A model explaining patterns of geographic character variation in *Cordylus cordylus* (Reptilia; Cordylidae) in the south-western Cape, South Africa

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A model is proposed for the evolution of three morphotypes of the girdled lizard *Cordylus cordylus* (Linnaeus) in the south-western Cape. The available data are interpreted as indicating that a vicariant splitting of a warm-adapted ancestral population during the last glacial period occurred. Differential evolution of the two daughter populations in response to different environmental pressures resulted. One of the daughter populations remaining in the coastal lowlands to the west of the Cape Fold Mountains, became cold-adapted, an event which was followed by a rapid range expansion. The other daughter population to the south and east of the Cape Fold Mountains apparently experienced less severe climatic conditions, maintained a larger population size, and for these reasons remained warm-adapted. During the subsequent warmer, interglacial period the now cold-adapted daughter population was again fragmented into two populations. Of these, one is presently found along the south-western coast and the other along the higher peaks of the western section of the Cape Fold Mountains. On the other hand the amelioration of the climate during the interglacial allowed the warm-adapted daughter population to the south and east to expand its range, eventually penetrating into the areas formerly occupied by the cold-adapted populations. Subsequently zones of secondary contact were established. In the area under discussion similar patterns of contraction and expansion can be observed in other closely related species. Our data support the turnover-pulse hypothesis of Vrba (1985).

'n Model word voorgestel vir die evolusie van drie morfotipes van die gordelakkedis *Cordylus cordylus* in die suidwes-Kaap. Die beskikbare inligting dui daarop dat 'n vikariante deling van 'n warm-aangepaste voorvaderlike populasie gedurende die laaste ystydperk plaasgevind het. Differensiële evolusie van die twee dogterpopulasies a.g.v. verskillende omgewingsdrukke het gevolg. Een van die dogterpopulasies, in die kuslaaglande wes van die Kaapse Plooiberge, het aangepas geraak by koue toestande, 'n gebeurtenis wat 'n vinnige gebiedsuitbreiding tot gevolg gehad het. Die ander dogterpopulasie suid en oos van die Kaapse Plooiberge het meer gematigde omgewingstoestande ondervind en het warm-aangepas gebly. Gedurende die daaropvolgende warmer interglasiale periode is die nou koud-aangepaste westelike dogterpopulasie weer in twee populasies opgebreek. Een van hierdie populasies kom vandag langs die suidwestelike kus voor terwyl die ander op hoë pieke in die westelike seksie van die Kaapse Plooiberge aangetref word. Die warmer interglasiale periode het aan die anderkant 'n aansienlike gebiedsuitbreiding by die warm-aangepaste binnelandse populasie tot gevolg gehad, tot in areas wat voorheen deur koud-aangepaste, melanistiese populasies beset was. Uiteindelik het sones van sekondêre kontak tussen die oorblywende koud-aangepaste en warm-aangepaste populasies ontstaan. In die area onder bespreking is soortgelyke patrone van uitsetting en inkrimping ook by naverwante spesies waarneembaar. Ons inligting ondersteun die 'turnover pulse'-hipotese van Vrba (1985).

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The taxonomic status of the melanistic rough-scaled girdled lizard, *Cordylus cordylus niger,* occurring in the Cape Peninsula and the Saldanha-Langebaan area, is considered one of the most pressing herpetological problems in the Cape Province (Visser 1971; Branch 1981). This melanistic form is regarded by some authors as a colour variant of the typical form (FitzSimons 1943), others see it as a subspecies (Rose 1926; Essex 1927; Power 1930; Loveridge 1944), while it is also proposed that it could be a separate species (Visser 1971). This 'embarrassing state of affairs' (Visser 1971, p. 18) prompted an in-depth investigation of geographic character variation in the *C. cordylus* complex in the south-western Cape (Mouton 1987). This investigation revealed the existence of three distinct morphotypes of the nominate species, namely a coastal melanistic form (= *C.c. niger),* a montane melanistic form (previously undescribed) , and a typical form (= *C.c. cordylus).* The purpose of this report is to advance hypotheses on the evolution of the three morphotypes in accordance with the methodology of speciation analysis proposed by Vuilleumier (1980) and Cracraft (1982).

The main causes of geographical variation in populations are usually divided into two major components, namely populations responding to different environments, and the restricted gene flow between spatially separated populations (Lane & Marshall 1981). Where environmental conditions change gradually over a given area, gradual changes in certain characters of a species will be caused, resulting in regular gradients of variability or clines (Calhoon & Jameson 1970; Vogt & Jameson 1970; Moodie and Reimchen 1976; Lane & Marshall 1981). Clines may be expressed in many characters and may be the result of any number of geographically variable conditions (Lane & Marshall 1981). Different characters will, however, react differently to different environmental factors and will not necessarily vary geographically together. The characters expected to show smooth clinal trends are those which are strongly influenced by selection mediated through environmental pressures. Features such as body size and pigmentation, for example, normally vary in a regular manner, usually in association with climatic conditions (Porter 1972; McMahon & Bonner 1983). These characters may be reliable indicators of ecological relationships but do not normally reflect phylogenetic patterns. Endler (1982, p.449) concluded that 'good taxonomic characters are supposed to drift, so they should reflect the true phylogenetic pattern if they were not subject to selection'.

Workers in biogeography have lately become divided into groups specializing in either ecological or historical aspects, usually to the exclusion of alternative hypotheses (Endler 1982; examples: MacArthur 1972; Briggs 1974; Platnick & Nelson 1978; Rosen 1978; Van Dijk 1982). To date there have been very few attempts to determine the relative importance of both history and ecology. Endler (1982, p.450) states: 'Organisms are subject to current ecology and history. The effects of the two can operate in various ways, sometimes yielding the same patterns. This makes it very difficult to distinguish between the two factors, and to estimate their relative importance. It is exceptionally important to consider several hypotheses, and test for all possible consequences of each hypothesis.' In the present study a special attempt is made to consider both ecological and historical factors in explaining the observed patterns of character variation in *C. cordylus* in the south-western Cape.

Most hypotheses on the causes of speciation and extinction centre around the opposing perspectives of internalism versus environmentalism and gradualism versus punctuationalism (Vrba 1985). Neo-Darwinists, for example, do not consider changes in the physical environment as necessary for speciation to occur and believe that interspecific competition and dispersal and radiation into available niches act as initiating causes of speciation and extinction (Vrba 1985) . The Neo-Darwinistic view accordingly predicts random and indiscrete patterns of lineage turnover against time.

