

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
<i>burchellii</i>		X			X	
<i>ericoides</i>		X	X			
<i>esterhuyseniae</i>	Y					
<i>filiformis</i> subsp. <i>filiformis</i>	X	X			X	
<i>filiformis</i> subsp. <i>glutinosa</i>	X	X				
<i>galpinii</i>			Y			
<i>paleacea</i>		X	X		X	
<i>paludosa</i>		Y				
<i>pendula</i>						Y
<i>quadrifaria</i>				X	X	X
<i>truncata</i> subsp. <i>monticola</i>	X	X				
<i>truncata</i> subsp. <i>truncata</i>	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
<i>comosa</i>	Northern Cape	X	X		X		
<i>falcifolia</i>	Eastern Cape		X				X
<i>nivicola</i>	Northern Cape	X	X				
<i>rubra</i>	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
<i>obtusifolia</i>	Widespread in Northern, Western and Eastern Cape	X	X	X	X	X	X
<i>rigida</i>	Coastlines of KwaZulu-Natal, Western and Eastern Cape	X	X	X			X
<i>corymbosa</i>	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
<i>drakensbergensis</i>	Endemic	South Africa	KwaZulu-Natal, Bergville District in northern Drakensberg
<i>montana</i>	Near-endemic to Great Escarpment of southern Africa	High-mountain areas: Angola Zimbabwe Mozambique Namibia South Africa Swaziland Lesotho	Huíla Plateau, Lubango and Cheila Mountains Nyanga Manica and Sofala Moltkeblick on the Auas Mountains Limpopo Province, Mpumalanga, KwaZulu-Natal, Free State, and Eastern Cape Mbabane Widespread
<i>montivaga</i>	Near-endemic to Great Escarpment of southern Africa	Zimbabwe Mozambique South Africa Swaziland	Chimanimani Mountains Manica and Sofala Limpopo Province, Mpumalanga, KwaZulu-Natal, Western and Eastern Cape 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.

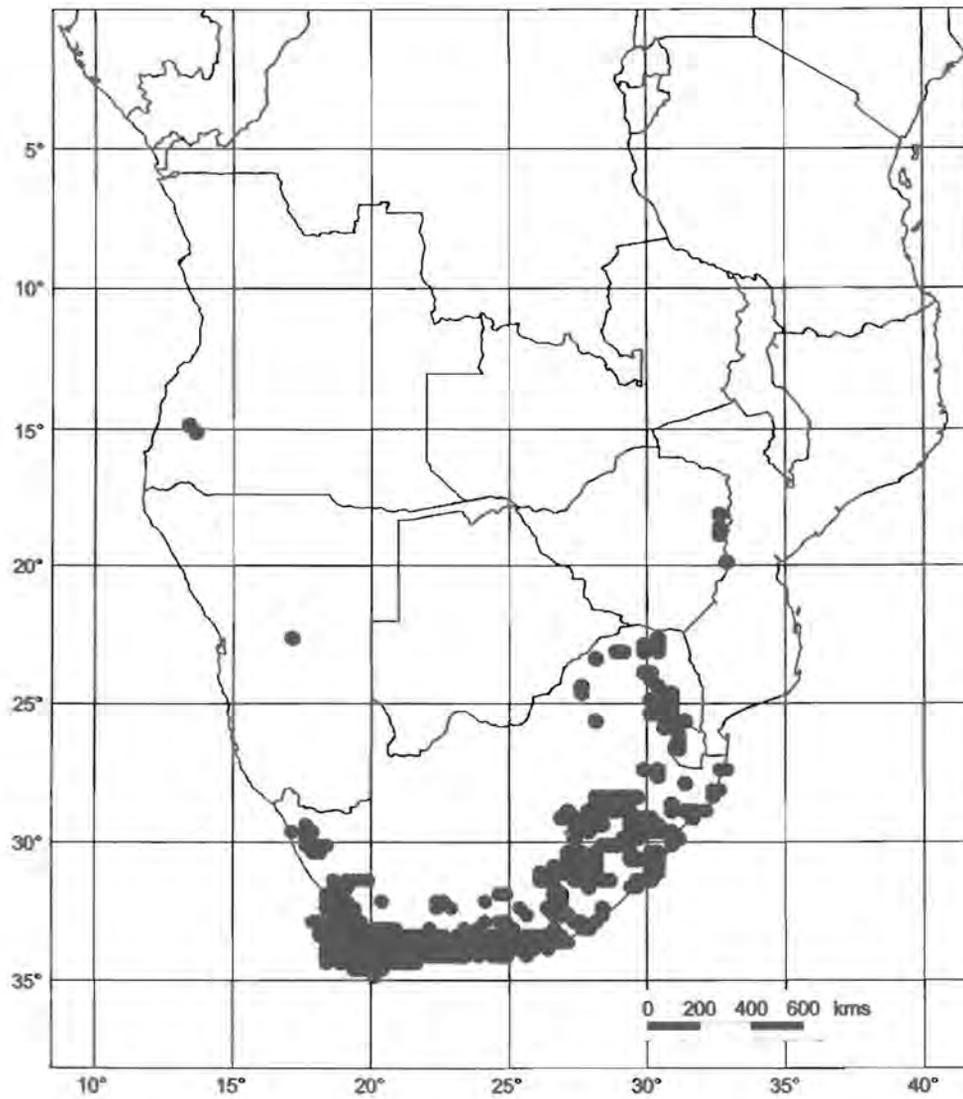


FIGURE 5.1.—Known distribution of genus *Passerina*.

