

Phytogeography of *Passerina* (Thymelaeaceae)

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Keywords: Afromontane, Cape Floristic Region, distribution, endemism, fynbos, grassland, *Passerina* L., phytogeography, Red Data List, relict, Thymelaeaceae

ABSTRACT

Passerina L. comprises 20 species and four subspecies of microphyllous, wind-pollinated shrubs. Once considered cosmopolitan, the genus as currently defined, is endemic to southern Africa. Endemism within the genus is highest in the Cape Floristic Region (CFR), where all members show morphological and anatomical adaptations to the winter rainfall and dry warm summers of the Mediterranean or semi-Mediterranean climate of the region. The Western Cape is the centre of diversity for *Passerina*, from where certain species extend to the west, north and east. The outlier populations of *Passerina montana* Thoday on the interior plateau of South Africa and Zimbabwe, as well as the Auas Mountains in Namibia, most probably originated in the CFR and formed part of a previously wider northern temperate Afromontane grassland-dominated vegetation during the Quaternary, of which relicts remained in the high mountain areas. *P. burchellii* Thoday and *P. paludosa* Thoday have the most restricted distribution and are regarded as Vulnerable. All other species are either widespread or under no immediate threat.

INTRODUCTION

Meisner (1840, 1857) redefined *Passerina* L. by clarifying the taxonomic position of 92 'species exclusae', thus changing the status of the genus from cosmopolitan to endemic in southern Africa, an opinion also reflected in the now outdated taxonomic revision of the group by Thoday (1924). A recent monograph of *Passerina* recognized 20 species and four subspecies (Bredenkamp 2002; Bredenkamp & Van Wyk 2003); these are listed in Tables 1 and 2. All members of *Passerina* are woody, evergreen shrubs or subshrubs with microphyllous leaves and small, rather insignificant wind-pollinated flowers. It is the only exclusively anemophilous genus of the Thymelaeaceae and the plants usually grow gregariously.

Taking the most southerly distribution of *Passerina montivaga* Bredenkamp & A.E. van Wyk into consideration, no less than 18 species of *Passerina* occur in the Cape Floristic Region (CFR). The CFR is also acknowledged as the smallest of the world's six floristic kingdoms (Van Wyk & Smith 2001). Following a taxonomic revision of *Lachnaea* L. (Thymelaeaceae), Beyers (2001) reviewed 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 paper we follow the interpretation of Goldblatt & Manning (2000), which identifies the following six principal local centres of endemism: the Northwestern (NW), Southwestern (SW), Agulhas Plain (AP), Karoo Mountain (KM), Langeberg (LB) and Southeastern (SE) Centres.

Species of *Passerina* endemic to the CFR (Table 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, 2001). Most species in the CFR are associated with fynbos, a sclerophyllous vegetation type on oligotrophic soils derived mainly from quartzitic Cape Supergroup rocks. 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; forest 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.

Species near-endemic to the CFR are more widespread (Table 1). They have adapted to a wider amplitude of environmental conditions: where ranges extend north of the southern Cape mountain ranges, they are often adapted to arid karroid vegetation and summer rainfall; certain species are adapted to forest margins and others tolerate periodic falls of snow at high altitudes.

The few species of *Passerina* endemic to the northern Drakensberg or near-endemic to the Great Escarpment of southern Africa (Table 2) are associated with the high moisture levels prevalent on the eastern escarpment and conditions of summer rainfall. These plants are often found in the ecotonal belt between forest and grassland; they also grow along streams and riverbanks and on mountain slopes.

In this contribution we describe, for the first time in one paper, the patterns of geographical distribution shown by members of *Passerina*. Patterns are interpreted in terms of geology, climate, vegetation type and historical change, and the conservation status of threatened taxa is suggested.