In contrast, the turnover-pulse hypothesis of Vrba (1985) is an expression of a strong environmentalistic viewpoint. According to this hypothesis forcing by the physical environment is necessary for speciation, extinction and most migratory events to occur. Accordingly 'most lineage turnover in the history of life has occurred in pulses, nearly synchronous across diverse groups of animals and in predictable synchrony with changes in the physical environment' (Vrba 1985, p. 232). In other words non-random and discrete patterns of lineage turnover against time are predicted. The hypothesis of Vrba involves a combination of evolutionary notions, namely conservatism, habitat specificity of species, vicariance and punctuated equilibrium. In our study these notions were evaluated by careful consideration of the observed patterns of morphological character variation seen against the palaeoenvironmental history of the region.

Materials and methods

The distribution patterns of the three morphotypes of *C. cordylus* identified in the section of the Cape Province south of 32°30′ latitude and west of 19°30′ longitude (Mouton 1987) (Figure 1) form the basis of this report. Available literature on palaeoclimatology and palaeogeography (Tankard 1976; Deacon 1983a,b; Vogel 1985; Deacon & Deacon 1986; Tyson 1986) was studied and was implemented in the evolutionary models.

Results and discussion

Topographically the study area can be described as consisting of the Cape Fold Mountains and the bordering coastal platform with its extension, the continental shelve, that has been variously exposed through changes in sea level in the past. The coastal platform is bisected into a western and an eastern section along an imaginary line from Cape Hangklip to Worcester (Figure 1). Important features of the western section are the several offshore islands, as well as two major peninsulas, the Cape Peninsula and the Langebaan Peninsula (Figure 1).

In terms of climate the following are considered relevant: The Effective Temperature map of Stuckenberg (1969) indicates cooler zones (ET = 14–15 °C) along the immediate south-western coast and along the Cape Fold Mountains (Figure 2). These two cooler zones are separated by a warmer zone (ET = 15–16 °C) along the coastal lowlands (Figure 2). Along the southern coast there is no cooler zone along the coast, the warmer 15–16 °C ET zone extending from the coastline to the Cape Fold Mountains (Figure 2). The cooler zone along the west coast is a direct effect of the cold Benguela Current, which brings cool waters northward against the west African coast (Schulze 1965; Brown & Jarman 1978) . In addition there is an upwelling of cold water from the ocean depths off shore (Hart & Currie 1960; Schulze 1965). The air cooled by the passage of the prevailingly south and south-west winds over the belt of cold water stabilizes the temperature of the coastal areas (Meigs 1966). Fog is another result of the cool belt of offshore water. As the wind blows from the warmer part of the ocean across the cool belt near shore, thick fog or low stratus cloud forms and is blown over the land (Meigs 1966). At Saldanha Bay, for example, a mean of 128 misty days per annum are experienced (Scheurkogel, Page, Schumann, Tebutt & Thomas 1973). The effect of the cold Benguela Current is most pronounced along the Namib coast and decreases southwards and northwards.

Information on climatic changes during the Late Pleistocene and Holocene is particularly relevant to this study. During the last 500 000 years the extent of the polar ice sheets fluctuated in the form of regular pulses (van Donk 1976; Imbrie & Palmer-Imbrie 1979) with a periodicity of some 100 000 years. The glacial periods, characterized by globally cooler and generally drier climates, are interrupted by shorter periods of warmer and generally wetter climates (Hays, Imbrie & Shackleton 1976; Kukla 1977). The best dating

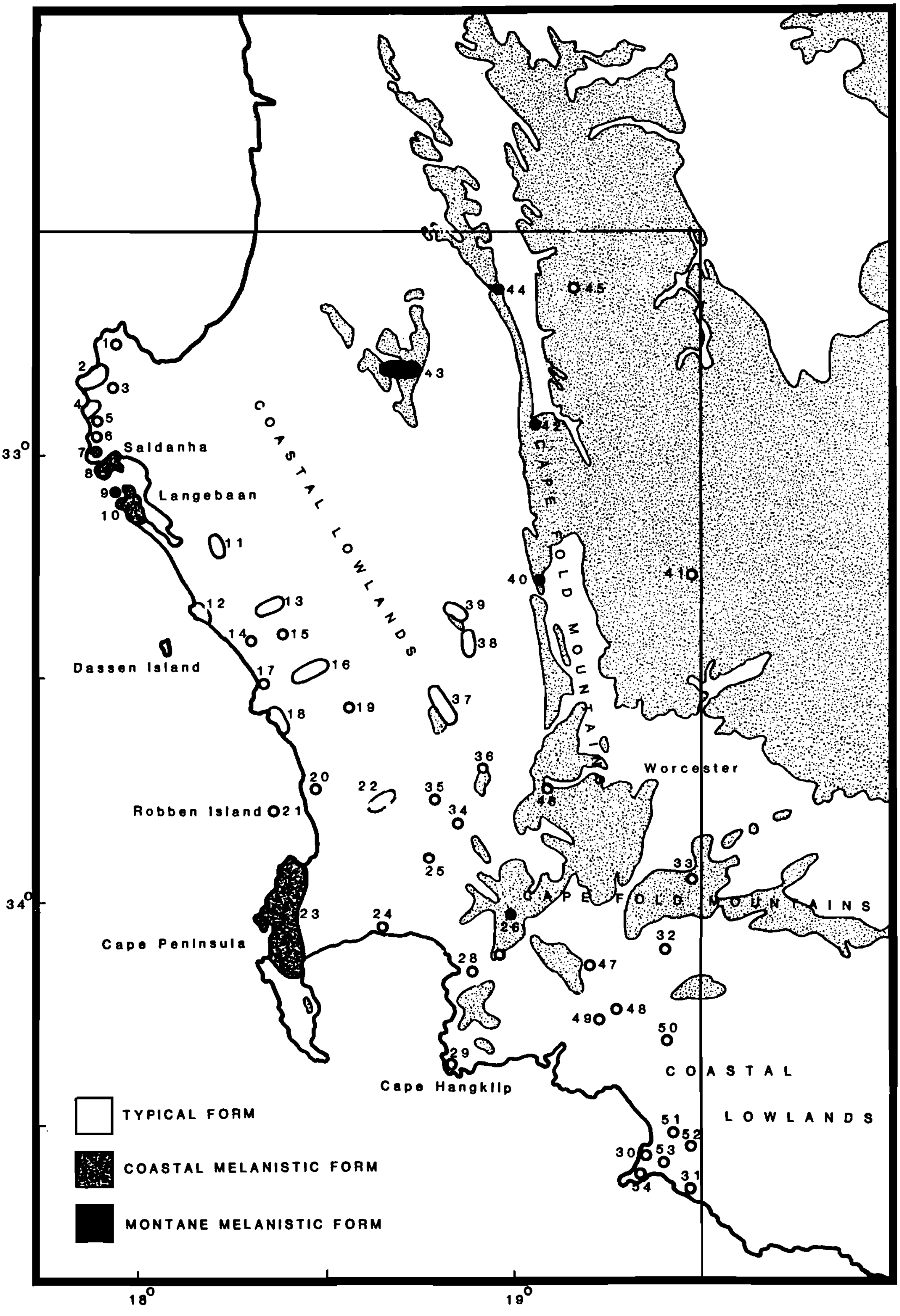

Figure 1 Geographic distribution of the three phenotypic forms of *C. cordylus* in the study area (the 500 m contour line is shaded).

