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Phenotypic variation among populations of *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape Province, South Africa

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In order to elucidate the taxonomic status of the melanistic, girdled lizard, *Cordylus cordylus niger*, occurring in the Cape Peninsula and the Saldanha Bay area, South Africa, character variation among populations of the *C. cordylus* complex in the section of the Cape Province south of 32°30′ latitude and west of 19°30′ longitude was analysed. Variation for 92 external morphological characters at 54 localities was determined. Distinct patterns of interlocality variation were observed in only eight characters, but interestingly, these patterns were concordant in all eight cases. The observed patterns are interpreted as indicating that three phenotypic forms of the nominate species occur in the south-western Cape, namely a coastal melanistic form (= *C. c. niger*), occurring in insular and peninsular situations along the coast; a montane melanistic form occurring at relatively high altitudes along the western section of the Cape Fold Mountains; and the typical form (= *C. c. cordylus*), occurring commonly along the coastal lowlands, but also further inland at some places.

Ten einde die taksonomiese status van die swart gordelakkedis, *Cordylus cordylus niger*, wat in die Kaapse Skiereiland en die Saldanhabaai-omgewing voorkom, op te klaar, is eienskapvariasie tussen bevolkings van die *Cordylus cordylus*-kompleks in die deel van die Kaapprovinsie suid van 32°30′ breedtegraad en wes van 19°30′ lengtegraad ondersoek. Variasie in 92 uitwendige morfologiese kenmerke tussen 54 lokaliteite is bepaal. Duidelike patrone van interlokaliteit-variasie is slegs in agt eienskappe waargeneem, maar opvallend is die feit dat die patrone in al agt gevalle ooreenstem. Die resultate word vertolk as aanwysend dat drie fenotipiese vorme van *Cordylus cordylus* in die suidwes-Kaap voorkom, naamlik 'n kus-melanistiese vorm in skiereiland- en eiland-situasies langs die suidwes-kus; 'n berg-melanistiese vorm teen relatiewe hoë hoogtes langs die westelike deel van die Kaapse Vouberge; en die tipiese vorm wat algemeen voorkom in die kuslaaglande, maar ook hier en daar in die binneland aangetref word.

The taxonomy of the common Cape girdled lizard, *Cordylus cordylus*, is at present considered one of the most pressing herpetological problems in southern Africa (Broadley 1971; Branch 1981). Loveridge (1944), Wermuth (1968), and Welch (1982) list 10 races of *C. cordylus*, but other authors regard many of these as distinct species, albeit without detailed motivation (FitzSimons 1943; Broadley 1971; Visser 1971; Branch 1981). In the Cape Province five races, i.e. *C. c. cordylus, C. c. niger, C. c. minor, C. c. lawrenci* and *C. c. tasmani*, are recognized (Loveridge 1944; Wermuth 1968; Welch 1982). Although the taxonomic status of all of these is uncertain, Branch (1981, p.161) states: 'The most obvious and pressing problem remains the status of the small, melanistic, rugose *niger*'.

Since the early 1700's two distinct forms of *C. cordylus* were recognized in the south-western Cape. These are the above-mentioned melanistic form, *C. c. niger*, at that time only known from the Cape Peninsula, and a form of varying colour, *C. c. cordylus*, occurring widely along the southern coastal regions of the Cape Province. The melanistic form was initially considered to be a distinct species (Seba 1735; Cuvier 1829), but subsequent workers (Rose 1926; Essex 1927; Power 1930; Loveridge 1944) saw it as a race of the non-melanistic *C. c. cordylus*. Power (1930) and Loveridge (1944) distinguished *C. c. niger* from *C. c. cordylus*, not only on colour, but also on several other characters. According to these workers, in *C. c. niger*, 10 longitudinal rows of ventral scales occur, the median subocular reaches the lip, the head shields are smooth, the occipitals rectangular and smooth, and the vertebral series of dorsal scales strongly keeled. In *C. c. cordylus*, on the other hand, the median subocular does not reach the lip, 12 longitudinal rows of ventral scales occur, the head shields are rugose, the occipitals are irregular in form and rugose, and the vertebral series of dorsal scales smooth. It was also believed that the melanistic form is smaller in body size than the typical form (Loveridge 1944; Branch 1981).

FitzSimons (1943), however, treated the black form as a colour variant of the typical form. He based his decision on the fact that an overlap in most of the characters described by Power (1930) and Loveridge (1944) occurs and because isolated black specimens occur throughout the range of *C. c. cordylus*. Visser (1971) pointed out the similarities between *C. c. niger* and *C. peersi*, another melanistic form occurring in Little Namaqualand. He suggested that *C. c. niger*, although close to *C. c. cordylus*, might prove to be a subspecies of *C. peersi*. Branch (1981) recognizes the status of the two forms as problematic but opted to follow FitzSimons in regarding the black form a colour variant of the typical form.

C. c. niger was originally known only from the Cape Peninsula but was later also found in the Saldanha Bay area and on Jutten Island (FitzSimons 1943). Mouton (1985, 1986) subsequently pointed out several other melanistic *C. cordylus* populations along the western section of the Cape Fold Mountains. A preliminary analysis indicated that these populations show similarities to the coastal melanistic populations although they are not identical. A new genus and species, *Calyptoprymnus verecundus*, described by De Vis (1905) on a single specimen, presumably from the Solomon Islands, was shown by Moody (1977) to be a *synonym* of *C. cordylus niger*. Moody recognized *C. c. niger* as a South African endemic.

To date, investigations regarding the taxonomic status of *C. c. niger* have been primarily concerned with establishing morphological differences between the melanistic and non-melanistic populations. As *C. c. niger* and *C. c. cordylus* were reported to be sympatric on the Cape Peninsula (Loveridge 1944) and occur in such close proximity elsewhere, past workers have been inclined to view these two as conspecific, which discouraged detailed investigation of their relationships

up to now. No attempt, for example, has been made to establish geographical patterns of phenotypic variation and to study the processes responsible for these observed patterns.

According to Vuilleumier (1980) and Cracraft (1982) any taxonomic analysis should ultimately be a speciation analysis. They recognize the following main stages in any such analysis (Cracraft 1982, p.412).

(i) 'The geographical distribution of the forms studied is determined.

(ii) Phenotypic variation, the structure of any clines and zones of secondary contact are determined and any hibridization occurring described.

(iii) The degree to which the genealogical relationships of the forms studied coincide in space with patterns of other taxa occurring in the same area is determined.

(iv) Literature on present ecological characteristics is studied and augmented by fieldwork. Literature on Plio-Pleistocene palynology, palaeoclimatology and palaeogeography is studied to get an idea of times of isolation, forming of barriers, and of secondary contact.

(v) A synthesis of all the data is made in a descriptive scenario according to present ideas on speciation.'

An intensive analysis, based on the above-mentioned methodology, has been carried out to determine the taxonomic status of *C. c. niger*. Observed distribution patterns as well as patterns of phenotypic variation among populations of *C. cordylus* in the south-western Cape are reported on here. In subsequent reports possible causal factors of the observed patterns will be discussed. This conforms with the principles of Eldridge & Cracraft (1980, p.4) that: 'Initially the study of pattern must be divorced as much as possible from the study of process, to provide an unbiased baseline for the evaluation of alternative hypotheses about process.'