MATERIAL AND METHODS

All infrageneric taxa of *Passerina* were studied during extensive field work covering the complete geographi-

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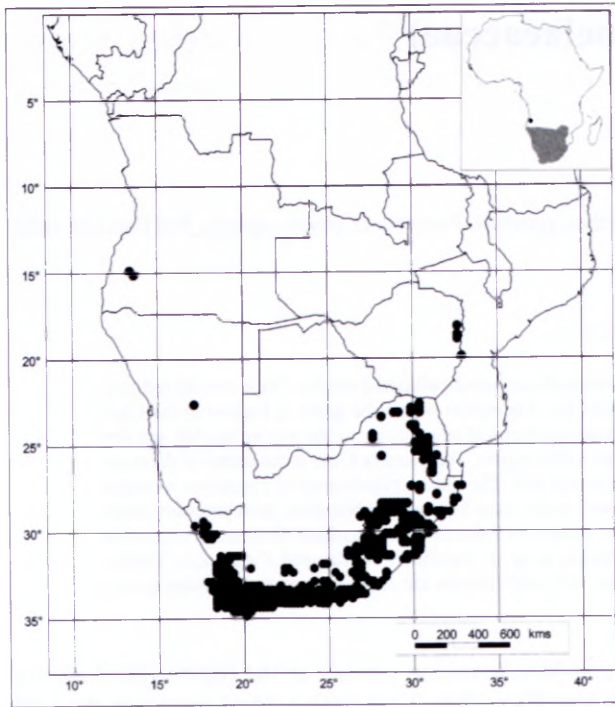


FIGURE 1.—Known geographical distribution of the genus *Passerina*. Distribution in Angola on Huila Plateau near Lubango and Chela Mountains is shown in insert.

cal range of the genus. Live material was collected, as far as possible, from at least five different localities for every taxon. Habitat and distribution data from 22 national and international herbaria were compiled in a Microsoft Access Database and integrated with the Pretoria Computerised Information System (PRECIS), from which distribution maps for all taxa were generated. For mapping purposes the degree square system was used (Edwards & Leistner 1971). Categories used to indicate Red List status of taxa are based on the criteria of the IUCN Species Survival Commission (2000).

OBSERVATIONS

The combined distribution of all species of *Passerina* is shown in Figure 1. The number of species per one-degree square is indicated in Figure 2. In *Passerina* the highest numbers of species per one-degree square are concentrated in a belt including those grids between 33° and 34°S and 18° to 27°E. The CFR (mainly Western Cape) is clearly the centre of diversity for *Passerina*, from where certain species extend to the west, north and east (see also Bredenkamp & Van Wyk 2001). The highest numbers of species occur in the grids 3321 (Ladismith), 3322 (Oudtshoorn) and 3419 (Caledon). The highest