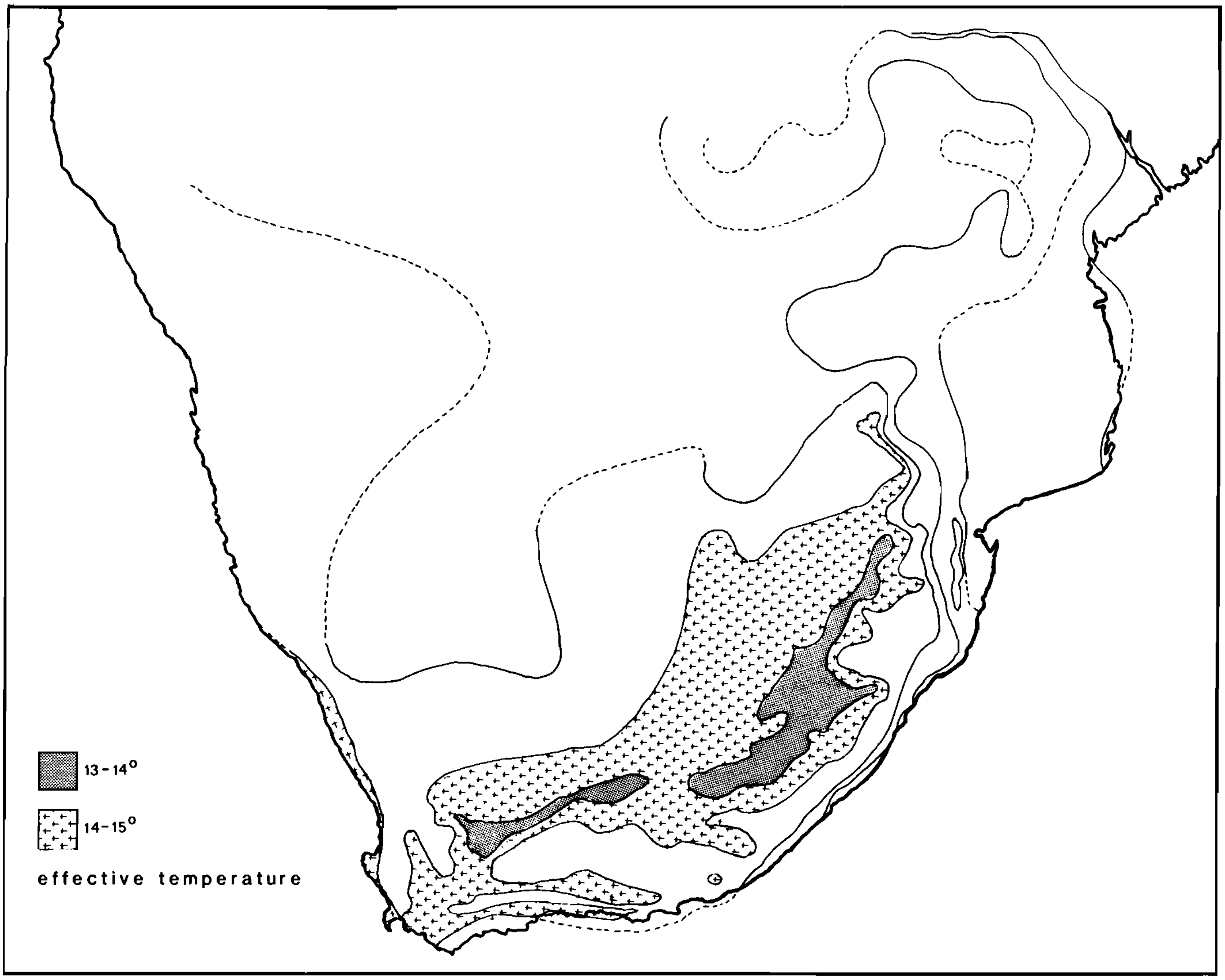

Figure 2 Effective temperature map for Southern Africa [redrawn from Stuckenberg (1969)].

resolution for climatic changes is for the last 40 000 years for which a good radiocarbon chronology is available (Tankard 1976; Deacon 1983a; Vogel 1985; Deacon & Deacon 1986). From approximately 40 000 BP a relatively long period of cool moist conditions led up to the Last Glacial Maximum which covers a time range between about 25 000 and 17 000 BP (Deacon & Deacon 1986). At approximately 18 000 BP conditions were the most severe of the glacial cycle and were essentially cold and dry, with temperatures 5–6°C lower than at present (Deacon 1983a; Deacon & Deacon 1986; Tyson 1986). After about 16 000 BP a relatively rapid amelioration of the climate took place (Deacon 1983b; Deacon & Deacon 1986), which was accompanied by a renewed onset of humidity coming to an end at about 11 000 BP (Vogel 1985). After this, two wet / dry cycles followed with the highest temperatures in mid-Holocene time i.e. at approximately 5 000 BP (Vogel 1985).

A time-depth plot of sea level for South Africa over the last 47 000 years (Tankard 1976) suggests that between 47 000 and 25 000 BP a sea level maximum at approximately –20 m occurred. The curve furthermore suggests a rapid fall of sea level with the advance of the Last Glacial Maximum and that a minimum sea level of –130 m was reached at 17 000 to 18 000 BP. Opinions differ about the course of sea level rise following the Last Glacial Maximum. Generally there appears to have been an initial rapid rise, but the rate apparently decreased with time. The present sea level was reached at approximately 5 000 BP (Tankard 1976). According to Fairbridge (1961) sea levels oscillated after 5 000 BP with maxima exceeding the present level with 3–5 m.