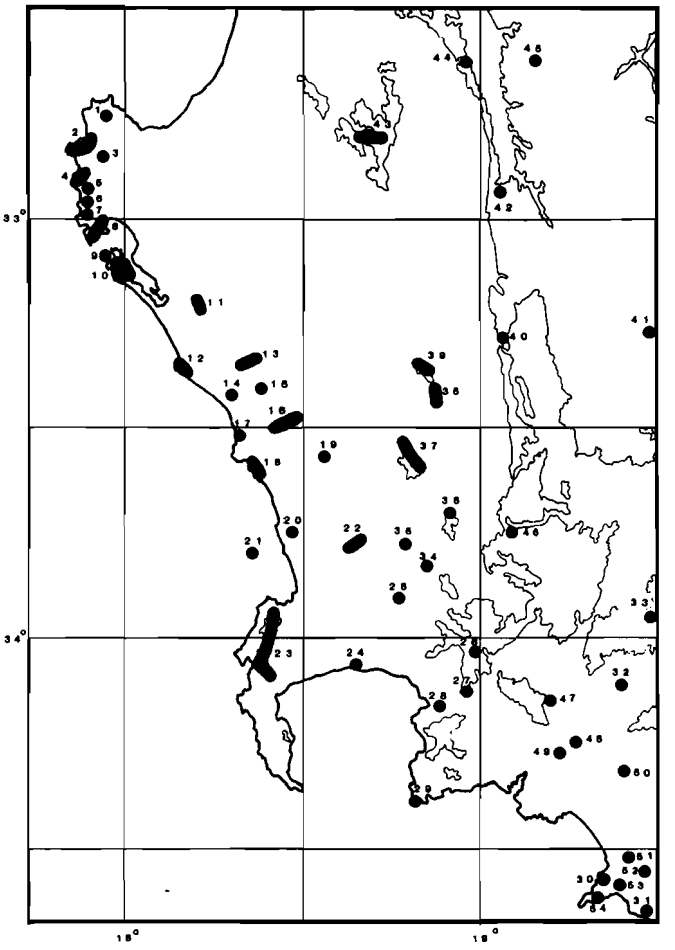

Figure 1 Localities and compound localities in the study area at which *C. cordylus* occurs.

Materials and Methods

Study area and sample localities

The section of the Cape Province south of 32°30′ latitude and west of 19°30′ longitude, including all the islands along the west coast, were surveyed (Figure 1). Along the coastal lowlands almost every isolated hill or rocky outcrop was investigated, but along the Cape Fold Mountains only readily accessible localities were visited.

In the analysis of geographic character variation it is important to obtain enough specimens from a representative number of localities to ensure that local variations are accounted for (Thorpe 1976). In the present study sufficient localities were sampled but too few specimens were obtained from some of them. As was suggested by Sokal (1965) this problem was amended by the pooling of localities after a preliminary investigation of character variation was done. It is believed that pooling in this case can be justified by the fact that the localities included in a compound locality are geographically close to each other in a seemingly unchanging environment so that gene flow can occur freely between them. Even by pooling localities a desired minimum number of six individuals was not obtained in a few cases. Any inaccuracy, because of small sample sizes will, however, be counteracted by the fact that a large number of localities were sampled in a relatively small study area.

Characters investigated

Variation in 92 external morphological characters was examined (Appendix 1). These included 50 qualitative, 22 meristic, and 20 mensural characters. Those characters in which distinct patterns of geographic variation were observed, are reported on here. Results obtained for other characters are available from the author. Variation in the following characters is discussed.

Colour

For the purposes of the present study individuals were considered either melanistic or non-melanistic in colour. Differentiation was clear-cut and there was no need for special apparatus or methods to categorize individuals.

Subocular state

Specimens were classified on whether the median subocular scale reached the lip or not (Figure 2). The frequency of occurrence of a median subocular reaching the lip (hereafter referred to as the MSr state) at each locality, was expressed as a percentage of the total sample size. To account for intra-specimen variation the right and left sides of the specimen were treated separately. The number of recorded cases is therefore double the number of specimens investigated.

Prefrontal state

The two prefrontal scales were classified as either in contact mesially or separated by a suture of the frontonasal and the frontal (Figure 3). The frequency of occurrence of the separated state (hereafter referred to as the Ps state) was determined for each sample locality and was expressed as a percentage of the sample size.

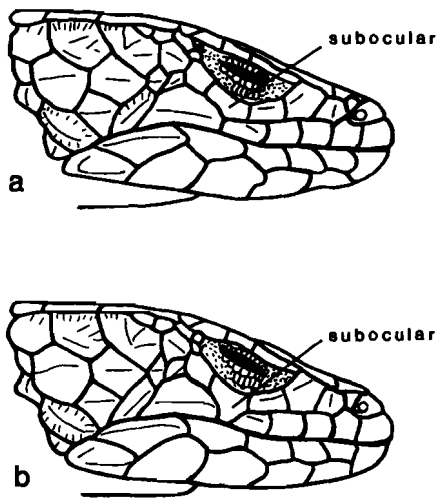

Figure 2 Lateral view of the head of *C. cordylus* showing the median subocular (a) not reaching the lip, and (b) reaching the lip.

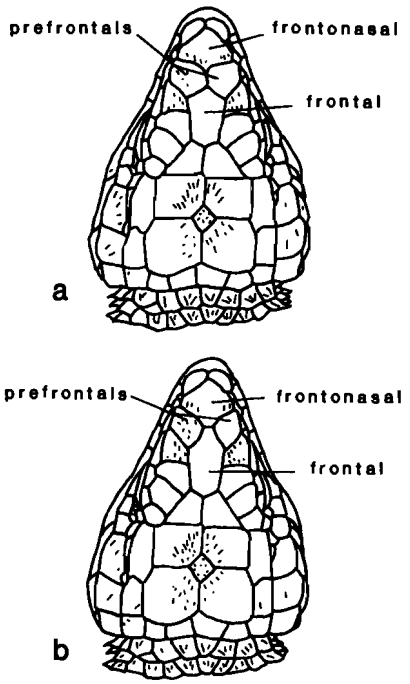

Figure 3 Dorsal view of the head of *C. cordylus* showing the prefrontal scales (a) in contact and (b) separated.

Longitudinal rows of ventrals

In specimens from the study area the number of longitudinal rows of ventral scales, counted midway across the ventrum between fore and hind limbs, was either 10 or 12. The frequency of occurrence of 10 rows of ventrals (hereafter referred to as the V10 state) was determined for each of the sample localities and was expressed as a percentage of the sample size.

Texture of dorsal head shields

The posterior part of the head, including the anterior parietals, the interparietal, and the posterior parietals, was considered separately from the anterior part of the head. The following character state combinations were considered:

Anterior, as well as posterior scales smooth.
Anterior scales smooth, posterior scales rugose.
Anterior scales slightly rugose, posterior scales rugose.
Anterior as well as posterior scales rugose.

The frequency of occurrence of each character state combination was determined for each sample locality and was expressed as a percentage of the sample size.

Occipital shields

The shape, texture and spinosity of the occipital shields were determined. Three character state combinations were recognized:

Occipitals quadrangular to rectangular, smooth and non-spinose.
Occipitals quadrangular to rectangular, rugose and/or spinose.
Occipitals irregular in form, rugose and/or spinose.

The frequency of occurrence of each of the character state combinations was determined for each locality.

Number of femoral pores

Since the right and left pore counts often differ, total counts were used. Mean total pore counts, standard deviation and range were determined for all the sample localities.

Snout-vent length

Snout-vent length was measured from the tip of the snout to the vent. The mean, standard deviation and range were determined for all sample localities.

Results and discussion

The localities and compound localities from which *C. cordylus* were collected in the study area are shown in Figure 1 and listed in Appendix 2. The localities are numbered from 1 – 54 and will be referred to by these numbers throughout. Sample sizes are given in Table 1. To see the distribution of *C. cordylus* in the study area in perspective, Figure 1 should be compared with Figure 4, which gives the total number of localities visited. The uncollected area in the north-eastern part of the study area is a sandy stretch void of any rocky outcrops, an area expected to be totally unsuitable for rupicolous cordylid lizards.

