

Taxonomic status of the melanistic forms of the *Cordylus cordylus* complex (Reptilia: Cordylidae) in the south-western Cape, South Africa

P. le F.N. Mouton* and J.H. van Wyk

John Ellerman Museum, Department of Zoology, University of Stellenbosch, Stellenbosch, 7600 Republic of South Africa

Received 4 October 1988; accepted 29 June 1989

The taxonomic status of the two melanistic morphotypes belonging to the *Cordylus cordylus* complex in the south-western Cape, South Africa, is considered. It is proposed that the coastal melanistic form, previously described as subspecies of *C. cordylus*, be considered a separate species, while the previously unknown montane melanistic form is also described as a new species. Areas of uncertainty, which may affect the status of the two melanistic species in the future, are discussed.

Die taksonomiese status van die twee melanistiese morfotipes behorende tot die *Cordylus cordylus*-kompleks in die suidwes-Kaap, Suid-Afrika, word bespreek. Daar word voorgestel dat die kus-melanistiese vorm, wat voorheen as 'n subspesie van *C. cordylus* beskryf is, as 'n aparte spesie beskou moet word. Die voorheen onbekende berg-melanistiese vorm word ook as 'n nuwe spesie beskryf. Gebiede van onsekerheid wat moontlik die status van die twee melanistiese spesies in die toekoms kan beïnvloed, word bespreek.

*To whom correspondence should be addressed

The melanistic girdled lizard, *Cordylus cordylus niger* Cuvier, occurring in the Cape Peninsula and the Saldanha–Langebaan areas, has for many years presented a taxonomic problem (Branch 1981; Mouton 1987). Initially described as a distinct species by Cuvier (1829), subsequent workers (Rose 1926; Essex 1927; Power 1930; Loveridge 1944) saw it as a subspecies. FitzSimons (1943) points out the overlap in distinguishing character states between the melanistic and nominate forms and holds the opinion that *C. c. niger* is simply an ecological colour variant not worthy of subspecific status. Visser (1971) mentions the possibility that *C. c. niger* and the nominate form do not constitute a monophyletic group, pointing out similarities between *C. c. niger* and another melanistic taxon, *Cordylus peersi* from Little Namaqualand. More recently opinions seem to favour the view of FitzSimons (1943) that the melanistic form is an ecological colour variant and the name *C. c. niger* has gradually started to disappear from checklists and everyday discussions (Branch 1981).

Unfortunately most of the above opinions on the taxonomic status of the melanistic form lack a sound factual basis. Recently, however, Mouton (1987) conducted an in-depth analysis of geographic character variation among populations of the *Cordylus cordylus* complex in the south-western Cape in order to elucidate the taxonomic status of *C. c. niger*. Results obtained from this analysis highlighted a unique pattern of geographic character variation which constitutes the basis of this discussion.

Mouton (1987) described the *C. cordylus* complex in the south-western Cape as consisting of three morphotypes, namely a melanistic coastal form (= *C. c. niger*) occurring in insular and peninsular situations along the south-western coast (Figure 1), a second, previously unknown melanistic montane form occurring at isolated localities along the extreme western borders of the Cape Fold Mountains, from Landdroskops in the south to the

Piketberg Mountains in the north (Figure 1), and the typical form (= *C. c. cordylus*) extensively distributed along the south-western coastal lowlands, but also, at

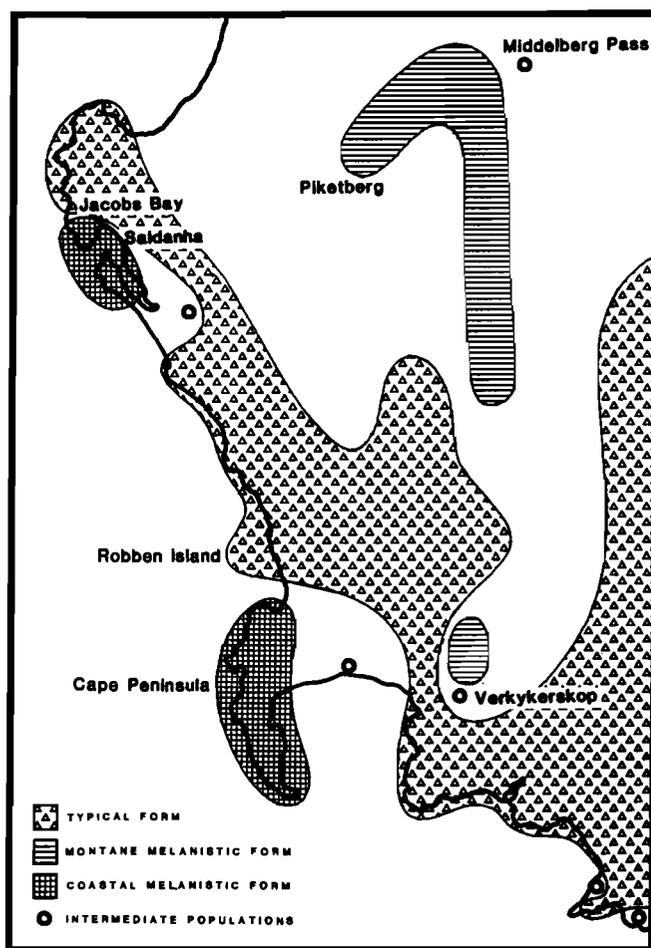


Figure 1 Geographic distribution of the three morphotypes belonging to the *Cordylus cordylus* complex in the south-western Cape.