The geographical distribution of the three morphotypes of *Cordylus cordylus* identified by Mouton (1987) in the south-western Cape, is depicted in Figure 1. The coastal melanistic form occurs only in insular and peninsular situations along the south-western coast, i.e. on the Cape Peninsula, the Saldanha–Langebaan area and on Jutten Island. The montane melanistic form, on the other hand, occurs at isolated localities at relatively high altitudes along the extreme western borders of the western section of the Cape Fold Mountains. The typical form occurs mainly along the coastal lowlands, but populations of this form are also to be found on Robben Island (Figure 1, Locality 21) and at relatively high altitudes in the Cape Fold Mountains (Figure 1, Localities 33 & 46). This form also has a wide distribution outside the south-western Cape, mainly along the southern coastal regions of South Africa, but also reaching further inland in the eastern Cape as far as the southern Orange Free State (Figure 3).

Apart from colouration the two melanistic morphotypes have a few, seemingly non-adaptive character states in common. There are 10 longitudinal rows of ventral scales, a subocular scale reaching the lip, and separated prefrontal scales (Mouton 1987). In the typical form, however, 12 longitudinal rows of ventral scales occur, the median subocular scale does not reach the lip and the prefrontal scales are in contact (Mouton 1987). A contact zone between the coastal melanistic and typical forms has been identified at Jacobs Bay, immediately to the north of Saldanha Bay (Figure 1) (Mouton 1987). A similar contact zone on the northern slopes of Table Mountain has been described by Loveridge (1944). A few populations with intermediate character suites have also been identified in the study area (Mouton 1987) (Localities 11, 24, 27, 30, 45; Figure 1). Invariably these populations are located in close proximity to present melanistic populations.

To explain the isolated melanistic *Cordylus cordylus* populations in the south-western Cape the following hypotheses are considered:

(i) The ecological hypothesis: The observed pattern of morphological variation in *Cordylus cordylus* (Mouton 1987) may be a manifestation of present gradients in the physical environment over the study-area. The distribution of the melanistic *C. cordylus* populations in the south-western Cape does not correlate with vegetation type, substrate type or rainfall patterns but does correlate with temperature patterns (Mouton 1986a). Strong selective pressures in terms of thermoregulation may be operative in insular and peninsular situations (Mertens 1934; Carlquist 1965) and at high altitudes (Fuggle 1981) and melanism may be a response to these cooler environments. The thermoregulatory advantages of melanism in cool environments have been pointed out by several workers in the past (Atsatt 1939; Cole 1943; Fitch; 1955; Bartlett & Gates 1967; Norris 1967; Gibson & Falls 1979).

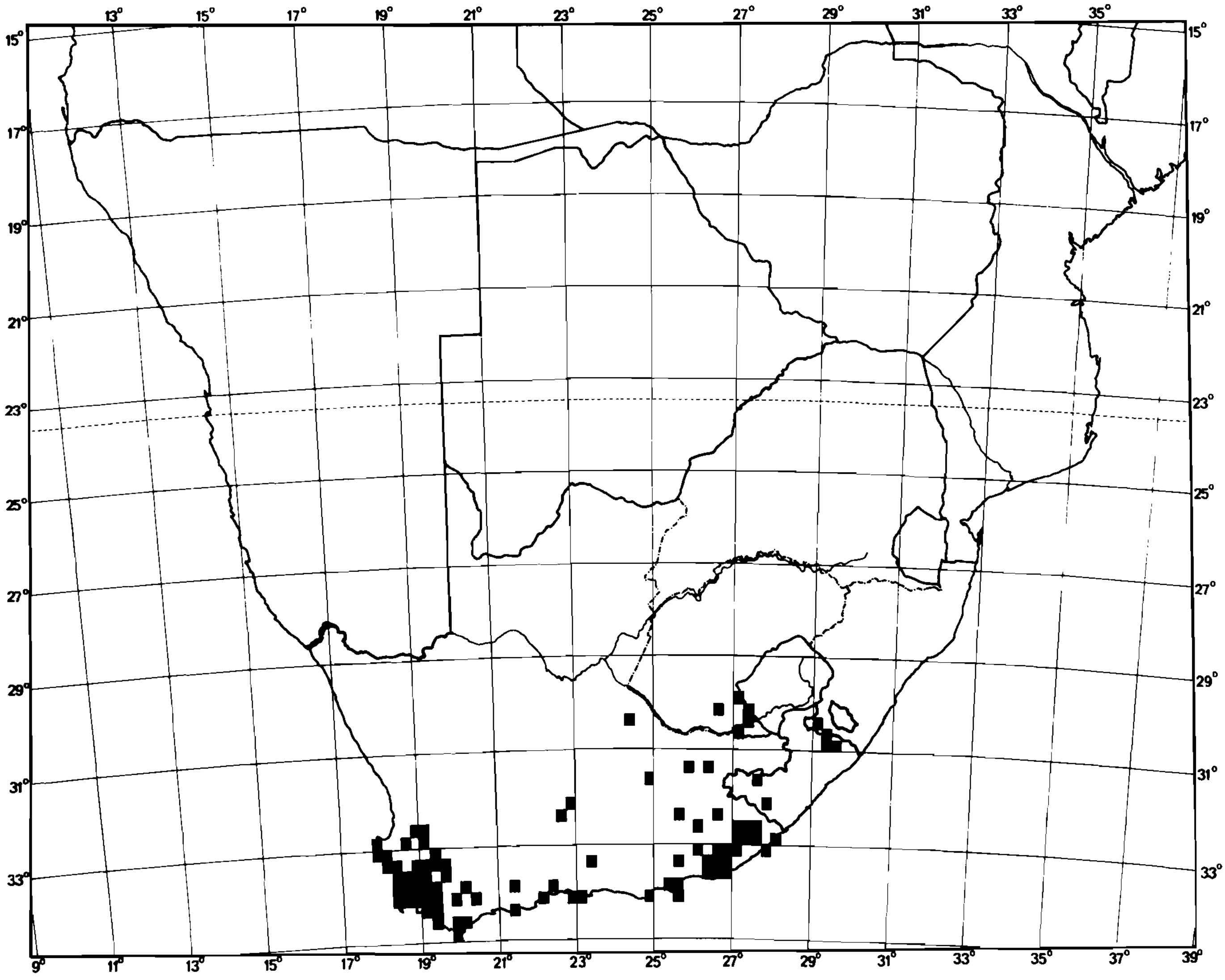

Figure 3 The distribution of the typical form of *C. cordylus* in southern Africa (distributional records obtained from the literature).