The distribution of melanistic *C. cordylus* populations in the study area is depicted in Figure 5. Noteworthy is the fact that along the coast melanistic populations are restricted to insular and peninsular situations, whilst inland they occur exclusively at relatively high altitudes along the western flank of the Cape Fold Mountains. Non-melanistic populations, on the other hand, were recorded from sea-level to mountain top (Locality 47) and also from Robben Island.

The frequency of occurrence of the MSr and V10 character states at the sample localities is presented in the form of a scatter-diagram in Figure 6. There is striking clustering representing the absence of both character states and the presence of both character states, respectively. Both character states are present at all localities where melanistic populations occur. With the exception of Locality 7, the frequency of occurrence of both character states in the melanistic populations is higher than 75%.

Although both the MSr and V10 character states are absent at most 'non-melanistic' localities, either one or both states are present at some localities (Figure 6). With the exception of Localities 11, 14 and 45, the frequency of occurrence of the two character states is, however, less than 50% at these localities. The V10 character state was recorded at only five 'non-melanistic' localities and interestingly the MSr state is also present at these five localities.

Table 1 Frequency of occurrence (%) of the four head shield texture combinations at the 54 sample localities in the study area. A = anterior and posterior scales smooth; B = anterior scales smooth, posterior scales rugose; C = anterior scales slightly rugose, posterior scales rugose; D = anterior and posterior scales rugose; *N* = sample size

Locality	*N*	A	B	C	D
1	3	0	100	0	0
2	15	7	80	13	0
3	11	0	0	91	9
4	5	0	40	60	0
5	11	0	0	64	36
6	6	0	100	0	0
7	13	46[a]	15	39	0
8	9	78[a]	22	0	0
9	9	100[a]	0	0	0
10	24	83[a]	13	4	0
11	10	0	60	0	40
12	3	0	0	100	0
13	12	0	17	83	0
14	2	0	0	100	0
15	3	0	100	0	0
16	11	0	82	9	0
17	5	0	80	20	0
18	6	0	17	50	33
19	3	0	67	33	0
20	2	0	0	100	0
21	15	0	33	47	20
22	4	0	100	0	0
23	16	100[a]	0	0	0
24	12	0	17	83	0
25	4	25	25	50	0
26	5	0	0	100	0
27	11	9	9	73	9
28	11	0	0	82	18
29	12	8	50	42	0
30	4	0	0	100	0
31	5	0	40	60	0
32	6	0	0	100	0
33	4	0	50	50	0
34	4	0	75	0	25
35	7	0	14	86	0
36	1	0	0	100	0
37	10	0	60	40	0
38	5	0	20	60	20
39	4	0	0	75	25
40	7	0	0	0	100
41	2	0	50	50	0
42	8	0	0	25	75
43	7	0	0	0	100
44	5	0	0	0	100
45	11	0	0	9	91
46	7	0	14	86	0
47	4	0	25	75	0
48	10	0	50	50	0
49	10	0	30	50	20
50	7	0	71	29	0
51	6	0	67	33	0
52	8	0	88	12	0
53	6	0	67	17	16
54	8	0	50	38	12

[a]Coastal melanistic localities

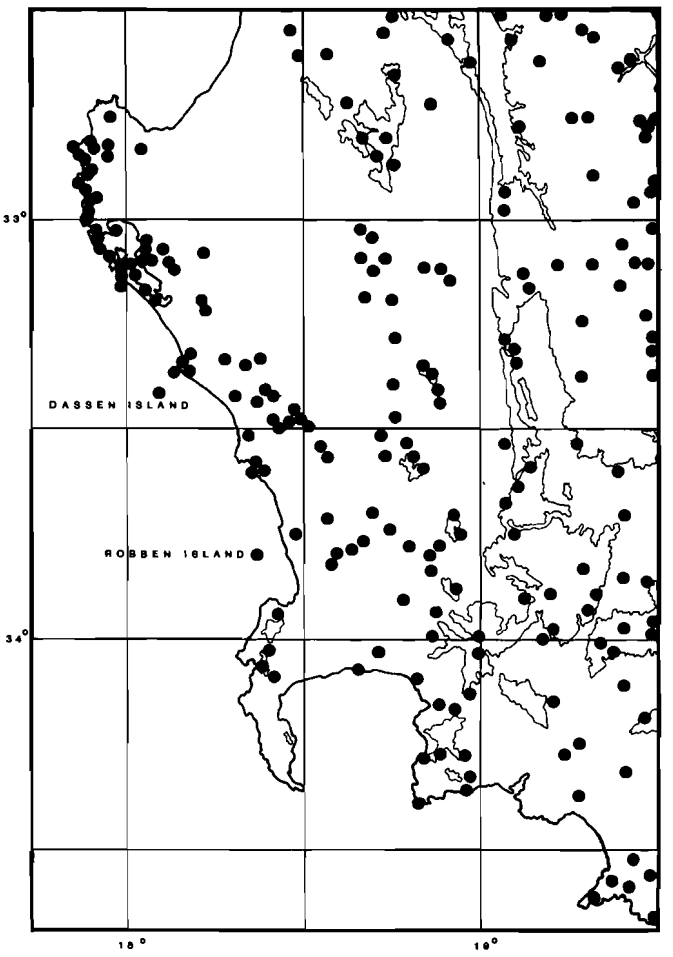

Figure 4 Localities visited in the study area.

The occurrence of both the MSr and V10 character states in non-melanistic populations obviates the possibility that the correlation between the occurrence of melanism, a median subocular scale reaching the lip, and 10 rows of ventral scales, is the result of common epigenetic control.

To determine any possible clines in the MSr and V10 characters, the variation in frequency of occurrence was mapped (Figure 7). Localities at which a frequency of occurrence higher than 60% was recorded, were contoured and shaded. Note that Locality 7 at which the frequency of occurrence of the V10 state is lowest of all the 'melanistic' localities, is situated at the periphery of the Saldanha-Langebaan melanistic zone, which is characterized by a high frequency of occurrence of both character states. At Locality 6, however, only 2 km to the north of Locality 7, no individuals with 10 rows of ventrals were encountered. At the same locality the frequency of occurrence of the MSr state is less than 20%, while that recorded for Locality 7 is a high 96%. Specimens collected from Locality 6 were, without exception, non-melanistic, while both melanistic and non-melanistic individuals, as well as ones of mixed coloration occurred at Locality 7. Locality 27, where both character states are present, although at low frequencies, is located within 10 km of Locality 26, a 'melanistic' locality with a 100% incidence in both character states. Specimens from Locality 27 were dark with numerous white markings. Similarly, Locality 45, the only 'non-melanistic' locality at which a 100% incidence in both character states was recorded, lies geographically in close proximity to 'melanistic' Localities 42 and 44. Specimens from Locality 45 resemble those of Locality 27 in coloration. Locality 24, where both character states occur, is geographically situated near the Cape Peninsula melanistic population. The