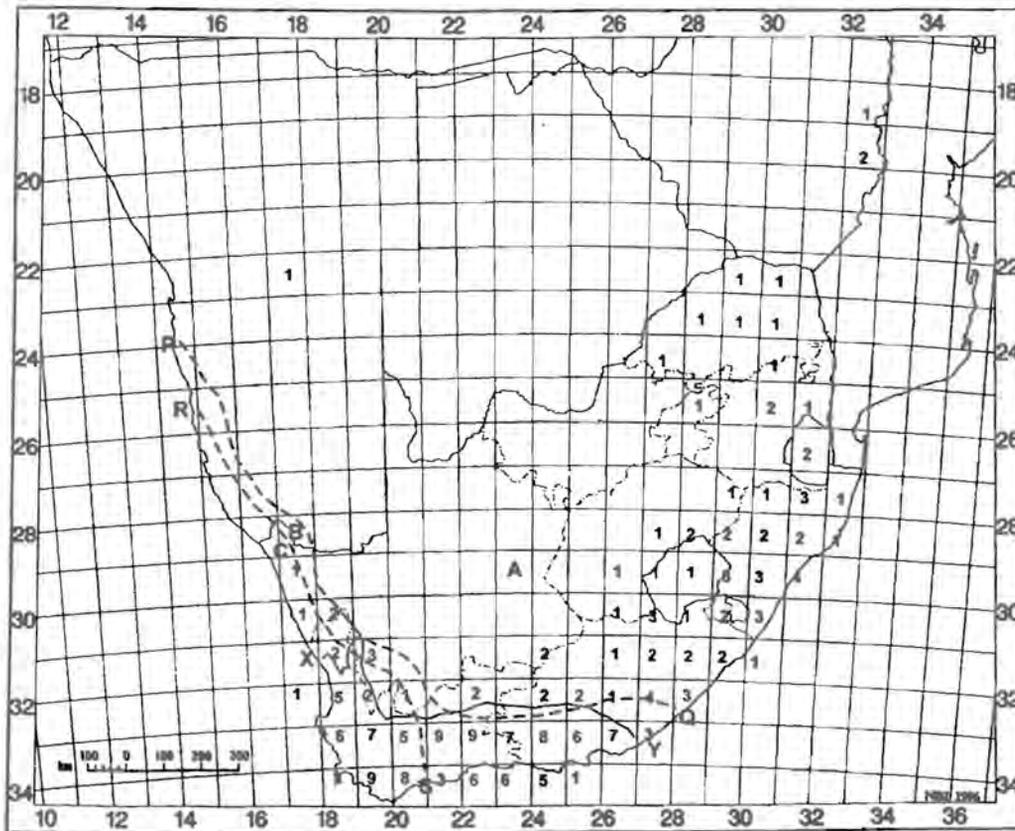


FIGURE 5.2.—Number of species per degree grid square in the distribution of *Passerina*. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops. Distribution outside South Africa shown in insert.

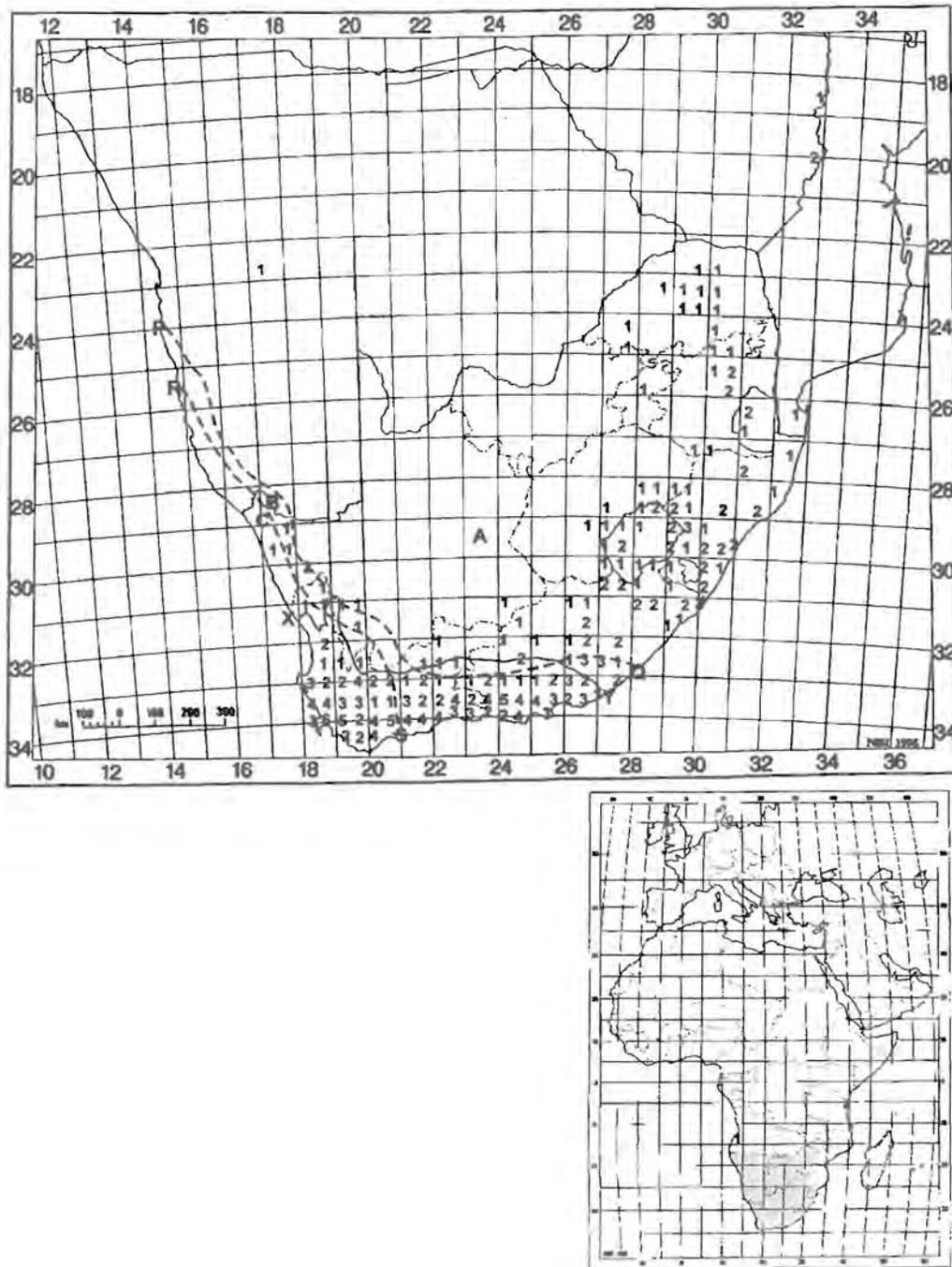


FIGURE 5.3.—Distribution of *Passerina*, with number of species per quarter degree grid square indicative of highest diversity of species. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops.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

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 Sneekrans 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 Mountains 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 Mountains. However, the specimens from both Auas and Huila are unmistakably *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 Mountains.