We, however, have serious doubts as to whether the observed patterns of morphological variation can be explained in terms of present environmental conditions only. Firstly, certain anomalies occur as far as the distribution of the non-melanistic morphotype is concerned. A population displaying all the features characteristic of the typical non-melanistic form is present on Robben Island. As this island is small (only ± 10 km^2) it should represent a similar thermal regime as the Cape, Saldanha and Langebaan peninsulas and Jutten Island where the coastal melanistic form occurs. However, none of the features, characteristic of the coastal melanistic populations, are present in the Robben Island population. Similarly, populations of the typical form are to be found in the Cape Fold Mountains at even higher altitudes than some of the populations of the montane melanistic form, for example at Du Toitskloof (Figure 1, Locality 46) and in the Riviersonderend Mountains (Figure 1, Locality 33). These populations are, however, not even darkly coloured and display none of the other features characteristic of the melanistic populations.

Secondly, if the observed morphological variation is in direct response to present gradients in the physical environment, it bears the implication that the whole set of morphological characters that vary together geographically, are individually determined by the same set of environmental pressures, or else are under the same epigenetic control. The latter argument can not be the case as in the intermediate populations (Mouton 1987) these characters are not linked. Although not entirely impossible it seems highly unlikely that 10 rows of ventral scales, a median subocular reaching the lip, and separated prefrontals evolved in response to thermal pressures. Even if all these character states are in response to environmental pressures, it is hard to believe that they can be governed by the same environmental pressures, causing them to vary together geographically.

In conclusion, therefore, we are of the opinion that the observed pattern of geographic character variation in *Cordylus cordylus* in the south-western Cape can not be adequately explained in terms of present environmental factors only.

(ii) The vicariance hypothesis: If the number of longitudinal rows of ventral scales, whether the median subocular scale does or does not reach the lip and whether or not the prefrontal scales are separated, are taken as non-adaptive traits, the particular character states must have originated through genetic drift. Accordingly these characters can be considered good indicators of taxonomic relationships (Endler 1982), implying that the two coastal melanistic populations on the one hand, and the five montane melanistic populations on the other hand, are sister populations respectively.

The possibility that the isolated melanistic populations simply originated by the accidental transport of individuals from one locality to the other might seem feasible in the case of the coastal melanistic populations, but must be rejected on several grounds. Firstly, the distinct pattern of distribution of the melanistic populations in the south-western Cape, in insular and peninsular situations along the coast and at relatively high altitudes along the extreme western borders of the Cape Fold Mountains, certainly does not support transportation as a vicariance mechanism. Secondly, at both the Cape Peninsula and Saldanha Bay, contact zones between the melanistic and typical forms have been identified (Loveridge 1944; Mouton 1987), implying that if melanistic individuals have been imported, by man or by sea, from either locality to the other, the imported melanistic individuals would probably have had to replace the typical form. This must be considered highly unlikely, as there are definite signs of hybridization between the two forms at these contact zones and any melanistic newcomers to either locality would have been genetically swamped by the typical form.

We therefore propose that the present pattern of distribution of melanistic populations along the south-western coast and along the western section of the Cape Fold Mountains resulted from the fragmentation of two melanistic populations, originally occurring at least from the Cape Peninsula to the Saldanha Bay area and from Landdroskop in the Hottentots Holland Mountains all along the western section of the Cape Fold Mountains to the Piketberg Mountains in the north. By implication the typical form, during or after fragmentation of the melanistic populations, must have dispersed into the coastal areas between the Cape Peninsula and Saldanha Bay and reached destinations at higher altitudes along the Cape Fold Mountains. Indeed, the zone of secondary intergradation between the melanistic and typical forms at Jacobs Bay (Figure 1, Locality 7) indicates that one of the three forms only recently arrived in the area thus coming into contact with the other forms.

During the proposed contraction and fragmentation of the two formerly large, continuous, melanistic populations it is to be expected that apart from the two coastal and five montane melanistic populations others could have prevailed, for some time at least, in suitable habitats along the coast or the Cape Fold Mountains. Since the typical and coastal melanistic forms, and probably the typical and montane melanistic forms as well, are able to interbreed, as is illustrated at Jacobs Bay, the melanistic populations not effectively isolated in peninsular and insular situations along the coast or at suitable altitudes along the mountains, could have been genetically swamped by interbreeding with the inmoving typical form. This would explain the occurrence of several populations showing characteristics of both coastal melanistic and typical forms and montane melanistic and typical forms, respectively (Mouton 1987) (at Localities 11, 24, 30 and 31; Figure 1). The overlap in certain characters, which hampered the delimitation of *C.c. cordylus* (= typical form) and *C.c. niger* (= coastal melanistic form) by previous investigators, most probably is the result of such former areas of interbreeding.

The degree of morphological similarity, the intermediate populations, as well as the zones of secondary intergradation described by Mouton (1987), are interpreted as indicating that interbreeding between the three forms is possible and that they are therefore closely related. Establishing the sequence of vicariant events through which the three forms originated, requires careful consideration of intraspecific relationships. The two forms sharing the most synapomorphies must have originated through the most recent vicariant event, while a preceding event must have given rise to the ancestor of these two forms and to the third form (Eldridge & Cracraft 1980). The two melanistic forms share more attributes with each other than with the typical form. Because of a total lack of information on intrageneric relationships it is not possible at this stage to determine through outgroup comparison whether the shared character states present synapomorphies or symplesiomorphies. It is, however, our contention that the geographical distribution of the two melanistic forms, i.e. restricted distributions in close proximity in the south-western Cape, indicates that these two forms are indeed sister forms.

We propose that an ancestral population, occurring from the south-western coastal regions eastwards over the mountains and some distance along the southern coast and also towards the interior, was divided by a vicariant event into an eastern population from which the typical form evolved, and a western population from which the two melanistic forms evolved. By a subsequent vicariant event the western population was split up to give rise to the two extant melanistic forms, which later were fragmented into the few isolated populations by contraction. The eastern typical form at this stage underwent a drastic range expansion and finally reached the south-western coastal lowlands, thereby geographically separating the two melanistic forms. During this range expansion several small, remaining melanistic populations were engulfed by the typical form, resulting in populations with intermediate character suites. Furthermore, zones of secondary contact, where hybridization is presently taking place, were inevitably formed between some of the remaining melanistic populations and the typical form, indicating that the process of assimilation is still in progress. The remaining coastal melanistic populations were probably for some time effectively isolated by their peninsular habitats and the resultant narrow potential contact zones. The melanistic populations are also thought to have selective advantages in terms of thermoregulation which hamper the process of assimilation. The montane melanistic populations, adapted to the relatively cold conditions at higher altitudes, are likewise isolated to a certain extent from the ingressing typical form.