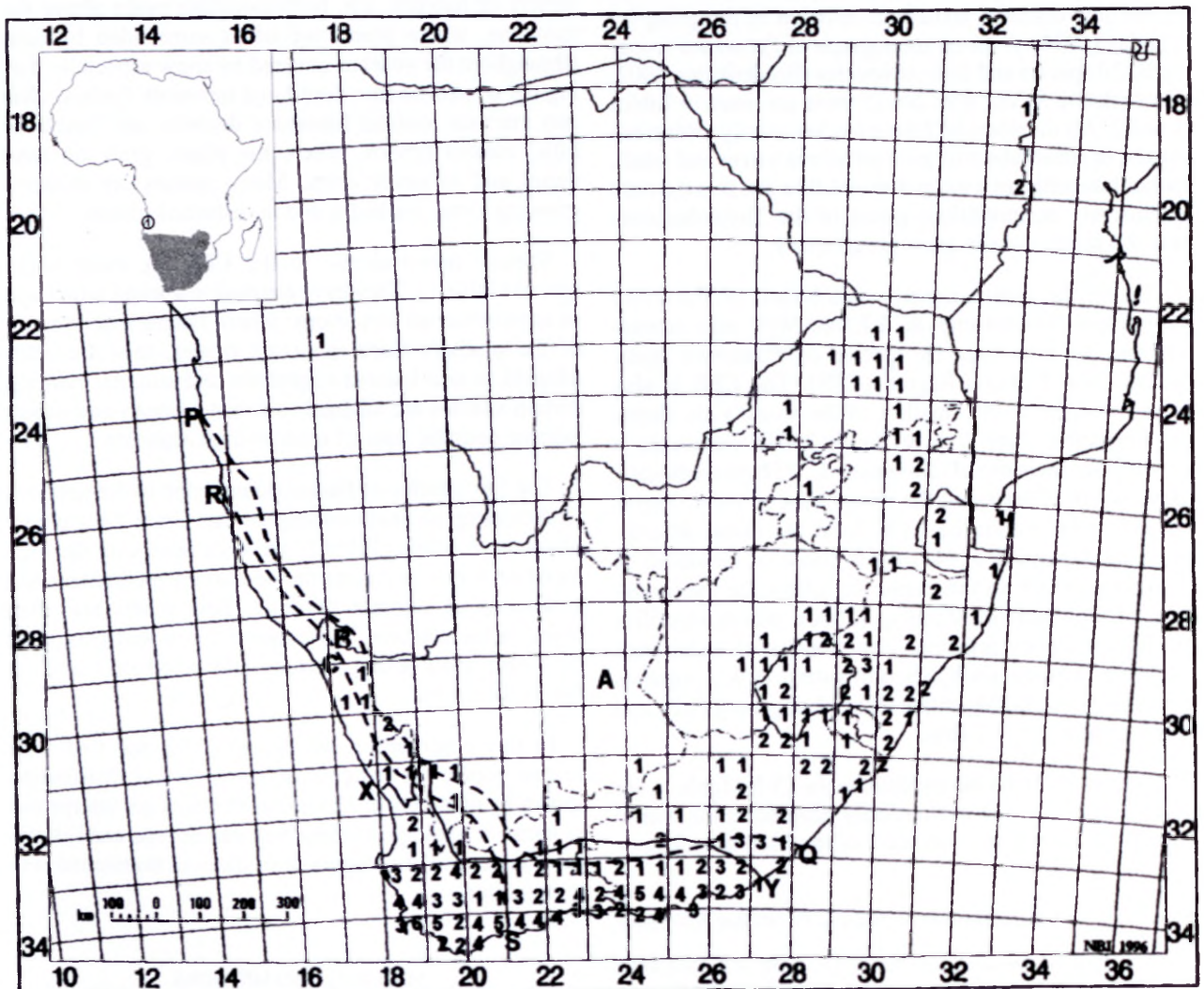


FIGURE 2.—Number of species of *Passerina* per one-degree grid square. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops. Distribution on Huila Plateau and Chela Mountains in Angola is shown in insert.

diversity of species (six per half-degree square) occurs in the False Bay area, from Seekoeivlei, including the Cape Flats, to De Mond at the Palmiet River (3418B) (Bredenkamp 2002). Levyns (1938) was the first to show that the Caledon District is the centre of species richness in the CFR with a reduction in numbers to the north and east. Oliver *et al.* (1983) regard the quarter-degree square 3418BB as the richest area in the CFR. Beyers (2001), also working in the Thymelaeaceae, found that the highest number of *Lachnaea* L. species occurred in the quarter-degree square 3319AD (Worcester).

Species endemic or near-endemic to the CFR (Table 1)

Passerina shows a high percentage of endemism within the CFR, as nine species out of 20 (45%), as well as the three subspecies, are endemic to this region. High percentages of species, 25%–65%, are also demonstrated in each of the local centres of endemism. *P. esterhuyseniae* (Northwestern Centre), *P. paludosa* (Southwestern Centre), *P. galpinii* (Agulhas Plain Centre) and *P. pendula* (Southeastern Centre) are all endemic to one local centre of endemism only.