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 *rbcL* 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 *Lachmaea* 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
<i>S. leptantha</i>	0	00000	00000	00000	-000	00-00	0—	-0000	-0020	00000	00000	0
<i>burchellii</i>	0	11201	11010	11101	00020	11111	10221	10211	02121	21111	11121	1
<i>comosa</i>	0	10001	11111	11101	01030	11110	11101	10201	02010	11111	10110	2
<i>drakens-</i>												
<i>bergensis</i>	0	01001	11210	11101	00020	11110	10201	10201	01111	11111	10110	3
<i>ericoides</i>	0	10101	11110	11101	00030	11011	10211	11221	11101	01111	10120	3
<i>ester-</i>												
<i>huyseniae</i>	0	20001	11110	11101	01020	11001	10110	10111	11220	21111	11100	3
<i>falcifolia</i>	0	00011	11310	11211	10120	11210	10201	00201	01101	01111	10100	5
<i>filiformis</i>	0	00001	11110	11101	00020	11210	10010	00201	01020	21111	10100	3
<i>galpinii</i>	0	00001	11110	11101	00020	11011	10000	00201	11002	01111	10110	3
<i>montana</i>	0	20001	11110	11311	01121	12-11	10211	10201	02101	01111	10121	6
<i>montivaga</i>	0	01010	11310	11211	10120	11210	10031	00101	02020	21111	10100	5
<i>nivicola</i>	0	02001	01110	11000	-000	11001	10010	00101	01000	01111	10100	0
<i>obtusifolia</i>	0	00001	11110	11101	02020	11010	10131	10201	12101	01111	10100	4
<i>paleacea</i>	0	20001	11110	11311	01131	12-01	10200	00121	10000	01111	11121	6
<i>paludosa</i>	0	01001	11010	11101	00010	11110	10031	00201	01022	21111	10120	2
<i>pendula</i>	0	01201	11210	11101	00020	11111	10121	10121	02101	01111	10121	1
<i>quadrifaria</i>	0	00001	11211	11101	00020	12-10	11101	10201	02021	11111	10120	3
<i>rigida</i>	0	20001	11110	11311	00131	11001	10201	11111	12101	01111	11121	6
<i>rubra</i>	0	00101	11210	11101	00020	11210	10201	00201	02001	01111	10100	3
<i>truncata</i>	0	10101	11110	11101	02030	12-11	10211	10211	12101	01111	10121	4
<i>corymbosa</i>	0	00011	11310	11311	10121	11210	10231	00201	02101	01111	10100	6

-, not applicable

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).

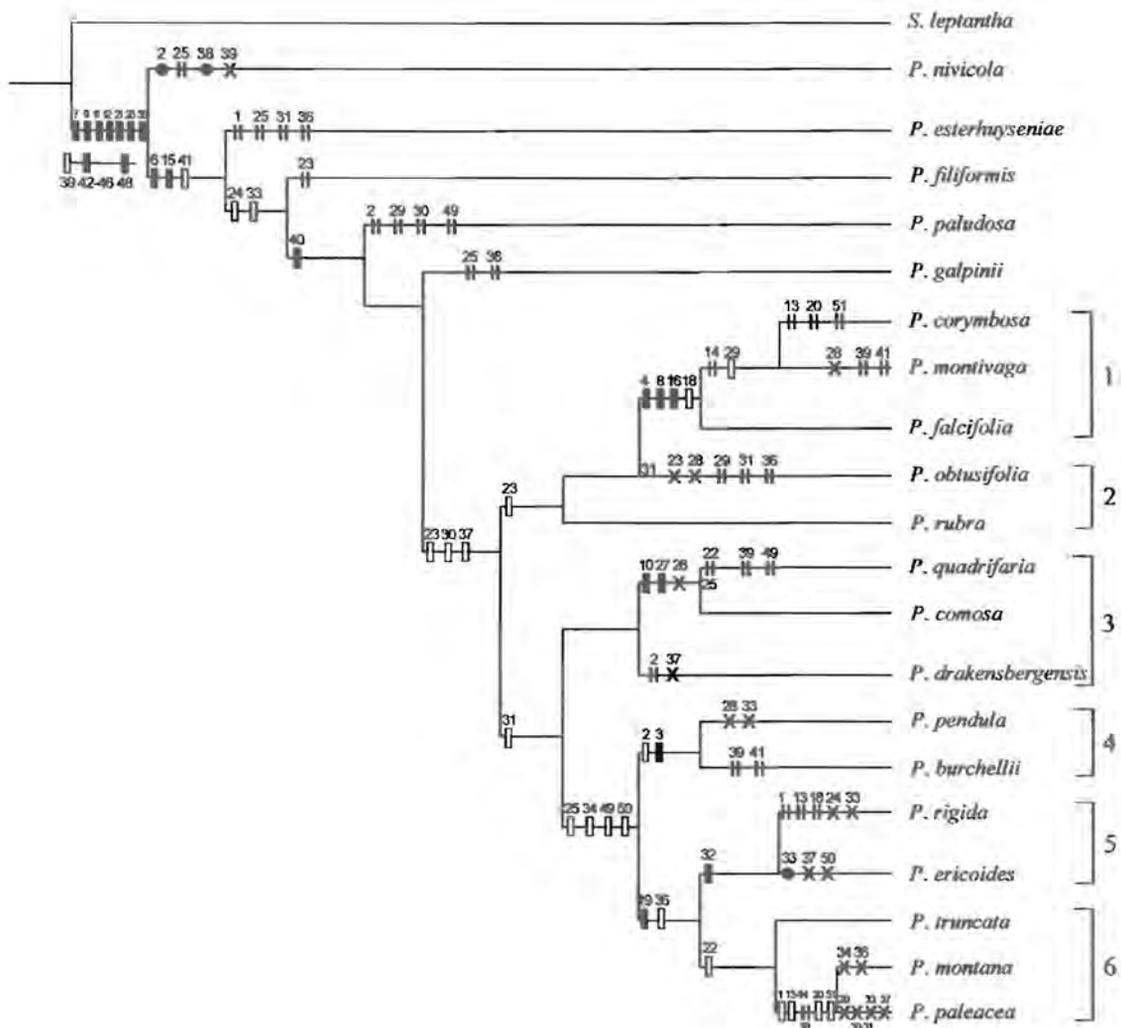


Figure 6.1.—Estimate of possible phylogenetic relationships in the genus *Passerina* as obtained in analysis A. For details see text. Symbols used: |, synapomorphy showing no homoplasy; |, synapomorphies showing reversal higher up in the cladogram; X, reversals; |, convergencies; ●, autapomorphies not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

