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).