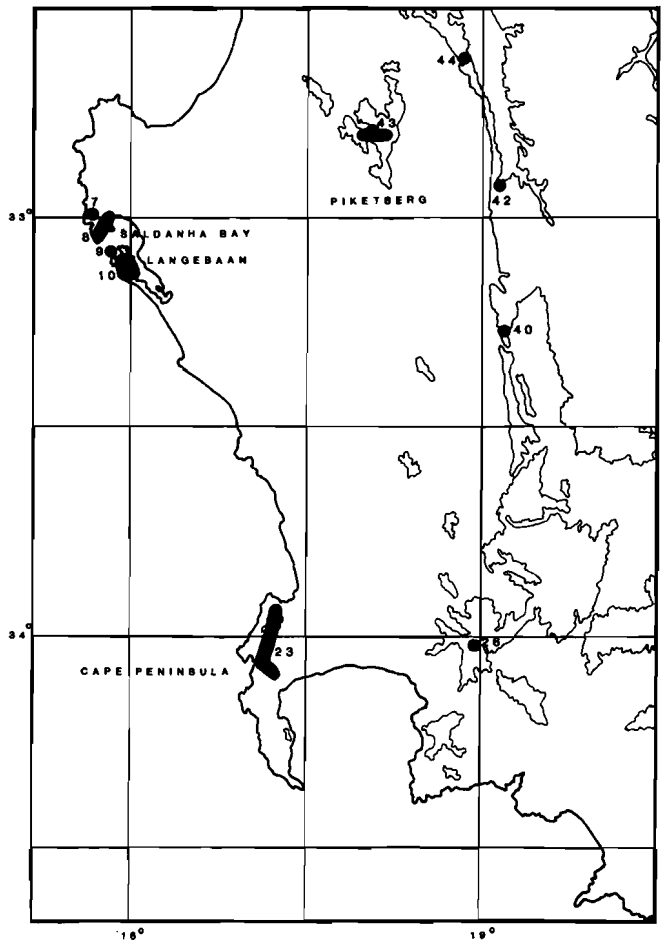

Figure 5 The distribution of melanistic *C. cordylus* populations in the study area.

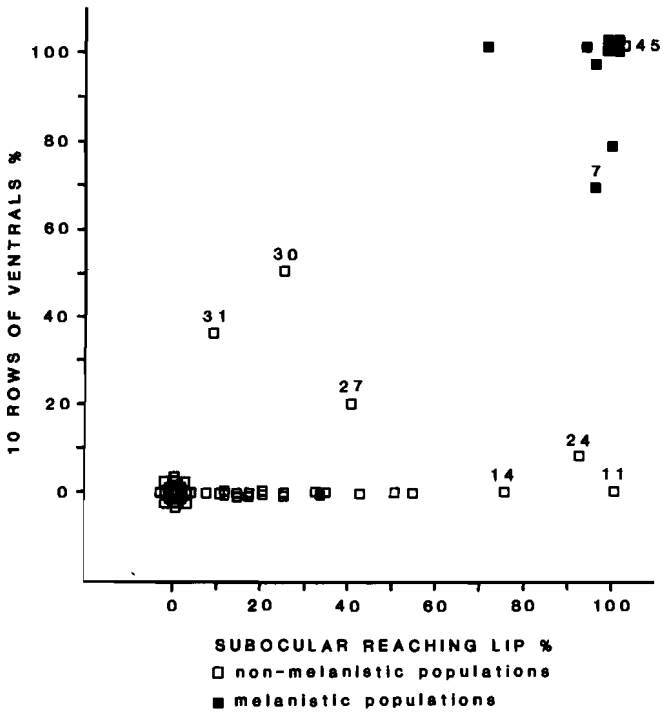

Figure 6 Scatter diagram showing the frequencies of occurrence of the V10 (Y axis) and MSr (X axis) character states at the 54 sample localities.

other two 'non-melanistic' localities at which both character states were recorded, Localities 30 and 31, lie in close proximity along the southern coastline.

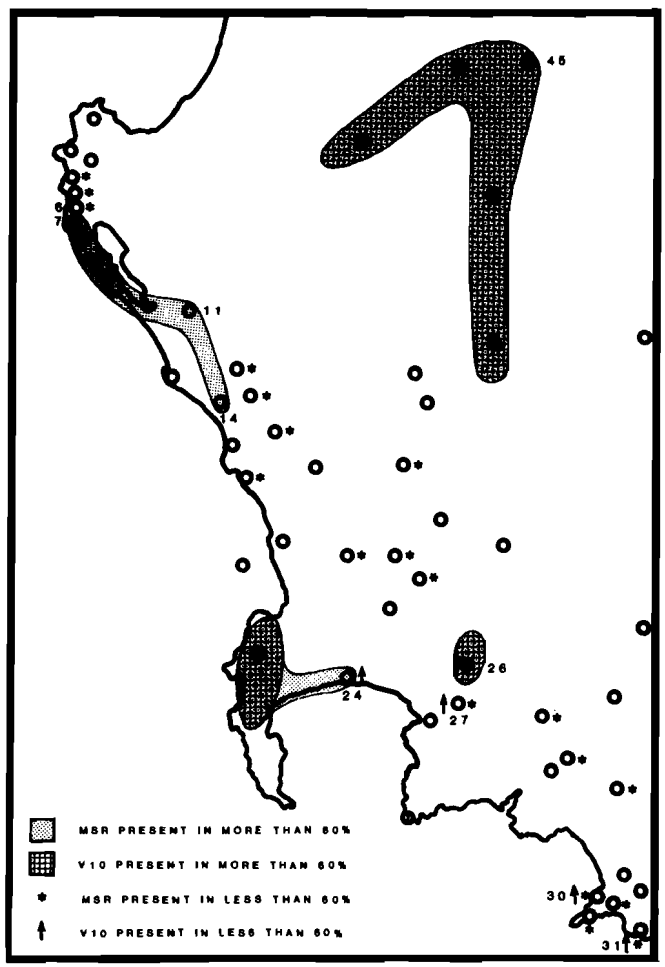

Figure 7 Contour map showing the geographic distribution of frequencies of occurrence of the V10 and MSr character states higher than 60%.

Although the MSr character state was recorded at many 'non-melanistic' localities in the coastal lowlands west of the Cape Fold Mountains, no smooth clinal trends were observed in the frequency of occurrence in this character state. The melanistic population at Locality 11, with a 100% occurrence of both character states, lies geographically in close proximity to the Saldanha-Langebaan melanistic zone.

Three melanistic zones, with a frequency of character state occurrence higher than 75%, can be recognized in the study area. The first is in the Saldanha-Langebaan area, a second in the Cape Peninsula and another along the western flank of the Cape Fold range. These three areas are geographically separated from each other by non-melanistic zones with a low frequency of occurrence in both character states. Furthermore, along the coast the melanistic populations seem to be restricted to peninsular and insular situations. Even the non-melanistic populations at Localities 30 and 31 in which both character states are present, occur in or near semi-peninsular circumstances.

Separated prefrontals (Ps character state) were recorded in eight populations (Figure 8). All but two of these were melanistic. The Ps character state is present in all the coastal melanistic populations, with the highest incidence in the Saldanha-Langebaan area. This character state is, however, present in only one of the five montane melanistic populations (Locality 43), which is geographically close to the Saldanha-Langebaan zone of high incidence.

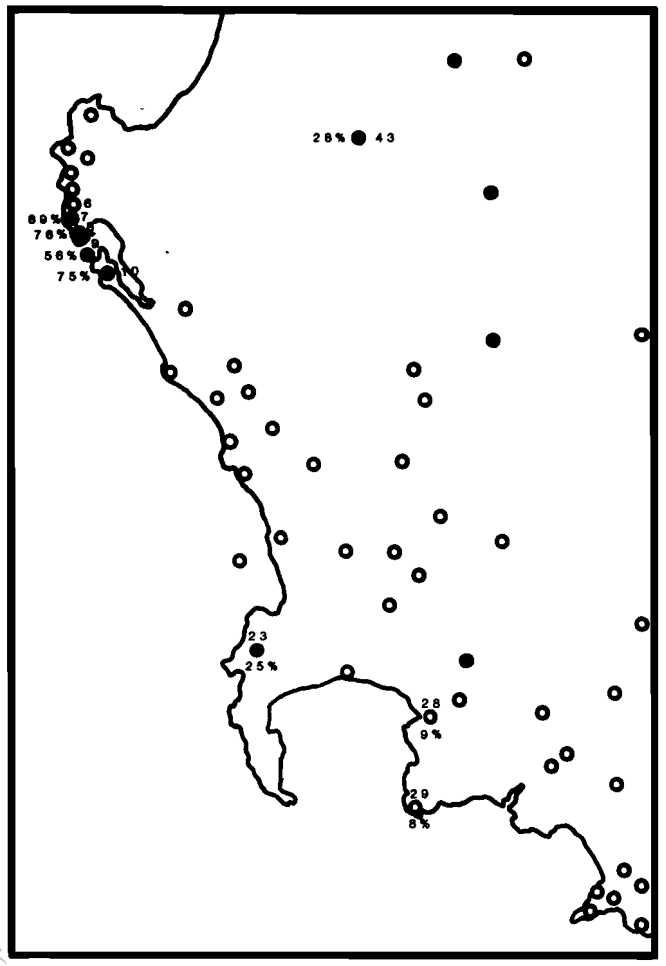

Figure 8 The geographic distribution of separated prefrontals in the study area. The frequency of occurrence is given at those localities where the Ps state is present.

