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.