Although the information at hand suggests a contraction of formerly large, melanistic populations, and an almost simultaneous expansion in the range of the typical form, no reference has so far been made to possible causal factors. In this regard the occurrence of melanism itself may be highly informative. Although melanism in the study-area can to a degree be correlated with current environmental conditions, it also ties in with a whole set of non-adaptive characters. This is interpreted as indicating that the acquisition of the characters, including melanism, predates the vicariant event which split up the western ancestral population into the two melanistic forms. In view of its significance in thermoregulation, the association of melanism in reptiles with cold environments (Carlquist 1965; Norris 1967), and the present day relatively cold habitats of the melanistic populations found in the study area, we assume that *C. cordylus* acquired its melanism during a very cold period. As a rule, colouration in lizards is subjected to strong environmental pressures (Porter 1972; Endler 1978). Relatively quick changes in colouration may result from a change in climate. It is therefore highly unlikely that the melanism under discussion evolved in the very distant past. We therefore assume that the observed melanism evolved during the last major cold period and not prior to that.

We propose that prior to the advance of the Last Glacial Maximum at 40 000 BP or even earlier, an ancestral non-melanistic population occupied the south-western Cape. This form occurred from the western coastal regions over the Cape Fold Mountains, extending some distance to the east along the southern coast and into the interior (Figure 4, Stage 1). This form was adapted to the relatively warm environment of that time. With the onset of cooler conditions after 40 000 BP, conditions along the coast and the Cape Fold Mountains in particular, soon became too harsh for populations of the warm-adapted ancestral form. This form eventually became extinct in these two 'inhospitable' zones and the former range of the ancestral form was accordingly split into two. A population persisted in the relatively warmer coastal lowlands west of the Cape Fold Mountains, with a second population persisting in the warmer interior areas or southern coastal areas east of the Cape Fold Mountains (Figure 4, Stage 2).

We are of the opinion that during the last glacial period the influence of the cold Benguela Current on the climate of the south-western coastal regions was more pronounced than at present. With the lowering of the sea level and resultant exposure of the continental shelve during the glacial period (Tankard 1976), the Benguela Current and upwelling system would in effect have been located nearer to the coastline and would have had a greater stabilizing influence on the coastal temperatures. The incidence of fog might also have been much greater than at present. We agree with the general opinion that the climates would have been much drier than at present (Deacon 1983a), but predict that limited sunshine hours were experienced along the south-western coastal regions, because of a high incidence of fog and low stratus clouds. In the interior and eastern parts of southern Africa, however, much less adverse climatic conditions would have been in effect.

As the climate progressively deteriorated the western coastal population came under more severe pressure than the eastern population and underwent further contraction. At a certain stage the gene pool of this population became small enough to ensure the rapid spread of favourable morphological adaptations,

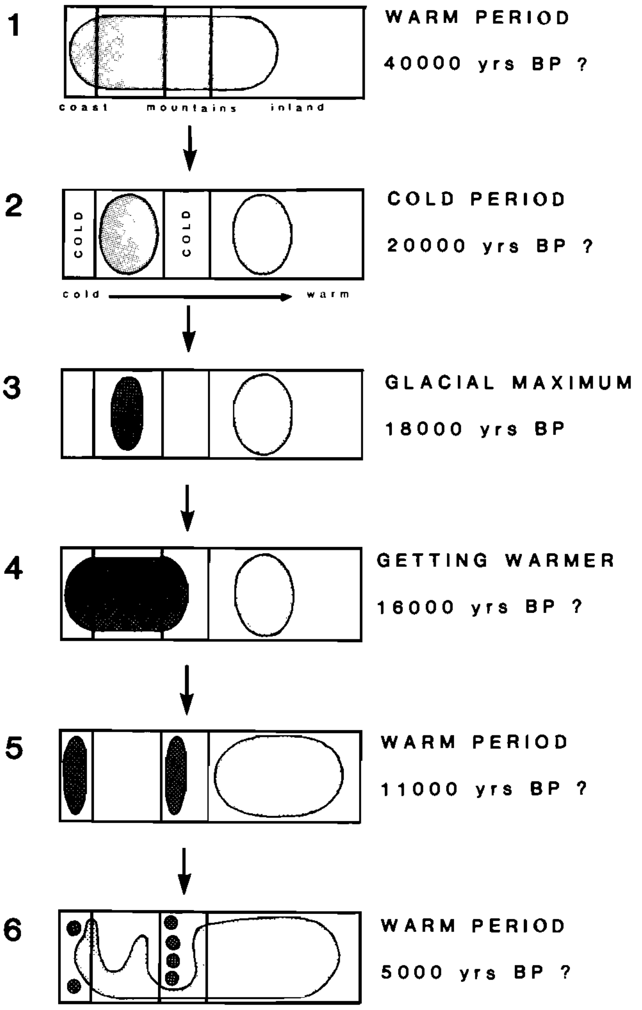

Figure 4 Proposed stages in the evolution of the three phenotypic forms of *C. cordylus.*

induced through selection by strong environmental pressures on the perifery of the population, throughout the entire population. With the onset of the Last Glacial Maximum 18 000 to 16 000 BP, melanism had evolved in the coastal lowland population (Figure 4, Stage 3). Conversely, the population east of the Cape Fold Mountains, not being subjected to such harsh climatic conditions in their refuge area, experienced no comparable selection pressures. One of or both the western and eastern populations apparently acquired certain derived character states through genetic drift in small gene pools.

This proposed sequence of events is in agreement with the notions of Vrba (1985) that evolution is normally conservative and that evolutionary change does not take place unless forced by changes in the physical environment and, furthermore, that environmental pressures are only rarely strong enough that not only contraction of range but also evolutionary change or extinction results. In the case of the western population the threshold of organism–environment interaction was exceeded which left the option of adaptive change or extinction. In the case of the eastern population environmental stimulus was only strong enough to induce contraction of range but not evolutionary change.

We propose that at the onset of the amelioration of the climate following the Glacial Maximum, at 16 000 BP, a rapid expansion in the range of the now cold-adapted population west of the Cape Fold Mountains took place and this form invaded the zone along the coast and also occupied the Cape Fold Mountains (Figure 4, Stage 4). During the early phases of amelioration of the climate the warm-adapted, inland population experienced at most only a slight range extension.