The Northwestern Centre has a relatively high concentration of *Passerina* species, as 40% of the species occur there. The occurrence of 65% of *Passerina* species in the Southwestern Centre, confirms that the grids 3419 (Caledon) and 3418 (Simonstown) can be regarded as centres of total species richness [Levyns (1938) and Oliver *et al.* (1983)]. 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). Thirty percent of *Passerina* species occur in this centre. The percentages of *Passerina* species represented in the Karoo Mountain Centre (25%) and the Langeberg Centre (35%) are relatively low, and no *Passerina* species are endemic to either of these Centres. The Southeastern Centre has a relatively high concentration of *Passerina* species, with 40% of the species occurring there.

Species considered near-endemic to the CFR are *Passerina comosa* and *P. nivicola*, distributed from the CFR to the Northern Cape and *P. falcifolia*, *P. rubra* and *P. truncata* subsp. *truncata* distributed from the CFR to the Eastern Cape. *Passerina nivicola*, restricted mostly to mountainous areas, is possibly still under-collected.

Species endemic to the Northern, Western and Eastern Cape and KwaZulu-Natal (Table 1)

P. obtusifolia and *P. corymbosa* (= *P. vulgaris*) are so-called Cape ubiquitous (Weimark 1941) as they are very common and adapted to a wide range of Cape habitats. Their distributions currently include all the Centres within the CFR and both occur in three other South African provinces. *Passerina rigida* is confined to coastal areas from South Africa's western coast to the northeastern coast of KwaZulu-Natal.

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

Endemism of *Passerina drakensbergensis*, *P. montana* and *P. montivaga* is indicated in Table 2.

Based on fossil 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, temperate 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 for the presence of such fynbos 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). A phylogenetic study by Bredenkamp (2002) indicates that *Passerina filiformis* and *P. paludosa* (both common in the Cape Peninsula) are probably the most primitive extant members of the genus, and *P. truncata*, *P. montana* and *P. paleacea* as the most advanced. We hypothesize that *P. montana* probably originated from an ancestor in the CFR and adapted to the environmental conditions of the high-mountain Afromontane grassland, which had a wider northerly distribution during the Quaternary. Because of environmental changes since the beginning of the Quaternary, the boundaries of the Grassland and Savanna Biomes changed, resulting in relicts of Afromontane grassland and fynbos elements in high-altitude areas such as Nyanga, the Huila Plateau and the Auas Mountains. 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, the Eastern Zimbabwe Highlands and Angola (Huila Plateau). Although this broad pattern of distribution (Cape centre, eastern African extension with reduced species) is common to other genera as well, *Passerina* is unusual because it is represented in all the more pronounced Afromontane refuges in southern Africa, especially those isolated western outliers in Namibia 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 expansion of at least certain elements of that flora took place along the west coast into present-day Namibia. Unfortunately the *Passerina* specimens from the Auas Mountains available to him were sterile, resulting in their incorrect identification as *P. truncata* (= *P. glomerata*). As the most northerly known distribution of *P. truncata* at the time was Steinkopf in Namaqualand, he concluded that *P. truncata* once ranged further north through Namibia to the Auas Mountains. However, the specimens from both Auas and Huila are unmistakably *P. montana*, a species

TABLE 1.—Endemism of *Passerina* species in Cape Floristic Region (CFR), as well as in various provinces of South Africa