At Locality 7 the Ps frequency was as high as 69% whilst at Locality 6, only 2 km to the north, this character state was completely absent. This abrupt transition in the frequency of occurrence of the Ps character state coincides with the equally abrupt change in coloration, the MSr state, and the V10 state, as was pointed out in the previous section.

The populations at Localities 28 and 29 were the only non-melanistic populations at which individuals with the prefrontals separated were encountered. The frequency of occurrence is, however, exceptionally low, with only one individual per locality displaying this character state.

The frequency of occurrence of the four different head shield texture combinations recorded at the sample localities, is listed in Table 1. From this table it is evident that, as far as the texture of the head shields is concerned, three distinct groups can be discerned. In all the coastal melanistic populations the head shields, both anteriorly and posteriorly, are smooth in most specimens. The head shields are, however, rugose to strongly rugose in most specimens from montane melanistic populations. In most non-melanistic specimens the anterior shields vary from smooth to slightly rugose, with the posterior shields being rugose. Of all the coastal melanistic populations the frequency of occurrence of the smooth/smooth character state is lowest at Locality 7. However, 2 km to the north at Locality 6, all specimens have the anterior shields smooth and the posterior shields rugose. This abrupt transition again exactly coincides with the transition in the MSr, V10, and Ps character states as previously discussed.

The frequency of occurrence of each of the occipital character state combinations at the sample-localities is listed in Table 2. As far as this character is concerned two distinct

Table 2 Frequencies of occurrence of the three occipital character state combinations recorded at the 54 sample localities in the study area. A = occipitals quadrangular to rectangular, smooth and non-spinose; B = occipitals quadrangular to rectangular, rugose and/or spinose; C = occipitals irregular in form, rugose and/or spinose; *N* = sample size

Locality	*N*	A	B	C
1	3	0	33	67
2	15	0	0	100
3	11	0	0	100
4	5	0	0	100
5	11	0	18	82
6	6	0	33	67
7	13	84[a]	8	8
8	9	89[a]	11	0
9	9	100[a]	0	0
10	24	100[a]	0	0
11	10	0	20	80
12	3	0	0	100
13	12	0	25	75
14	2	0	0	100
15	3	0	0	100
16	11	0	36	64
17	5	0	20	80
18	6	0	0	100
19	3	0	33	67
20	2	0	0	100
21	15	0	7	94
22	4	0	25	75
23	16	81[a]	19	0
24	12	0	0	100
25	4	0	0	100
26	5	0	0	100
27	11	0	0	100
28	11	0	0	100
29	12	0	0	100
30	4	0	0	100
31	5	0	0	100
32	6	0	0	100
33	4	0	0	100
34	4	0	0	100
35	7	0	0	100
36	1	0	0	100
37	10	0	30	70
38	5	0	20	80
39	4	0	0	100
40	7	0	0	100
41	2	0	50	50
42	8	0	0	100
43	7	0	0	100
44	5	0	0	100
45	11	0	0	100
46	7	0	14	86
47	4	0	0	100
48	10	0	20	80
49	10	0	40	60
50	7	0	0	100
51	6	0	0	100
52	8	0	0	100
53	6	0	0	100
54	8	0	12	88

[a]Coastal 'melanistic' localities

groups can be recognized. In the coastal melanistic populations, the occipital shields are rectangular, smooth to very smooth, and non-spinose. At all the other localities, including the montane 'melanistic' localities, the occipital shields are irregular in form, rugose and spinose to various degrees.

Once again an abrupt transition in this character is detectable between Localities 7 and 6. At Locality 7 the occipitals were of the typical coastal melanistic type in 84% of the specimens examined, while at Locality 6 the occipitals were rugose and spinose in all individuals.

Mean total femoral pore counts, standard deviations and ranges recorded at the sample localities are given in a modified Dice-Leraas diagram (Figure 9). Pore counts vary from 8 – 20 and in most cases intra-locality variation is high. Little inter-locality variation was observed, but coastal 'melanistic' pore counts tend to be higher than normal. The mean pore count recorded at Locality 41, although high, is not considered to be of any significance because of the small sample size.

There is again an abrupt change in mean pore counts between Localities 6 and 7, which again coincides with the transitions in all the characters discussed so far. No differences in mean pore counts between montane melanistic and non-melanistic populations seem to exist.

Interestingly, the total femoral pore count recorded by Loveridge (1944) for *C. c. niger* is 10 – 18, while in the present survey, counts for individuals from Saldanha Bay and the Cape Peninsula (= *C. c. niger*) varied from 14 – 20. The total pore count of 10 – 18 for *C. c. cordylus* as reported by FitzSimons (1943) and Loveridge (1944) is in agreement with my counts for non-melanistic specimens (= *C. c. cordylus*).

Mean snout-vent length, standard deviation and range, recorded at each sample locality, are depicted in a modified Dice-Leraas diagram in Figure 10. Standardization in this character was not possible, but since the majority of specimens examined were adults, it is believed that a fair picture of the geographic variation in this character was obtained. In comparing values, minimum values should be ignored, since these usually represent subadult specimens in the samples. Emphasis should be placed on the mean and maximum values recorded.

From Figure 11 it is clear that specimens from montane 'melanistic' localities (Localities 26, 40, 42, 43, and 44) were without exception notably smaller than specimens from other localities. Mean snout-vent lengths at these localities were less than 65 mm in all cases, while the maximum individual values recorded never exceeded 70 mm. Maximum individual values