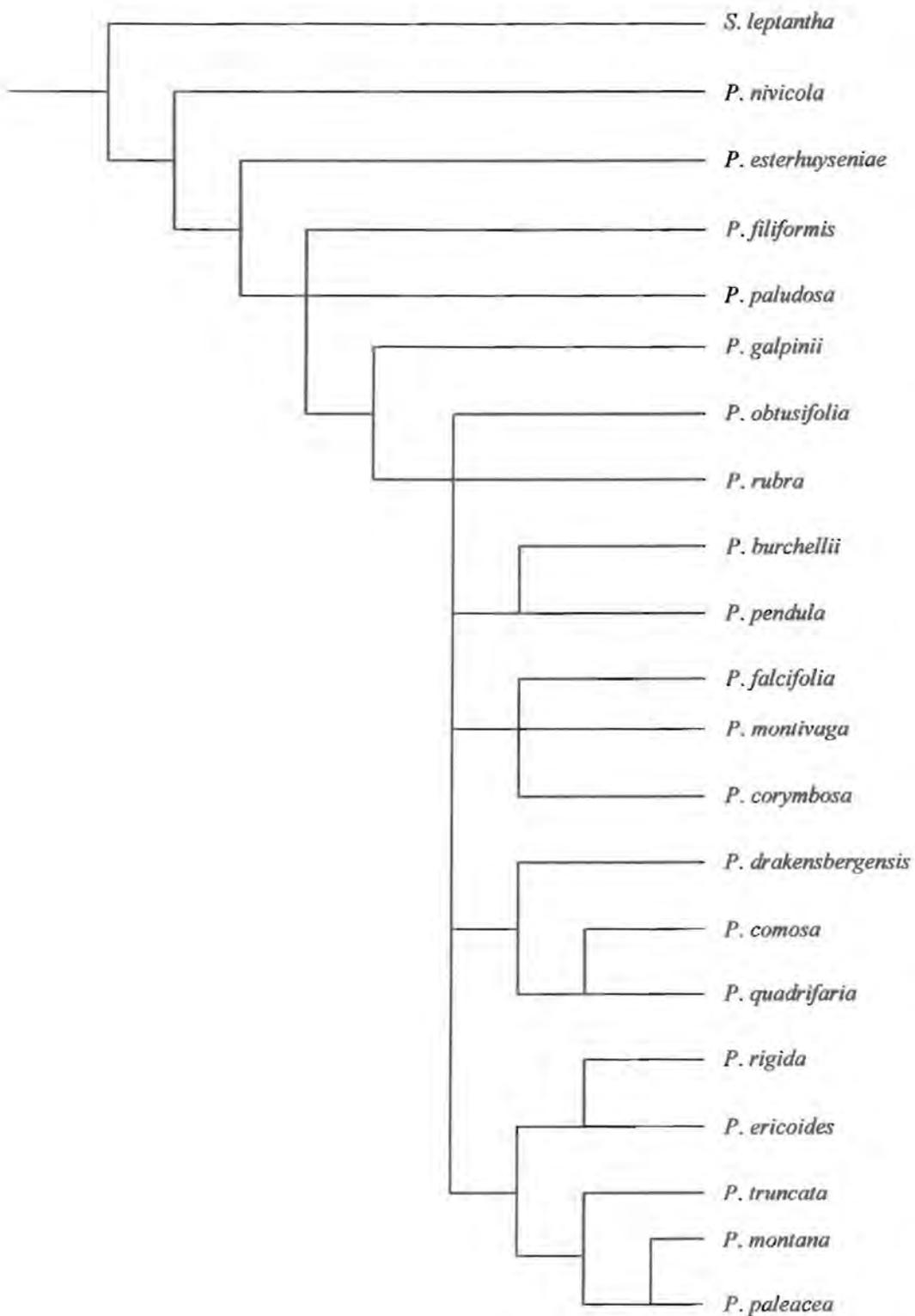


FIGURE 6.2.—Nelson consensus tree obtained in analysis A, after applying selective character weighting and using the program HENNIG 86.

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).

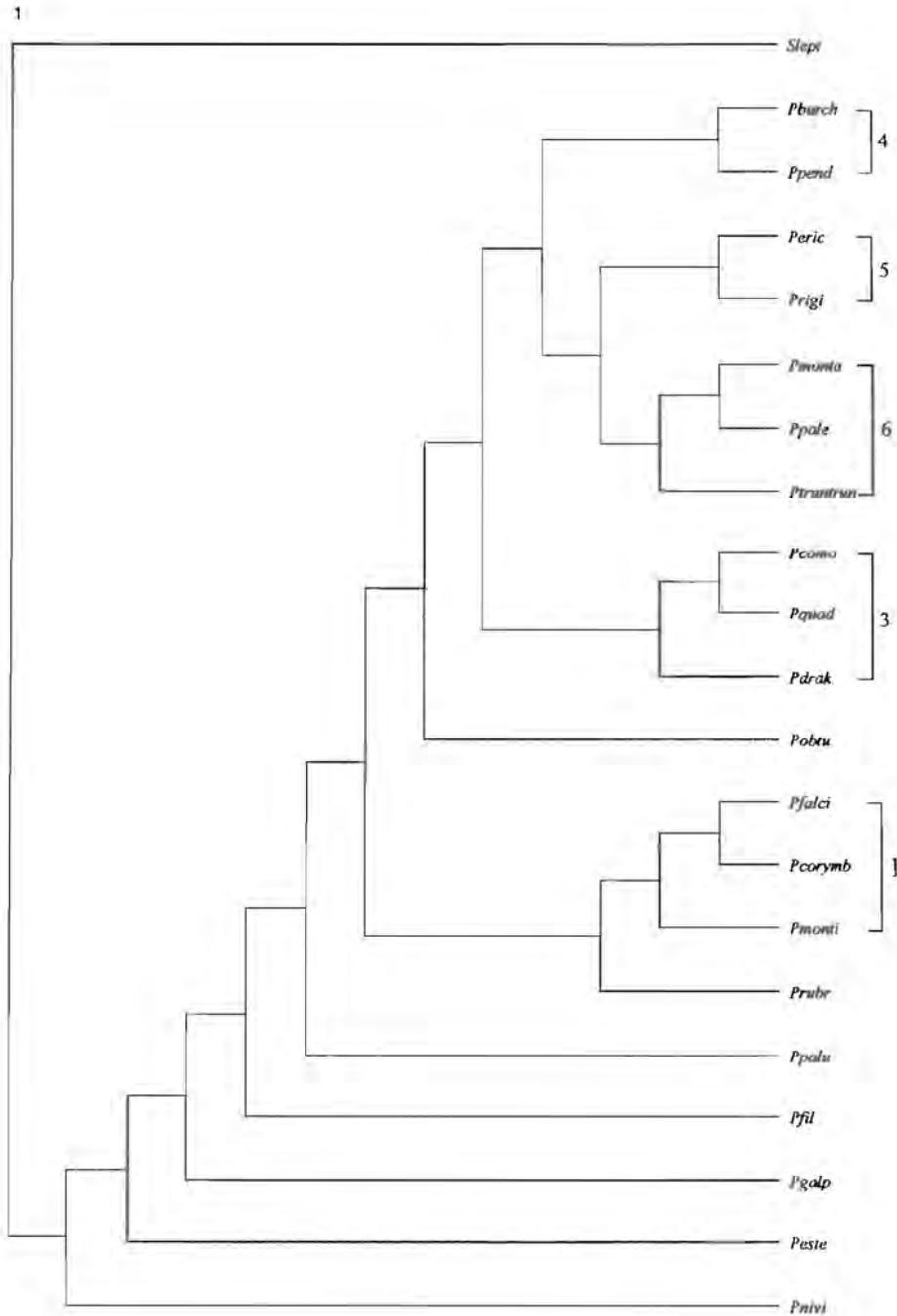


FIGURE 6.3.—Estimate of phylogenetic relationships in the genus *Passerina* as obtained in analysis B, after applying selective character weighting and using the Heuristic search of the PAUP 4.0 for Macintosh software package.