Taxa	Habitat & altitude	Centres of endemism										*Conserv. status	
		NW	SW	AP	KM	LB	SE	NC	WC	EC	KZN		
Species and subspecies endemic to CFR													
<i>burchellii</i> Thoday	High mtns		▲ Genaden-dai, Villiersdorp			▲ Towerkop at Ladismith							VU D2
<i>ericoides</i> L.	Beaches and salt marshes		▲ Melkbosstrand and Cape Peninsula, eastward	▲ De Mond in Bredasdorp Dist.									NT
<i>esterhuyseniae</i> Bredenk. & A.E. van Wyk	Mountain Fynbos (Rebello 1998), mtn summits	◆ Groenberg, Koppoort in Cederberg											LC
<i>filiformis</i> L. subsp. <i>filiformis</i>	Rocky areas, east-facing mtn slopes	▲ Piquetberg, south-eastward	▲ Cape Peninsula, eastward			▲ Attaquaskloof							LC
<i>filiformis</i> L. subsp. <i>glutinosa</i> (Thoday) Bredenk. & A.E. van Wyk	Strandveld (Acocks 1988)	Doring Bay, southward	St Helena Bay										NT
<i>galpinii</i> C.H. Wright	Stony flats, coastal limestone deposits and limestone hills, 0–290 m		◆ Elm to Bredasdorp, eastward to Mossel Bay										LC
<i>paleacea</i> Wikstr.	Beaches and salt marshes		▲ Langebaan south- and eastward	▲ Bredasdorp Dist., eastward		▲ Stilbaai Dist.							LC
<i>pallidosa</i> Thoday	Marshy areas		◆ Muizenberg, Rondevlei Nature Reserve, Zee-koevlei and Strandfontein Road (Smuts 1996)										VU BIB2abcd

◆ spp. endemic to one centre of endemism only; ▲, spp. endemic to more than one centre of endemism; ●, spp. near-endemic to CFR; ■ spp. endemic to CFR and adjacent provinces of South Africa; NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern; NC, Northern Cape; WC, Western Cape; EC, Eastern Cape; KZN, KwaZulu-Natal. *Conserv. status: VU D2, Vulnerable; NT, Near Threatened; LC, Least Concern; VU B1B2abcd, Vulnerable.

TABLE 1.—Endemism of *Passerina* species in Cape Floristic Region (CFR), as well as in various provinces of South Africa (cont.)

Taxa	Habitat & altitude	Centres of endemism										*Conserv. status			
		NW	SW	AP	KM	LB	SE	NC	WC	EC	KZN				
Species and subspecies endemic to CFR (cont.)															
<i>pendula</i> Eckl. & Zeyh. ex Thodlay	Mtn slopes and river-banks, 383–600 m										◆ E Kouga to Great Winterhoek Mtns, upper Swartkops and Boesmans Rivers at Port Elizabeth				LC
<i>quadrifaria</i> Breidenk. & A.E.van Wyk	Rocky peaks and mtn summits, 1 500–1 670 m				▲ Langeberg and Swartberg		▲ Swartberg				▲ Kouga, Tsitsikamma and Great Winterhoek Mtns				LC
<i>truncata</i> (Meisn.) Breidenk. & A.E.van Wyk subsp. <i>monticola</i> Breidenk. & A.E.van Wyk	In rock crevices on mtn summits, 2 000 m	Clanwilliam, south- and eastward	Table Mtn, Helderberg, Hex River and Rivier-sonderend Mtns												LC
Species and subspecies near-endemic to CFR															
<i>comosa</i> C.H.Wright	Mtn summits, slopes, 1 000–1 200 m	● Roggeveld	● Tafelberg in Worcester Dist.		● Witteberg, Klein Swartberg							● Kamiesberg to Calvinia			LC
<i>fulcifolia</i> C.H.Wright	Mtn plateaus, southeast-facing slopes, 0–1 100 m		● Near Calcedon				● Mossel Bay to Port Elizabeth						● Somerset East Dist., Grahams-town to Boknes		LC

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TABLE 1.—Endemism of *Passerina* species in Cape Floristic Region (CFR), as well as in various provinces of South Africa (cont.)