The rapid amelioration of the climate after 16 000 BP soon rendered the coastal lowlands, its former refuge area, too warm for the now cold-adapted melanistic form. Consequently this form gradually disappeared from its former sanctuary area with the result that the range of the melanistic form was split in two. A melanistic population along the cooler south-western coast thus prevailed, whilst a second population prevailed along the relatively cool western section of the Cape Fold Mountains (Figure 4, Stage 5). According to the Effective Temperature map of Stuckenberg (1969) (Figure 3), the greater part of the western coastal lowlands in the study area falls within the 15–16°C ET range wheras the Cape Fold Mountains and a narrow strip along the south-western coast fall within the 14–15°C ET range. The 15–16°C ET strip interposed in the 14–15°C ET range corresponds with the gap between the coastal and montane melanistic forms. It is our contention that the establishment of the higher temperatures along the inland coastal lowlands since 14 000 – 12 000 years BP (Deacon 1983a) caused the vicariance of the ancestral melanistic population. With the further amelioration of the climate the warm-adapted inland population now rapidly expanded its range. This expansion, slow at first, soon gained momentum as, with an increase in temperature, more and more suitable habitats became available (Figure 4, Stage 5). Our notions conform to the ideas of Vrba (1985) that if the habitat of a species expands or shifts, then so does the distribution range of that species.

The very low sea level during the Last Glacial Maximum, in the order of – 130 m (Tankard 1976), and the rapid rise following the glacial maximum, must have had a pronounced impact on the range of the coastal melanistic form. At the height of the glacial maximum the coastline ran some distance seaward from the present and peninsulas and islands along the south-western coast would have been part of the mainland. The marine regression and cooler climate expanded the habitable area of the coastal form considerably. The rapid transgression caused by the global amelioration of the climate after 16 000 years BP, however, again diminished the coastal habitat, while the hotter zone between the coast and the mountains also expanded. The coastal melanistic form therefore was literally caught between, what for them was an expanding devillishly hot climate and a transgressing deep blue sea. Being highly rupicolous and thus unable to cross sandy barriers, it is not hard to imagine that many populations of the retreating coastal form succumbed to the transgression of the sea. This could in fact explain the absence of melanistic populations along the coastal stretch from the Cape Peninsula to the Saldanha–Langebaan area.

The comparatively high mountains in the Cape Peninsula would have offered a suitable 'inland' refuge to the coastal melanistic form in a rapidly changing climate. Although the hills in the Saldanha–Langebaan area are much lower than the Cape Peninsula mountains, they likewise offered a suitable retreat. The vital importance of the refuge areas is thought to have increased as the sea transgressed. The climate in these refuge areas probably remained cool as the areas were transformed into peninsulas and islands. The present melanistic populations in the Cape Peninsula and Saldanha–Langebaan area are accordingly viewed as the last survivors of a former continuous population along the south-western coast (Figure 4, Stage 6) .

The absence of melanistic populations on Dassen Island and Robben Island, which at present seemingly form suitable habitats for melanistic populations, can satisfactorily be explained in terms of the above-mentioned arguments. Both islands are at present only a few metres above sea level. Prior to becoming islands these areas probably either did not offer suitable refuges to the coastal melanistic form during the rapid amelioration of the climate or the populations succumbed to the joint effect of the marine transgression and the rapidly changing climate.

To date, the typical form has not been reported from the Cape Peninsula proper (Loveridge 1944; Visser 1971). The presence of the typical form on Robben Island today, however, suggests that it advanced this far before Robben Island was cut off from the mainland. Although the effective contact zone between the melanistic Cape Peninsula population and the ingressing typical form at that time must have been much broader than at present, it is believed that the sandy Cape Flats acted and still act as an effective barrier, preventing the typical form from reaching the Cape Peninsula. It is postulated that the ingressing typical form followed a route along the lower slopes of the mountain ranges, across the hilly area north of the Cape Flats, to reach the west coast and Robben Island (Figure 5).

The melanistic populations in the Saldanha– Langebaan area, because of a lack in altitude, we suggest were less well buffered by a better thermoregulatory ability and thus much more prone to swamping than the Cape Peninsula population. The fact that they prevailed in the Saldanha–Langebaan area suggests to us that the typical form only recently reached this far and only at a stage when the formation of the present peninsulas and islands was completed. The shortening of the effective zones of contact between the melanistic and typical forms by marine transgression, as well as the possible small selective advantage the melanistic form has in the peninsular and insular areas, may be slowing down the process of assimilation by the typical form. Indeed, the absence of the typical form on Dassen Island and the islands in the Saldanha Bay area indicates that these islands originated prior to the arrival of the northward dispersing typical form in the area. The typical form in our opinion, reached the Saldanha–Langebaan area at some stage later than 5 000 BP, the time at which present sea level was reached (Tankard 1976).

The present day intermediate population at the Gansbaai peninsular area suggests that a melanistic population survived here for some time. The Gansbaai peninsular area lacks the altitude of the Cape Peninsula and the neighbouring cold Benguela Current of the Saldanha–Langebaan area. Furthermore, it is not as effectively isolated from the hinterland by sandy stretches as the Cape Peninsula and the Langebaan areas. The lack of those features that we consider to be key factors in the survival of the melanistic Cape Peninsula and Saldanha–Langebaan population made the Gansbaai area an easy target for the expanding typical form. Interbreeding on a large scale would eventually have produced the populations showing the mixture of characters we find at Gansbaai today.

Concordant patterns in other species

Our proposed model for the evolution of the three morphotypes of *C. cordylus* calls for a quotation from Cracraft (1982, p.413): 'We must estimate to what extent the genealogical relationships of the taxa under study, as translated in space, are concordant with the patterns of other taxa distributed in the same areas. Only in this way can we discover whether our taxa are part of a more generalized pattern of speciation or whether the history of this isolated group is largely unique and not explainable by the causes of some more general pattern'. According to the turnover–pulse hypothesis of Vrba (1985) diverse groups of animals will react in synchrony to changes in the physical environment. Although internal factors contribute to the nature and probability of speciations, external geographic factors determine the spatial distribution of turnover events during a pulse. In other words, closely related species with similar ecological requirements, i.e. where the internal factors are more or less similar, and occurring in the same geographical area, should respond in a similar fashion to changes in the physical environment. One way of testing our proposed model for intraspecific evolution in *C. cordylus*, therefore, is to look for concordant patterns in other closely related species in the south-western Cape.

Mouton (1986b) has already established that there is a high incidence of melanistic cordylid populations along the south-western coastal regions, corroborating our idea that climatic conditions along the south-western coastal regions were probably more adverse than in inland or southern coastal areas during the Last Glacial Maximum. Furthermore, the melanistic cordylid populations occur without exception as isolated populations either along the coast or at higher altitudes along the mountain ranges. This suggests the contraction of former larger melanistic populations.