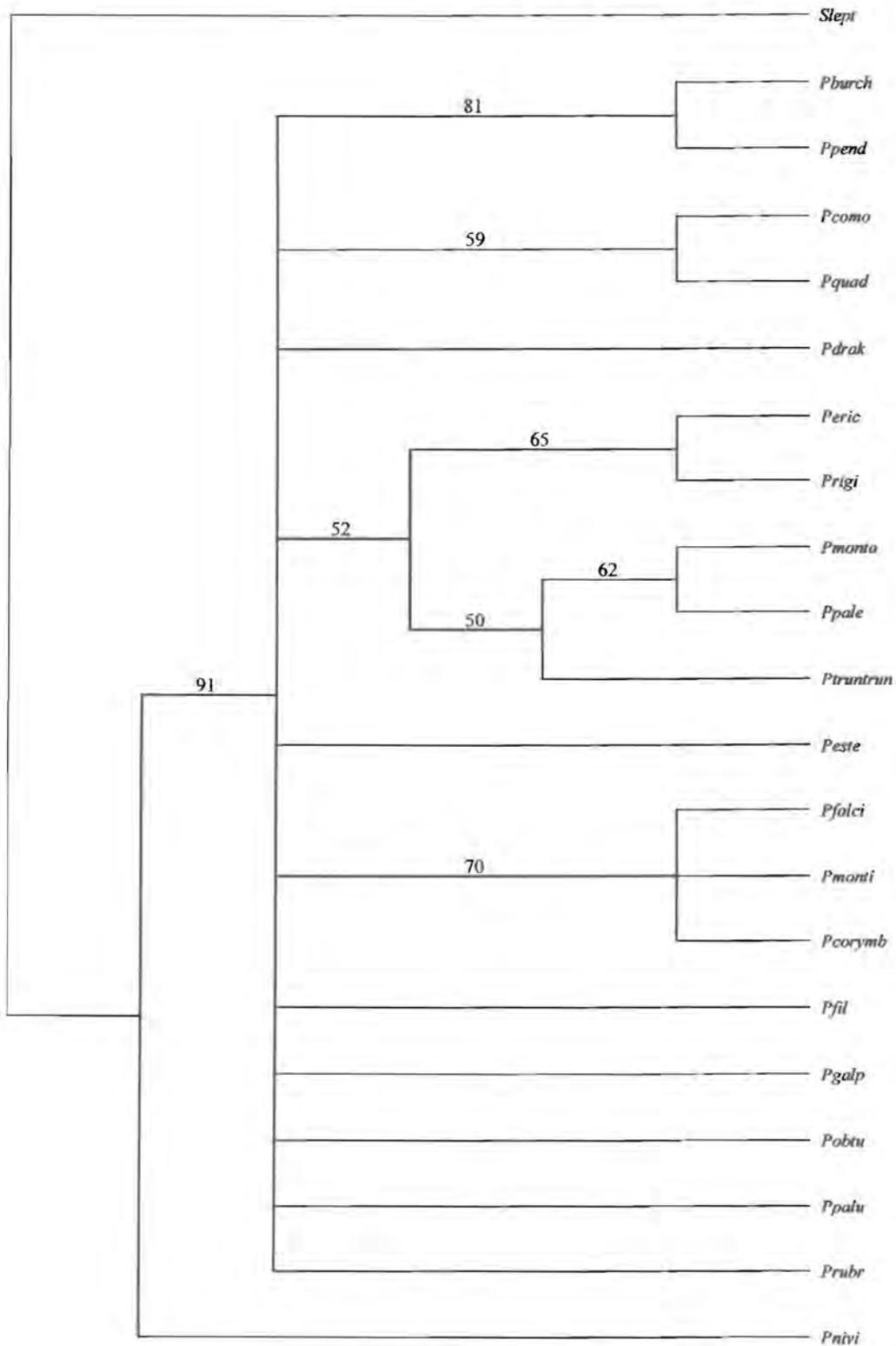


FIGURE 6.4.—Bootstrap values generated in analysis B, after applying selective character weighting and using the Heuristic search of the PAUP 4.0 for Macintosh software package.