Taxa	Habitat & altitude	Centres of endemism										*Conserv. status	
		NW	SW	AP	KM	LB	SE	NC	WC	EC	KZN		
Species and subspecies near-endemic to CFR (cont.)													
<i>nivicola</i> Bredenk. & A.E.van Wyk	Escarpment Mountain Renosterveld, Mountain Fynbos Renosterveld and Central Mountain Renosterveld (Rebello 1998)	● Ceres Dist.	● Tafelberg, Worcester Dist.									● Sneeukskrans in Roggeveld Escarpment	LC
<i>rubra</i> C.H.Wright	Calcareous soils, dunes, limestone		● Swellendam Dist., Bontebok National Park			● Muiskraal near Garcia Pass	● Sedgefield Dist. to Port Elizabeth, ancient dunes northward to Cradock					● Grahams-town Dist.	LC
<i>truncata</i> (Meisn.) Bredenk. & A.E.van Wyk subsp. <i>truncata</i>	Dry areas of Namaqualand, karoo environment, rocky slopes of several mtn ranges	● Vanrhynsdorp, southward	● Ceres Dist.		● Matjiesfontein, south-eastward							● Steinkopf, southward to Calvinia Dist.	LC
Species endemic to CFR and adjacent provinces of South Africa													
<i>obtusifolia</i> Thoday	Karoo habitats, north-facing aspect of mtns in sthn Cape, ecotone between Fynbos and Karoo, 670–1 400 m	■ Van Rhyn's Pass	■ Worcester and Caledon Dist., Hex River Mtns	■ Bredasdorp and Riversdale Dist.	■ Montagu and Ladismith Dist., Swartberg	■ Noukloof Nature Reserve to Ladismith, Langeberg	■ Steytlerville Dist. to Humansdorp, eastward to Port Elizabeth	■ Calvinia Dist.	■ Beaufort West Dist.	■ Lady Grey southward to Storms River, eastward to Grahamstown			LC

◆ spp. endemic to one centre of endemism only; ▲ spp. endemic to more than one centre of endemism; ● spp. near-endemic to CFR; ■ spp. endemic to CFR and adjacent provinces of South Africa; NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern; NC, Northern Cape; WC, Western Cape; EC, Eastern Cape; KZN, KwaZulu-Natal. *Conserv. status: VUD2, Vulnerable; NT, Near Threatened; LC, Least Concern; VUB1B2abcd, Vulnerable.

TABLE 1.—Endemism of *Passerina* species in Cape Floristic Region (CFR), as well as in various provinces of South Africa (cont.)

Taxa	Habitat & altitude	Centres of endemism										*Conserv. status						
		NW	SW	AP	KM	LB	SE	NC	WC	EC	KZN							
Species endemic to CFR and adjacent provinces of South Africa (cont.)																		
<i>rigida</i> Wikstr.	Along coast, littoral and hammock dunes, marshy places, river mouths	■ Lambert's Bay southward	■ Witsand River Mouth, along Cape Peninsula to Hermanus	■ Armiston to Mossel Bay							■ Buffalo Bay to Keur-boomsrivier				■ Jeffrey's Bay to Port Edward	■ Uvongo to Lake Sibayi	LC	
<i>corymbosa</i> Eckl. ex C.H. Wright	Mtn slopes, rear dunes along coast, riverbanks, roadsides, up to 1 300 m	■ Leipoldtville to Veldrift and Piquetberg	■ Hopefield to Cape Peninsula, eastward to Swellen-dam	■ Baardskeersbos to Riversdale and Mossel Bay Dist.	■ Laingsburg Dist. to Uniondale	■ Malgas to Mossel Bay	■ George Dist. to Port Elizabeth								■ Clanwilliam Dist., Nuweveld in Beaufort West Dist.	■ Lady Grey to Humansdorp, eastward to Gra-hamstown	■ Outliers at Ngome, Port Natal (Durban), Dumisa Station at Alexandra	LC
◆ + ▲ No. endemic spp. (CFR)		2	5	3	1	4	2											
● No. near-endemic spp. (CFR)		3	5		2	1	3					3			2			
■ No. endemic spp. (CFR & adjacent SA prov.)		3	3	3	2	2	3					1	2	3	2			
◆ + ● + ■ Total no. spp. (CFR & adjacent SA prov.)		8	13	6	5	7	8					4	2	5	2			
Percentage spp. (CFR & SA prov.)		40	65	30	25	35	40					20	10	25	10			
Percentage endemic spp. (CFR)		5	5	5	5	5	5											