In the study area there is a high degree of concordancy in the geographical occurrence of melanistic populations of different species. In the Saldanha–Langebaan area the areal extent of a melanistic *C. polyzonus polyzonus* population coincides almost exactly with that of the melanistic *C. cordylus* population, while along the Cape Fold Mountains the distribution of *Pseudocordylus capensis capensis* practically coincides with that of the montane melanistic populations of *C. cordylus.*

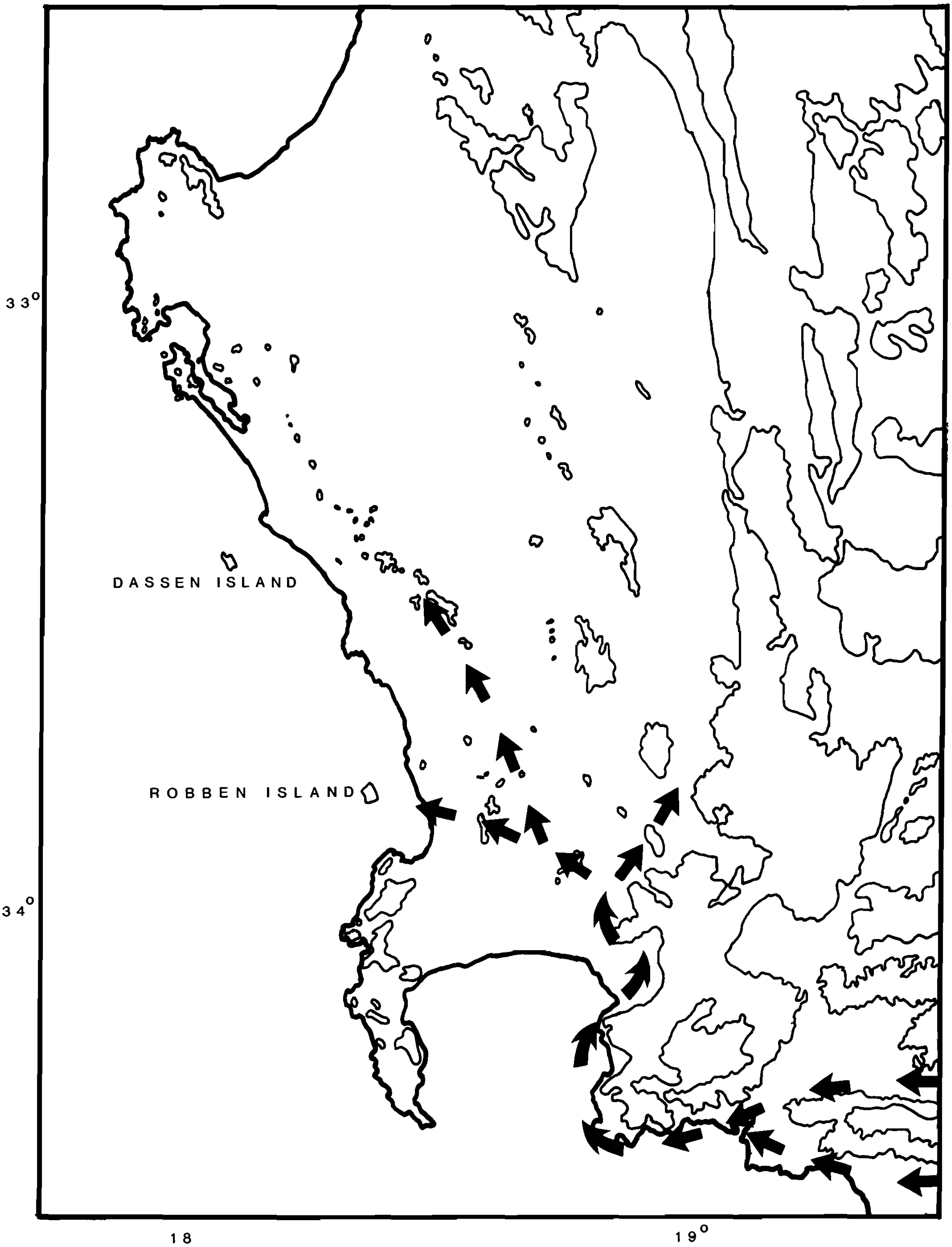

Figure 5 Proposed immigration route of the typical form of *C. cordylus* into the western coastal lowlands.

Preliminary results from our collections of *C. polyzonus polyzonus* indicate that several morphotypes of this species occur. In the Saldanha Bay area three forms, which seem to be different morphotypes of this species, meet. Brownish and turquoise forms occur over vast inland areas in the Cape Province, but only a few melanistic populations occur along the west coast, from Saldanha Bay in the south to the Orange River in the north. The observed pattern of distribution of the colour variants of this species could be interpreted as indicating that a large melanistic population along the western coast contracted, while inland brown and turquoise colour variants expanded their range. A thorough analysis of geographic character variation among all populations of this species in the western part of the Cape Province is, however, needed as the final test of this hypothesis. The collection of the necessary data is now in progress and the analysis is in preparation.

Pseudocordylus capensis capensis occurs at isolated localities along the Cape Fold Mountains as far north as Pakhuis Pass near Clanwilliam (Mouton 1986a). In fact, Branch (1981) considers the population at Pakhuis Pass to be intermediate between *P.c. robertsi,* occurring near van Rhynsdorp, and *P.c. capensis.* This pattern of geographical variation in the morphology in this melanistic species along the western section of the Cape Fold Moutains, might be interpreted as indicating that a cold-adapted ancestral form, during the last glacial period, ranged as far north as the Gifbergen near Van Rhynsdorp. The subsequent amelioration of climates would have led to fragmentation of the range, isolating populations. Again more information is needed to test this hypothesis.

In summary, therefore, concordant patterns of geographic variation in morphology can be observed in other cordylid species. These species are closely related to *C. cordylus* and have similar habitats. Furthermore, these patterns seem to underscore the hypothesis that melanism in *C. cordylus* evolved during the Last Glacial, and that the rapid amelioration of climates following the Last Glacial Maximum, led to the contraction of cold-adapted melanistic populations and paved the way for expansion of warm-adapted, non-melanistic, inland populations.

Studies done at our laboratories have indicated that the melanistic forms of *C. cordylus* display, except for melanism, several other physiological traits which might be interpreted as adaptations to cooler environments where limited sunshine prevails. The results (to be published elsewhere) underscore our hypothesis that the melanistic forms represent relict cold-adapted forms.

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