelaeales–Tiliales (Malvales-kompleks) word op grond van die eksotegmiese palissadeweefsel onderskei. 'n Malvales-verwantskap vir die Thymelaeaceae word sterk deur die molekulêre filogenie, asook blommorfologie, anatomie, embriologie en palinologie ondersteun.

'n Kladistiese studie gebaseer op morfologiese en anatomiese kenmerke van die blare en blomme ondersteun *Passerina* as 'n monofiletiese groep. Die taksonomiese en filogenetiese waardes van die stel kenmerke is ook beoordeel en die mees betekenisvolle plesiomorfiese en sinapomorfiese kenmerke is uitgewys. Gegrond op die verspreiding en uitbeelding van plesiomorfiese kenmerke, word *P. filiformis* en *P. paludosa* as morfologies die naaste verwant aan die hipotetiese voorouer van die genus beskou.

# CURRICULUM VITAE

Christina Lindith Bredenkamp (née Keyser) was born in Luckhoff in 1947. She attended the Hoër Meisiesskool Stoffberg in Brakpan and matriculated in 1964. She studied at the University of Pretoria and was awarded a B.Sc. degree in 1967. In 1968 she obtained the Higher Education Diploma at the Pretoria Teachers' Training College and followed a career in education from 1969–1983. In 1984 she received the B.Sc. (Honns.) *cum laude*, followed by a research project on the taxonomy of the genus *Vitex* L. (Verbenaceae) between 1995 and 1998, culminating in an M.Sc. degree from the University of Potchefstroom for C.H.E. She was employed at the H.G.W.J. Schweickerdt Herbarium, University of Pretoria, between 1988 and 1990 and as senior researcher at the Education Assessment Group of the Human Sciences Research Council between 1990 and 1992. Since 1992 she has been employed at the National Botanical Institute, where she has developed a special interest in the Thymelaeaceae, resulting in the monograph of the genus *Passerina*. She has had the opportunity to extend her interest into management and has also served as Assistant Curator: Information (National Herbarium) for the last five years. She has collected plant specimens from many areas in southern Africa and is the author or co-author of 14 scientific publications. She is married to George Johannes Bredenkamp and has three children, Danie, Elmarié and Nicolene.

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1. BREDENKAMP, C.L., BOTHA, D.J. & HAMILTON-ATWELL, V.L. 1986. A new technique for preparing pollen of the genus *Vitex* for scanning electron microscopy. *Proceedings of the Electron Microscopy Society of South Africa* 16: 93–95.
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