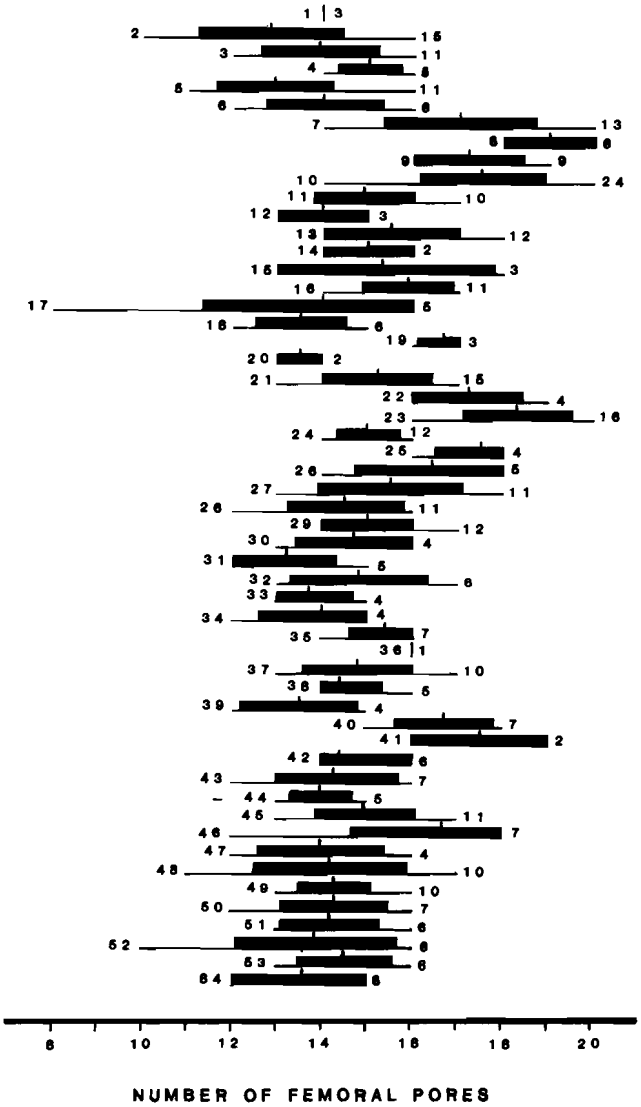

Figure 9 A modified Dice-Leraas diagram of the mean femoral pore counts (vertical line), standard deviations (solid bars) and the ranges (horizontal lines) recorded at the 54 localities in the study area. Locality number is given on the left and sample size on the right.

Figure 10 A modified Dice-Leraas diagram of the mean snout-vent lengths (vertical lines), standard deviations (solid bars) and the ranges (horizontal lines) recorded at the 54 localities in the study area. Locality number is given on the left and sample size on the right.

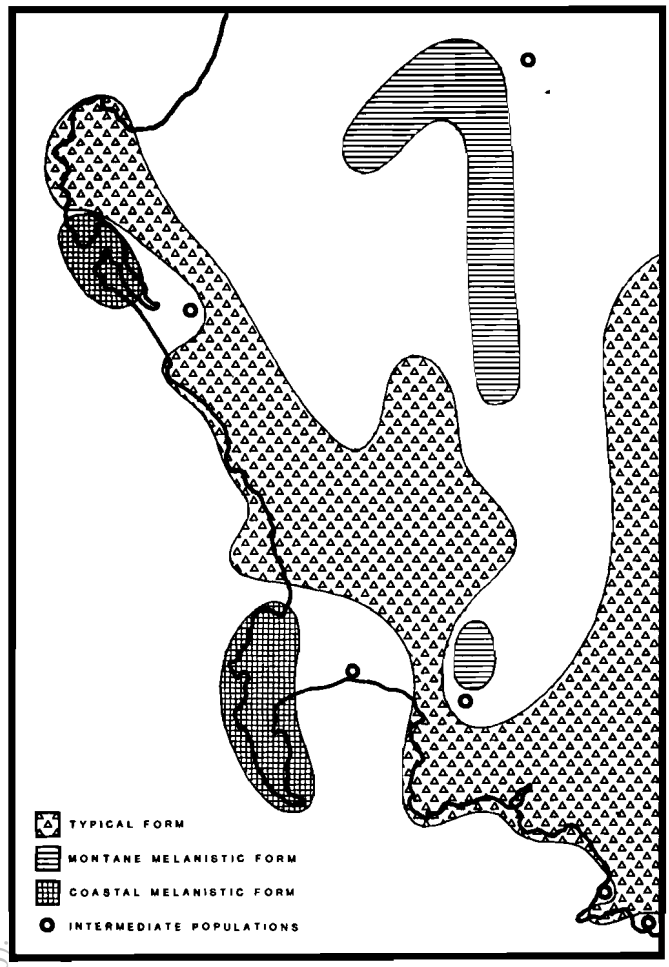

Figure 11 Geographic distribution of the three phenotypic forms of *C. cordylus*, as well as of intermediate populations, in the study area.

at the other localities range from 75 mm to as high as 98 mm.

No distinct differences in mean and maximum snout-vent lengths of the coastal melanistic and non-melanistic populations exist. Low mean and maximum head-body lengths were recorded at Localities 4, 5 and 6, whilst a much higher maximum value was recorded at Locality 7. Since body size could be affected differently by environmental parameters at the different localities, a much more sophisticated analysis is needed for micro-scale comparisons between sample localities. One should therefore treat these results with great caution.

It has been stated that *C. c. niger* is smaller in body size than the typical form (Loveridge 1944; Branch 1981). My data do not support this view and several specimens with head-body lengths in excess of 90 mm were collected at 'melanistic' Locality 10. Whereas the previous maximum head-body length recorded for *C. c. cordylus* (FitzSimons 1943) was 88 mm, the maximum value I recorded was 98 mm.

Summary and conclusions

Zones of homogeneity

Concordant patterns in the geographic distribution of several character states occur and three zones of homogeneity are recognized. For the sake of simplicity the populations in these zones will be regarded as phenotypic forms of *C. cordylus*.

Localities 26, 40, 42, 43 and 44 constitute the first zone of homogeneity and are referred to as the montane melanistic form of *C. cordylus*. This form is characterized by having 10 longitudinal rows of ventral scales and the median subocular scale reaching the lip in more than 75% of the individuals. The head shields of this form are rugose to strongly rugose, while the occipitals are irregular in shape, rugose and slightly spinose. Body length of the specimens examined does not exceed 70 mm. Separated prefrontals were encountered only in the Piketberg population (Locality 43). Individuals of this form are without exception melanistic, although sometimes with a white vertebral stripe.

The second zone of homogeneity is constituted by localities 7, 8, 9, 10 and 23. These populations will be referred to as the coastal melanistic form of *C. cordylus*. This form only occurs in peninsular and insular situations along the south-western coast. Although the whole of the Cape Peninsula has not been surveyed in this study (Figure 4) the melanistic population here is known to occur over almost the entire peninsula as far as Table Mountain in the north (Loveridge 1944; Visser 1971). The coastal melanistic form is characterized by having, like the montane melanistic form, 10 longitudinal rows of ventral scales and the median subocular scale borders on the lip in more than 75% of the individuals. The head shields are normally smooth, whilst the occipitals are rectangular in form, smooth and non-spinose. Although intra-population variation is great, a high number of femoral pores is characteristic of this form, usually in the order of 9 – 10 per side. The prefrontals are frequently separated by the frontal and frontonasal and this character state is most frequently encountered in the Saldanha-Langebaan area. Individuals of this form are without exception melanistic.

The third zone of homogeneity is constituted by most of the remaining sample localities in the study area, and is referred to as the typical form of *C. cordylus*. Although some individuals may be dark, none are ever truly melanistic. The typical form is characterized by having 12 longitudinal rows of ventrals in more than 75% of the individuals, while the head shields are normally smooth to slightly rugose anteriorly, and rugose to strongly rugose posteriorly. The occipital scales are normally irregular in form, rugose and slightly spinose. Typically the median subocular scale does not reach the lip. At localities where the subocular, in some individuals, does reach the lip, it does so in less than 60% of the individuals. The prefrontals are normally in contact behind the frontonasal; separated prefrontals were recorded in only two of 306 specimens of this form examined. In the study area the typical form occurs extensively along the coastal lowlands and lower mountain slopes.

Populations showing overlap in character states

At Localities 11, 24, 27, 30, 31, and 45 populations displaying combinations of the three character sets used to differentiate amongst the three forms of *C. cordylus*, occur. Of these the populations at Localities 11, 24, 27 and 45 occur geographically in close proximity to melanistic populations. The intermediate populations at Localities 30 and 31 are located in the vicinity of a peninsula thereby showing some resemblance to the coastal melanistic populations.

The geographic distribution of the three phenotypic forms, as well as of the intermediate populations, are depicted in a generalized scheme in Figure 11.