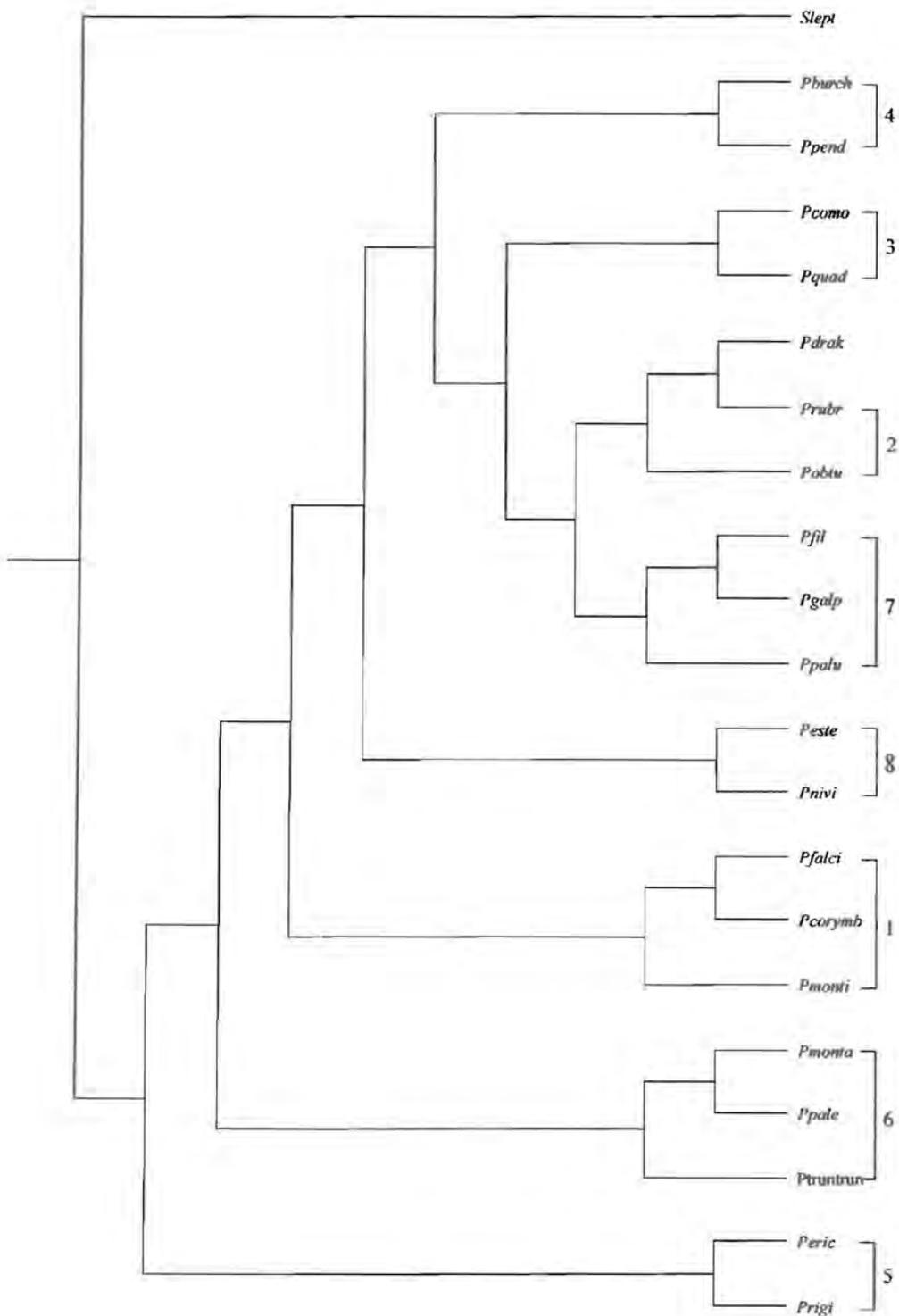


FIGURE 6.5.—Estimate of phylogenetic relationships in the genus *Passerina* as obtained in analysis C, after applying selective character weighting and using the UPGMA search of the PAUP 4.0 for Macintosh software package.

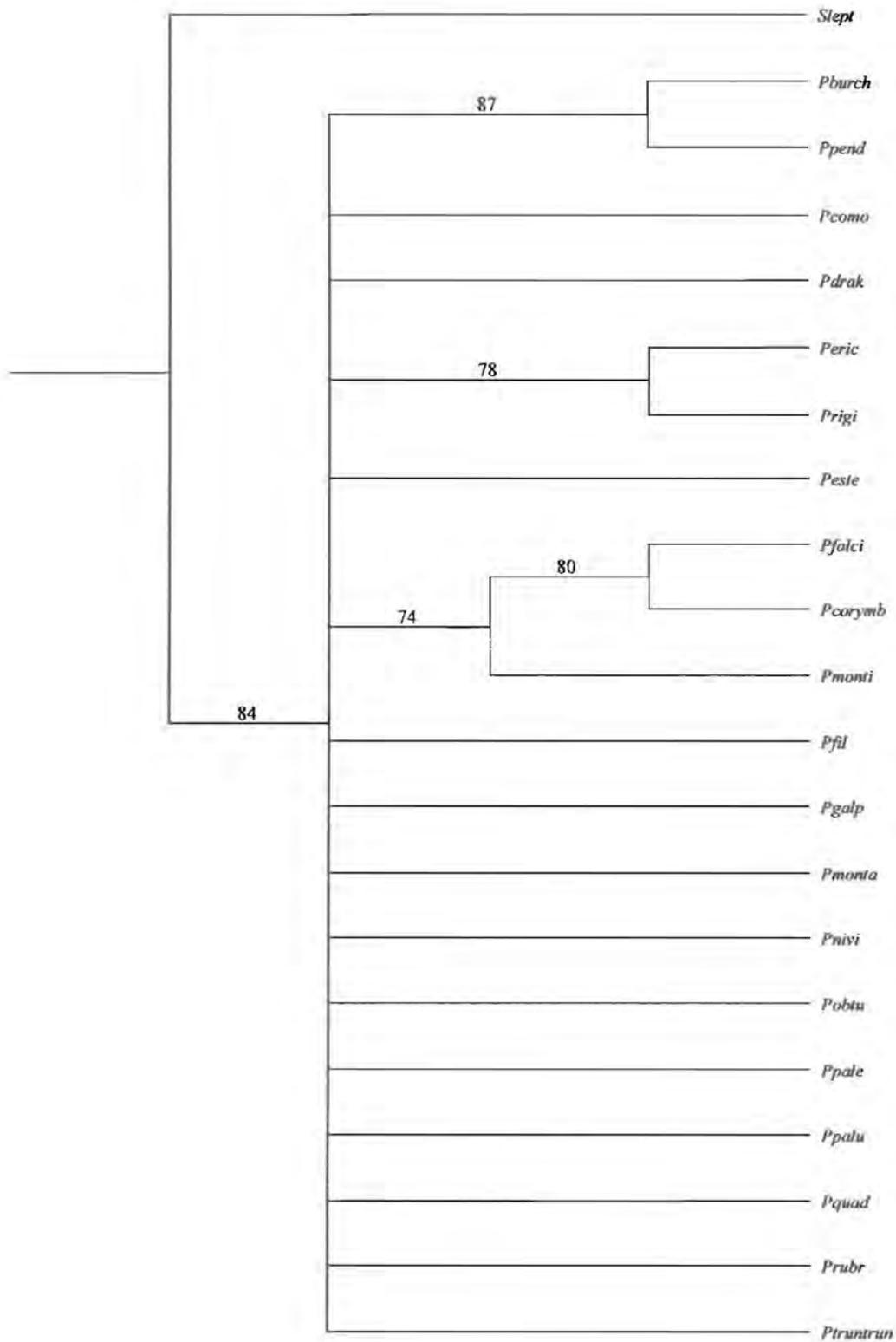


FIGURE 6.6.—Bootstrap values generated in analysis C, after applying selective character weighting and using the UPGMA search of the PAUP 4.0 for Macintosh software package.

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.