◆ spp. endemic to one centre of endemism only; ▲ spp. endemic to more than one centre of endemism; ● spp. near-endemic to CFR; ■ spp. endemic to CFR and adjacent provinces of South Africa; NW, Northwestern; SW, Southwestern; AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; SE, Southeastern; NC, Northern Cape; WC, Western Cape; EC, Eastern Cape; KZN, KwaZulu-Natal. *Conserv. status: VUD2, Vulnerable; NT, Near Threatened; LC, Least Concern; VUB1B2abed, Vulnerable.

TABLE 2.—*Passerina* species endemic or near-endemic to Great Escarpment of southern Africa, often with outliers in Afrotontane refuges

Species	Habitat & altitude	Status	South Africa	Swaziland	Lesotho	Zimbabwe	Mozambique	Angola	Namibia	*Conserv. status
<i>drakensbergensis</i> Hilliard & B.L. Burt	Transitional belt between forest and grassland, along streams, mtn slopes, 1 500–1 980 m	Endemic to Drakensberg Alpine Centre	KwaZulu-Natal, Bergville Dist. in mtn Drakensberg, Royal Natal National Park to Giant's Castle Game Reserve		Not yet recorded, but probably present along border with KZN					LC
<i>montana</i> Thoday	Bordering on montane forest, mtn slopes, stream and riverbanks, 1 200–3 000 m	Near-endemic to Great Escarpment of sthn Africa	Limpopo Province (Soutpansberg, Blouberg and Kraantzberg), Mpumalanga, Kwa-Zulu-Natal, Free State, and Eastern Cape	Mbabane	Widespread	Nyanga	Manica and Sofala	High mtn areas, Huila Plateau, Lubango and Chela Mtns	Moltkeblick on Auas Mtns	LC
<i>montivaga</i> Bredenk. & A.E. van Wyk	Ecotonal zone between forest and grassland, rocky mtn slopes, river valleys, 42–2 070 m	Near-endemic to Great Escarpment of sthn Africa	Limpopo Province, Mpumalanga, Kwa-Zulu-Natal, Western and Eastern Cape	Mbabane		Chimanimani Mtns	Manica and Sofala			LC

*Conserv. status: LC, Least Concern.

distributed mainly along the eastern Great Escarpment. The present distribution of *P. montana* renders Rennie's interpretation rather improbable.

CONCLUSIONS

In *Passerina* the highest numbers of species per one-degree square are concentrated in a belt between the 33° and 34°S and 18° to 27°E, occurring in the grids 3321 (Ladismith), 3322 (Oudtshoorn) and 3419 (Caledon). The highest diversity of species occurs in the False Bay area, from Seekoeivlei to the Palmiet River (3418B). Hence the CFR (Western Cape) is the centre of diversity for *Passerina*.

Passerina demonstrates a high degree of regional endemism, with 45% of the species endemic to the CFR. Of these endemics, 20% are endemic to one of four 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.

Passerina species that are near-endemic or endemic to the Great Escarpment probably originated in the CFR and adapted to conditions associated with the high-mountain Afromontane grassland, a vegetation type which is hypothesized to have had a much wider distribution during the Quaternary. The widely disjunct distribution of *P. montana* is probably due to subsequent environmental changes. The boundaries of the Grassland and Savanna Biomes shifted, resulting in relicts of temperate grassland and fynbos elements (such as *P. montana*) in isolated high-altitude refuges such as the Waterberg Plateau in Limpopo (South Africa), Nyanga-Chimanimani Highlands in eastern Zimbabwe, Huila Plateau in Angola and the Auas Mountains in Namibia.

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