Zones of secondary intergradation

In all the significant characters investigated, an abrupt transition in character state occurs between Localities 6 and 7. These two localities are within 2 km of one another. Locality 7 is included in the coastal melanistic form, but the frequency of occurrence of the character states characteristic of the coastal

melanistic form, was lowest at this locality. Specimens collected at Locality 6 conformed, without exception, to the general phenotype of the typical form. This pattern of abrupt change in phenotype is interpreted as being a zone of secondary intergradation between the coastal melanistic and typical forms. However, more research is needed to confirm this.

Shared characters

Characters which are shared by the coastal and montane melanistic forms, the coastal melanistic and typical forms, and the montane melanistic and typical forms, respectively, are listed in Table 3.

Table 3 Characters shared between the three phenotypic forms of *C. cordylus* occurring in the study area

Phenotypic form	Character
Coastal melanistic/ montane melanistic	(1) 10 longitudinal rows of ventral scales (2) median subocular reaching lip (3) melanistic (4) separated prefrontals (5) long hind limbs
Coastal melanistic/typical	(1) adult body size exceeds 70 mm
Montane melanistic/ typical	(1) head shields rugose (2) occipitals irregular in form, rugose and sometimes spinose (3) low number of femoral pores (4) prefrontals in contact

The results obtained in this study support the views of earlier workers (Rose 1926; Essex 1927; Power 1930; Loveridge 1944) that more than one phenotypic form of *C. cordylus* (*sensu latu*) occur in the south-western Cape. Final conclusions about the taxonomic status of the coastal *C. c. niger*, as well as the newly identified montane melanistic form will, however, have to await a determination of the relative importance of historical versus ecological causal factors responsible for the observed patterns of phenotypic variation.

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Appendix 1 Localities visited in the study area and specimens used in the analysis

1. Soetlandskop: 324416S/175723E. 3217 DB + DD Vredenburg. JEFB 383 – 385; 8.12.1983.
2. Tietiesbaai: 325009S/175183E. 3217 DB + DD Vredenburg. JEFB 539 – 544; 31.3.1984.
   Cape Castle: 324958S/175106E. 3217 DB + DD Vredenburg. JEFB 545 – 547; 31.4.1984.
   Hoedklip: 324945S/175107E. 3217 DB + DD Vredenburg. JEFB 548 – 551; 31.4.1984.
   Paternoster: 325313S/175240E. 3217 DB + DD Vredenburg. JEFB 377, 378; 7.12.1983.
3. Pelgrimsrust: 324924S/175358E. 3217 DB + DD Vredenburg. JEFB 568 – 578; 4.4.1984.
4. Trekoskraal: 325313S/175356E. 3217 DB + DD Vredenburg. JEFB 375, 376; 7.12.1983.
   Duminypunt: 325334S/175200E. 3217 DB + DD Vredenburg. JEFB 371 – 373; 7.12.1983.
5. Sandbaai: 325357S/175206E. 3217 DB + DD Vredenburg. JEFB 351 – 357; 7.12.1983.
   Groot Kreefgat: 325435S/175148E. 3217 DB + DD Vredenburg. JEFB 364, 365; 7.12.1983.
   Pêrlemoenbaai: 325506S/175242E. 3217 DB + DD Vredenburg. JEFB 367, 368; 7.12.1983.
6. Swartriet: 325739S/175356E. 3217 DB + DD Vredenburg. JEFB 553 – 555, 557 – 559; 1.4.1984.
7. Jacobsbaai: 325811S/175311E. 3217 DB + DD Vredenburg. JEFB 345 – 349; 5.12.1983.

Appendix 1 Continued

Mauritzbaai: 325837S/175250E. 3217 DB + DD Vredenburg. JEFB 560–567; 1.4.1984.

8. Saldanha: 330115S/175657E. 3317 BB Saldanha. JEFB 59; 17.4.1983.
   Malgaskop: 330200S/175537E. 3317 BB + 3318 AA Saldanha. JEFB 302–307; 5.12.1983.
   Môresonkop: 330129S/175531E. 3317 BB + 3318 AA Saldanha. JEFB 341, 342; 5.12.1983.
9. Jutteneiland: 330457S/175719E. 3317 BB + 3318 AA Saldanha. JEFB 314–322; 6.12.1983.
10. Postberg: 330646S/175719E. 3317 BB + 3318 AA Saldanha. JEFB 219–227; 1.12.1983.
    Oudepost: 330826S/180000E. 3317 BB + 3318 AA Saldanha. JEFB 263, 364; 2.12.1984.
    Plankiesbaai: 330754S/175822E. 3317 AA + 3318 BB Saldanha. JEFB 243–249; 1.12.1983.
    Kreeftekop: 330825S/175922E. 3317 AA + 3318 BB Saldanha. JEFB 258; 2.12.1983.
    Kreeftekop: 330812S/175839E. 3317 BB + 3318 AA Saldanha. JEFB 232–234; 1.12.1983.
    Konstabelberg: 330753S/180116E. 3317 BB + 3318 AA Saldanha. JEFB 267, 268; 2.12.1983.
11. Betjieskop: 331203S/181238E. 3317 BB + 3318 AA Saldanha. JEFB 492–496; 22.1.1984.
    Swartberg: 331300S/181317E. 3317 BB + 3318 AA Saldanha. JEFB 430–434; 22.1.1984.
12. Yzerfontein: 332052S/180848E. 3318 CA Yzerfontein. JEFB 84; 21.11.1981.
    Yzerfonteinrant: 332153S/181000E. 3318 AC Yzerfontein. JEFB 111, 112; 21.8.1983.
13. Klipberg: 332000S/181756E. 3318 AD Darling. JEFB 421–423; 12.12.1983.
    Bonteberg: 332121S/182015E. 3318 AD Darling. JEFB 654–662; 27.5.1984.
14. Rondeberg: 332518S/181756E. 3318 AD Darling. JEFB 104, 105; 20.8.1983.
15. Bokkop: 332511S/182238E. 3318 AD Darling. JEFB 34–36; 16.4.1983.
16. Bobbejaanberg: 332940S/182712E. 3318 AD Darling. JEFB 52, 53; 16.4.1983.
    Klavervlei: 332836S/182447E. 3318 AD Darling. JEFB 60–62; 19.6.1983.
    Waterkloof: 332820S/182836E. 3318 AD Darling. JEFB 28–33; 20.3.1983.
17. Kabeljoubank: 330025S/181858E. 3318 CB Melkbosstrand. JEFB 37–41; 19.3.1983.
18. Silwerstroomstrand: 333532S/182138E. 3318 CB Melkbosstrand. JEFB 54–57; 23.1.1984.
19. Kanonkop: 333316S/183312E. 3318 DA Philadelphia. JEFB 42–44; 18.6.1983.
20. Blouberg: 334457S/182747E. 3318 CB Melkbosstrand. JEFB 190, 191; 15.10.1983.
21. Robben Island: 334822S/182206E. 3318 CD Cape Town. JEFB 1356–1366; 9.11.1985. SAM 43932–43935.
22. Meerendal: 334700S/183700E. 3318 DC Bellville. JEFB 97–99; 17.9.1983.
23. Steenberg: 340508S/182525E. 3318 AB + AD Cape Peninsula. JEFB 1202–1211; 1.7.1985.
    Hout Bay: 340324S/182206E. 3418 AB + AD Cape Peninsula. JEFB 1213–1215; 1.7.1985.
    Table Mountain: 335721S/182502E. 3318 CD Cape Town. JEFB 1216, 1217; 1.7.1985.
24. Swartklip: 340421S/184042E. 3418 BA Mitchells Plain. JEFB 1331–1342; 2.11.1985.
25. Bottelaryheuwels: 335458S/185140E. 3318 DD Stellenbosch. JEFB 457–460; 6.1.1984.
26. Landdroskop: 340248S/185938E. 3418 BB Somerset West. JEFB 579–583; 8.1.1982.
27. Verkykerskop: 340606S/185821E. 3418 BB Somerset West. JEFB 999–1009; 9.2.1985.
28. Sir Lowry's Pass: 340806S/185537E. 3418 BB Somerset West. JEFB 1344–1354; 2.11.1985.
29. Kaap Hangklip: 342308S/185004E. 3418 BD Hangklip. JEFB 1305–1316; 27.9.1985.