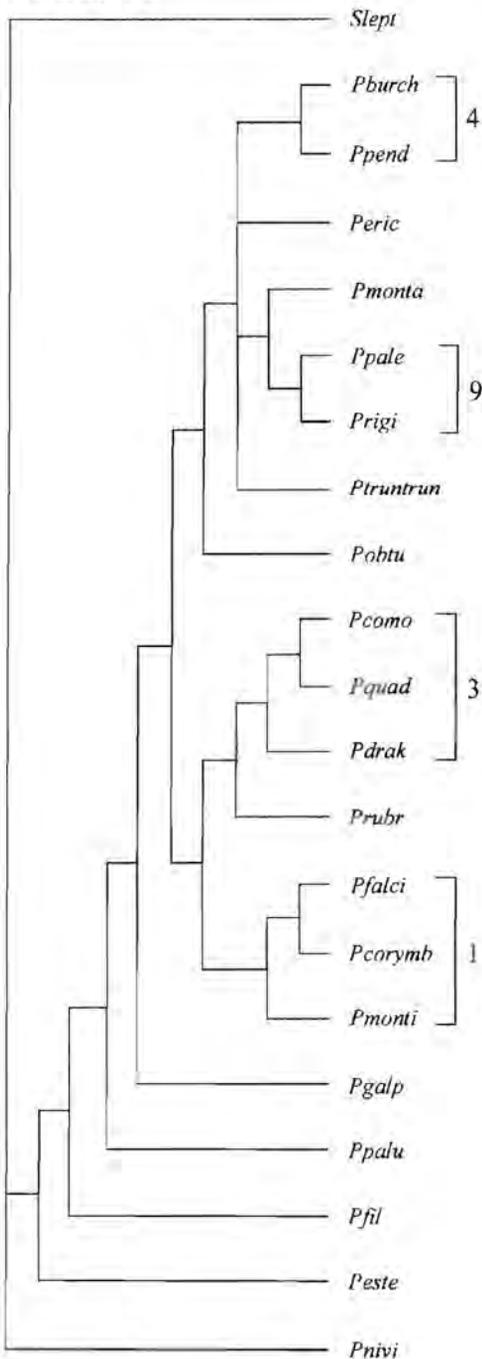
52 characters used.

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

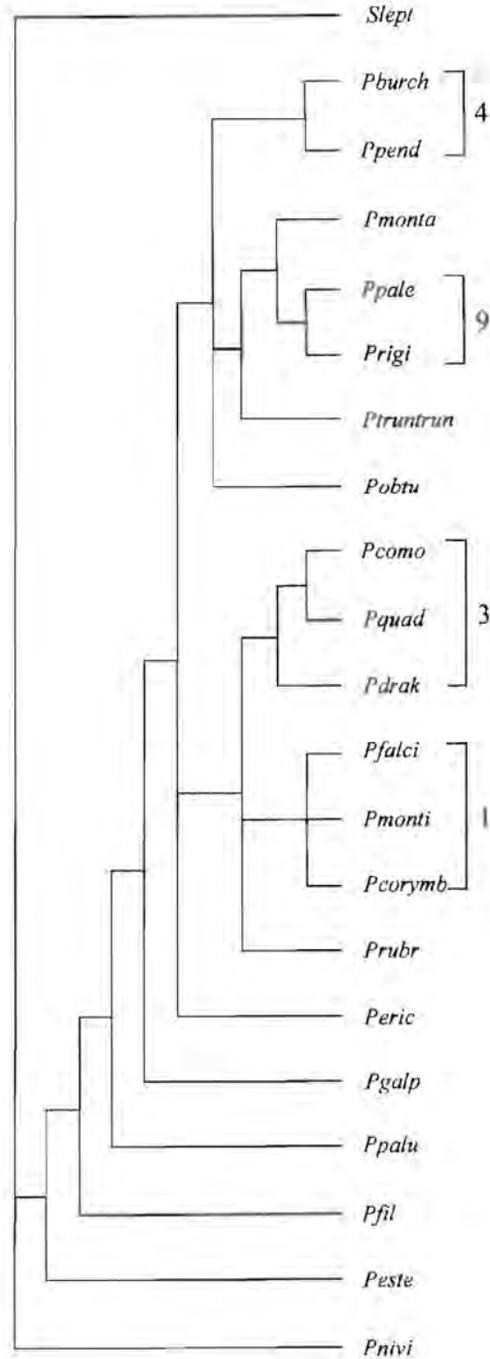


FIGURE 6.7.—Estimate of phylogenetic relationships in the genus *Passerina* as obtained in analysis D, without character weighting and using the Majority Rule and Adams options of the PAUP 4.0 for Macintosh software package.

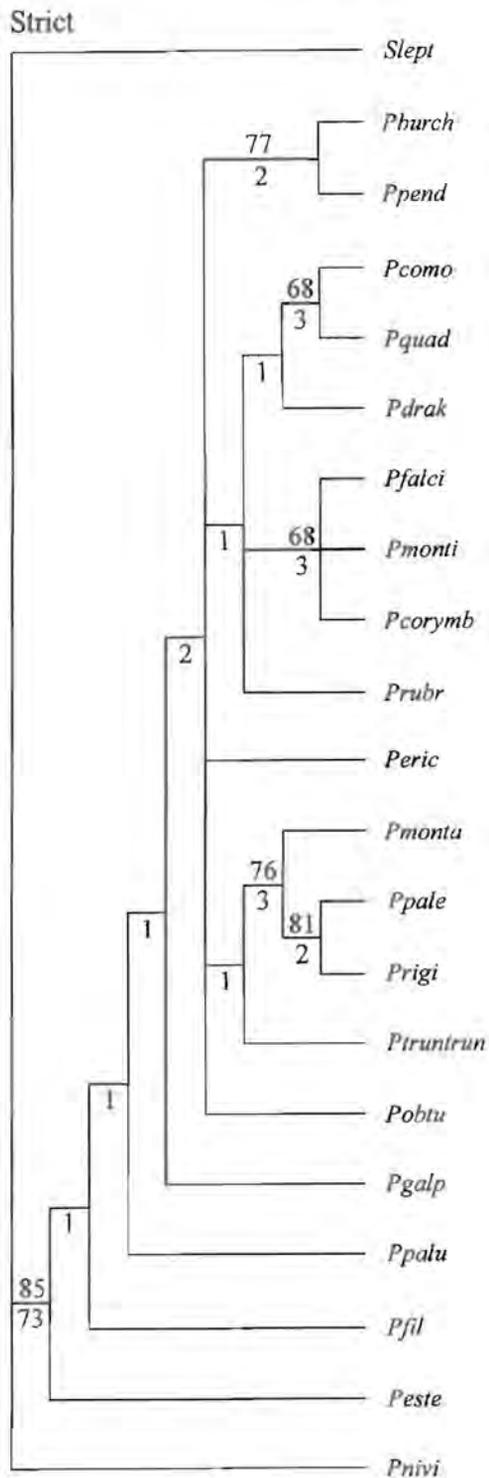


FIGURE 6.8.—Bootstrap values generated in analysis D, without character weighting and computing a strict consensus tree, using the PAUP 4.0 for Macintosh software package.