Appendix 1 Continued

30. The Kelders: 343246S/192231E. 3419 CB Gansbaai. JEFB 67–72; 2.4.1983.
31. Pearly Beach: 344015S/193023E. 3419 DA + DC Baardskeerdersbos. JEFB 79–83; 2.4.1983.
32. Vlaeberg: 3405S/1925E. 3419 AB Caledon. JEFB 891–896; 13.10.1984.
33. Suurberge: 3356S/1931E. 3319 DC Langvlei. JEFB 883–886; 29.9.1984.
34. Klapmutskop: 334911S/185140E. 3318 DD Stellenbosch. JEFB 118–121; 21.8.1983.
35. Joostenberg: 334631S/184724E. 3318 DD Stellenbosch. JEFB 45–51; 16.7.1983.
36. Paarlberg: 334136S/185427E. 3318 DB Paarl. JEFB 201; 16.10.1983.
37. Betel: 333424S/184835E. 3318 DB Paarl. JEFB 148, 149; 18.9.1983.
    Joubertskloof: 333227S/184714E. 3318 DB Paarl. JEFB 856–859; 750, 751.
    Besemgoedkop: 333237S/184813E. 3318 DB Paarl. JEFB 161, 162; 18.9.1983.
38. Porseleinberg: 332627S/185250E. 3318 BD Riebeeck Castle. JEFB 184, 185; 28.9.1983.
    Swartdam: 332416S/185314E. 3318 BD Riebeeck Castle. JEFB 129–131; 6.8.1983.
39. Kasteelberg: 332139S/185116E. 3318 BD Riebeeck Castle. JEFB 164, 165; 26.9.1983.
    Voorspoed: 332014S/184927E. 3318 BD Riebeeck Castle. JEFB 179,180; 28.9.1983.
40. Obiekwa: 331616S/190352E. 3319 AC Tulbagh. JEFB 970–977; 26.9.1985.
41. Hottentotskloof: 331515S/193629E. 3319 BC De Doorns. JEFB 65, 66; 18.9.1981.
42. Dasklippas: 325425S/190214E. 3219 CC Keerom. JEFB 63, 64; 28.5.1983. JEFB 585–587; 27.4.1984.
43. Perdekop: 324757S/183809E. 3218 DC Moravia. JEFB 473–476; 19.2.1984.
    Koggelmanderkop: 324808S/184237E. 3218 DC Moravia. JEFB 202–204; 19.11.1983.
44. Piekenierskloof: 323721S/185733E. 3218 DB Eendekuil. JEFB 1217–1222; 6.7.1985.
45. Middelbergpas: 323753S/190906E. 3219 CA Citrusdal. JEFB 1160–1170; 26.5.1985.
46. Du Toitskloof: 334258S/190502E. 3318 CA Bainskloof. JEFB 1375, 1376; 26.1.1986.
47. Welgemoed: 340719S/191406E. 3419 AA Grabouw. JEFB 1495–1498; 19.4.1986.
48. Avontuur: 341516S/191633E. 3419 AD Stanford. JEFB 1506–1515; 27.4.1986.
49. Perdekloof: 341745S/191338E. 3419 AC Hermanus. JEFB 1520–1529; 27.4.1986.
50. Shaw's Mountain Pass: 341845S/192420E. 3419 AD Stanford. JEFB 1463–1468; 15.3.1986.
51. Witkransberge: 343242S/192527E. 3419 CB Gansbaai. JEFB 1441–1446; 16.2.1986.
52. Byneskranskop: 343439S/192806E. 3419 CB Gansbaai. JEFB 1431–1438; 15.2.1986.
53. Franskraal: 343527S/192325E. 3419 CB Gansbaai. JEFB 1423–1428; 15.2.1986.
54. Dangerpoint: 343729S/191937E. 3419 CB Gansbaai. JEFB 1407–1414; 15.2.1986.

Appendix 2 External characters examined in *C. cordylus*

A. Morphometric characters

1. Length of head
2. Breadth of head
3. Depth of head
4. Length of frontonasal
5. Breadth of frontonasal
6. Length of frontal
7. Breadth of frontal

Appendix 2 Continued

8. Length of interparietal
9. Breadth of interparietal
10. Breadth of rostral
11. Depth of rostral
12. Length of mental
13. Breadth of mental
14. Breadth of largest gular
15. Length of ventrals
16. Breadth of ventrals
17. Length of forelimbs
18. Length of hindlimbs
19. Length of tail
20. Snout-vent length

B. Meristic Characters

1. Number of frontoparietals
2. Number of parietals
3. Number of occipitals
4. Number of temporals
5. Number of postoculars
6. Number of supraoculars
7. Number of supraciliaries
8. Number of suboculars
9. Number upper labials
10. Number of lower labials
11. Number of sublabials
12. Number of chin-shields
13. Number of gulars transversely between posterior sublabials
14. Number of transverse series of dorsal scales
15. Number of dorsal scales in longest row across middle of back
16. Number of transverse rows of ventrals
17. Number of longitudinal series of ventrals
18. Number of enlarged preanal scales
19. Number of scales under 4th toe
20. Number of scales under 4th finger
21. Number of femoral pores
22. Number of whorls in tail

C. Qualitative characters

1. Texture of head shields anteriorly
2. Texture of head shields posteriorly
3. Form of frontonasal
4. Frontonasal separated from nostril by suture of nasals or not
5. Frontonasal divided by median longitudinal suture or not
6. Frontonasal in contact on sides with loreal or separated
7. Nasals swollen or not
8. Position of nostril in nasal

Appendix 2 Continued

9. Nasals in contact behind rostral or not
10. Direction in which nostril faces
11. Prefrontals in contact behind frontonasal or not
12. Form of frontal
13. Frontal a little broader in front than behind or not
14. Form of interparietal
15. Interparietal produced anteriorly or not
16. Anterior pair of parietals slightly smaller than posterior pair or not
17. Form of occipital shields
18. Occipital shields spinose or not
19. Lower temporals keeled or not
20. Temporal spines present or not
21. Lower eyelid scaly and opaque or not
22. Loreal much smaller than preocular or not
23. Middle subocular reaching or not reaching lip
24. Which upper labial largest
25. Which lower labial largest
26. Posteriormost lower labial keeled or not
27. Which sublabial largest
28. Which sublabial smallest
29. Median gulars transversely enlarged or not
30. Gulars subimbricate or not
31. Small granular interstices between gulars and sublabials or not
32. Scales on neck strongly imbricate or not
33. Scales on side of neck keeled and spinose or not
34. Form of dorsal scales
35. Dorsal scales imbricate or not
36. Dorsal scales more or less smooth down middle of back or not
37. Dorsal scales keeled and mucronate towards sides or not
38. Posterior edges of dorsal scales more or less serrated or not
39. Scales on sides of body subequal in size to dorsals or not
40. Ventrals smooth
41. Form of ventrals
42. Scales of limbs above imbricate or not
43. Scales of limbs above strongly keeled or not
44. Scales of limbs above spinose or not
45. Scales of limbs above serrated or not
46. Scales of limbs below smooth or slightly keeled
47. Glandular scales in front of femoral pores or not
48. Tail with whorls of large, strongly keeled, spinose, serrated scales or not
49. Spines on tail strongest supero-laterally or not
50. Scales below tail elongate, obtusely keeled and mucronate or not.