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. exerted 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 mesophyll [15 (0)]. Autapomorphies characteristic of *P. nivicola* are tufted leaves [2 (2)] and the hairy apex of the outer sepal lobes [38 (2)]. The synapomorphic 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 synapomorphic 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 sclerenchyma 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 aspects:

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 rearrangements 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. *Pentameræ* and section II. *Tetrameræ*. *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 exerted 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 mesophyll [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 evolution 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 exerted 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 obtusulate 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 evolution 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 fibres 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 <i>P. montana</i> / <i>P. paleacea</i> clade, converging in <i>P. esterhuyseniae</i> and <i>P. rigida</i> .
2	Ciliate leaf margins (state 1) are synapomorphic for <i>P. pendula</i> and <i>P. burchellii</i> , converging in <i>P. drakensbergensis</i> , <i>P. montivaga</i> and <i>P. paludosa</i> . Tufted leaves (state 2) are autapomorphic for <i>P. nivicola</i> .
3	Rhombic leaves (state 2) are synapomorphic for <i>P. pendula</i> and <i>P. burchellii</i> .
4	The vascular bundle abaxially enclosed in V-shaped palisade parenchyma, in t/s (state 1) is synapomorphic for the <i>P. corymbosa</i> / <i>P. falcifolia</i> clade.
5	Turned off because of low CI and RI values.
6	Inverse-dorsiventral leaves (state 1) are synapomorphic for all clades in <i>Passerina</i> , except for that of <i>P. nivicola</i> which has isobilateral leaves.
7	Amphistomatic leaves represent the plesiomorphic state in <i>S. leptantha</i> Epistomatic leaves (state 1) are synapomorphic for all clades in <i>Passerina</i> .
8	Carinate leaves in t/s (state 3) are synapomorphic for the <i>P. corymbosa</i> / <i>P. falcifolia</i> clade.
9	The glabrous adaxial epidermis represents the plesiomorphic state in <i>S. leptantha</i> and the villous adaxial epidermis (state 1) is synapomorphic for all clades in <i>Passerina</i> .
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 <i>P. comosa</i> [a 'north-western endemic' of the Cape flora (Weimarck 1941)] and <i>P. quadrifaria</i> (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 <i>Passerina</i> .

12	Differentiated, smaller and irregularly shaped adaxial epidermal cells (state 1) are synapomorphic for all clades in <i>Passerina</i> .
13	Leaf structural type C (state 2) is synapomorphic for <i>P. montivaga</i> and <i>P. falcifolia</i> . Leaf structural type D (state 3) is synapomorphic for <i>P. montana</i> and <i>P. paleacea</i> and converges in <i>P. rigida</i> and <i>P. corymbosa</i> .
14	Extraxylary sclerenchyma fibres abaxially not enclosed by the vascular bundle sheath, often extending to the abaxial epidermis (state 1), are synapomorphic for <i>P. montana</i> and <i>P. paleacea</i> and the character converges in the clade <i>P. corymbosa</i> / <i>P. montivaga</i> .
15	A homogenous mesophyll is regarded as plesiomorphic and is present in <i>P. nivicola</i> . Palisade parenchyma adjacent to the abaxial epidermis (state 1) is synapomorphic for all other clades in <i>Passerina</i> .
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 <i>P. corymbosa</i> / <i>P. falcifolia</i> .
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 <i>P. corymbosa</i> / <i>P. falcifolia</i> clade and converges in <i>P. montana</i> , <i>P. paleacea</i> and <i>P. rigida</i> .
19	Homogenous mesophyll is plesiomorphic and present in <i>P. nivicola</i> . Increasing layers of palisade parenchyma are a xeromorphic adaptation and three layers (state 3) are synapomorphic for the clade <i>P. rigida</i> / <i>P. paleacea</i> .
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 <i>P. montana</i> / <i>P. paleacea</i> and convergent in <i>P. corymbosa</i> .
21	Monotelic synflorescences are regarded as plesiomorphic. Polytelic synflorescences (state 1) are synapomorphic of all the clades in <i>Passerina</i> .
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 <i>P. truncata</i> / <i>P. paleacea</i> and converges in <i>P. quadrifaria</i> .
23	Multiflowered spikes with more than 16 flowers (state 2) are synapomorphic for the clade <i>P. corymbosa</i> / <i>P. rubra</i> , with a reversal in <i>P. obtusifolia</i> and converging in <i>P. filiformis</i> .
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 <i>P. paludosa</i> / <i>P. paleacea</i> , with reversals in <i>P. rigida</i> and <i>P. paleacea</i> .
25	Long bracts (state 0) are regarded as plesiomorphic. Short bracts (state 1) are synapomorphic for the clade <i>P. pendula</i> / <i>P. paleacea</i> , converging in <i>P. nivicola</i> , <i>P. esterhuyseniae</i> and <i>P. galpinii</i> . Most taxa with short bracts have extended west-, north- and eastwards from the Western Cape, the centre of diversity for <i>Passerina</i> (Bredenkamp & Van Wyk 2000, 2001).
26	The absence of bracteoles (state 1) is synapomorphic for all clades in <i>Passerina</i> .
27	Differentiated floral bracts that are abaxially hairy (state 1) are an adaptation to dry summer conditions and are synapomorphic for <i>P. comosa</i> and <i>P. quadrifaria</i> .
28	Differentiated floral bracts that are adaxially villous (state 2) are synapomorphic for the clade <i>P. corymbosa</i> / <i>P. paleacea</i> , with reversals in <i>P. montivaga</i> , <i>P. obtusifolia</i> , <i>P. quadrifaria</i> , <i>P. comosa</i> and <i>P. pendula</i> .
29	Obtrullate floral bracts (state 3) are synapomorphic for <i>P. corymbosa</i> and <i>P. montivaga</i> , converging in <i>P. paludosa</i> and <i>P. obtusifolia</i> .
30	Differentiated floral bracts with a coriaceous texture (state 1) are synapomorphic for the clade <i>P. corymbosa</i> / <i>P. paleacea</i> , reversing in <i>P. paleacea</i> and converging in <i>P. paludosa</i> .
31	The absence of wings in differentiated floral bracts (state 1) is a synapomorphy of the clade <i>P. quadrifaria</i> / <i>P. paleacea</i> , reversing in <i>P. paleacea</i> and converging in <i>P. esterhuyseniae</i> and <i>P. obtusifolia</i> .
32	Fleshy fruit (state 1) is a synapomorphy of <i>P. rigida</i> and <i>P. ericoides</i> .

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

43	Exserted stamens (state 1) are an adaptation to wind pollination and are synapomorphic of all the clades in <i>Passerina</i> .
44	Extrorse anthers (state 1) are an adaptation to wind pollination and is synapomorphic of all the clades in <i>Passerina</i> .
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 <i>Passerina</i> .
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 <i>Passerina</i> .
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 <i>Passerina</i> .
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 <i>P. pendula</i> / <i>P. paleacea</i> , with convergence in <i>P. paludosa</i> and <i>P. quadrifaria</i> .
50	Ascending or spreading leaves are regarded as plesiomorphic. Appressed leaves (state 1), an adaptation to drier conditions, are synapomorphic for the clade <i>P. pendula</i> / <i>P. paleacea</i> , with a reversal in <i>P. ericoides</i> .
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 <i>P. montana</i> and <i>P. paleacea</i> and convergent in <i>P. corymbosa</i> .