places, occurring high up in mountains and also on Robben Island (Figure 1). The typical form also has a wide distribution outside the south-western Cape, mainly along the southern coastal regions, but also reaching further inland in the eastern Cape as far as the southern Orange Free State (De Waal 1978).

Apart from the three well-defined morphotypes, a few intermediate populations have also been described by Mouton (1987). Noteworthy is the fact that these populations without exception occur in the immediate vicinity of melanistic populations (Figure 1). Furthermore, a contact zone between the coastal melanistic form and the typical form has been identified at Jacobs Bay (Figure 1) where, in terms of external morphological characters, there is an abrupt change from the one form to the other.

In their proposed model for the evolution of the three morphotypes Mouton & Oelofsen (1988) argue that the melanistic populations are not simply ecological variants of the typical form, but that the observed pattern is historical in origin, only preserved by present environmental conditions. They interpret the available information as indicating that the melanistic populations are relict populations, which resulted from the contraction and fragmentation of formerly large melanistic populations along the south-western coast and along the Cape Fold Mountains. The typical form on the other hand, is seen as a newcomer to the south-western Cape through the expansion in range of a south-eastern population. The Last Glacial period and subsequent amelioration of the climate are seen as instrumental in the evolution of the melanistic forms. The intermediate populations are interpreted as products of the swamping of small remaining melanistic populations by the inmoving typical form.

Mouton & Oelofsen (1988) concluded that the three morphotypes recognized by Mouton (1987), form a monophyletic group, having originated from an ancestral form through a sequence of events from about 40 000 BP to about 11 000 BP. In their proposed model no statement, however, has been made regarding the taxonomic status of the three morphotypes. The purpose of this report is to consider the taxonomic status of the two melanistic forms.

Taxonomic status of the coastal melanistic form

The view of FitzSimons that the Cape Peninsula and Saldanha melanistic populations represent local adaptations to similar environmental conditions cannot be accepted without serious reservations. All indications are that these two coastal melanistic populations are genealogically related, although geographically separated by the typical form (Figure 1), and that they resulted from the contraction and fragmentation of a former large coastal melanistic population (Mouton & Oelofsen 1988). Furthermore the pattern of geographic character variation points to the typical form as a newcomer to the south-western Cape, having immigrated into the area from a south-eastern centre. The need to document, by means of formal taxonomy, the discrete identifiable clusters recognized by Mouton (1987) seems obvious,

bearing in mind the impact that knowledge of this pattern could have on future physiological and ecological studies as well as on our understanding of lizard speciation in the south-western Cape. The problem thus boils down to whether the coastal melanistic form should receive specific or subspecific status.

The nature of the contact zone between the coastal melanistic and typical forms at Jacobs Bay, just north of Saldanha Bay (Figure 1), probably holds the key to solving this problem. Mouton (1987) describes the Jacobs Bay locality as representing an abrupt change from the one morphotype to the other. A subsequent visit to Jacobs Bay revealed that the two morphotypes occur sympatrically at this locality along a narrow zone of 100–200 m. The melanistic form occurs abundantly among the rocks above the high-water mark, but towards the interior, at \pm 100–200 m from the shore is replaced abruptly by individuals of the typical form. Moving northwards along the shoreline there is likewise an abrupt transition from the melanistic to the typical form and from there on northwards individuals of the typical form occur from among the rocks along the shore to well into the interior. Along the narrow transition zone individuals of both morphotypes are found as well as an occasional odd individual seemingly representing hybridization between the two forms.

It stands to reason that a major analysis of this contact zone is necessary for a clear perspective of the amount of introgression taking place, of possible competitive exclusion, and of other eco-physiological factors that might be involved. The relevant picture emerging, however, is that of two distinct morphotypes predominating outside the contact zone, with limited introgression occurring only along a very narrow sympatric zone. Wiley (1981) is of the opinion that under such circumstances the parental morphotypes could be considered as separate species. If more pronounced introgression over a broader zone had been observed, the decision would probably have been in favour of one species, thus subspecific status. In the case under discussion it seems as if species-distinct characters are being selected for outside the zone of sympatry and that both morphotypes show independent species cohesion.

Mouton (1987) pointed out that a subocular reaching the lip, a diagnostic character of the melanistic form, is also found to be widely occurring among populations of the typical form (Figure 2), although at a much lower intra-population frequency. The presence of this character in populations of the typical form to the north of Jacobs Bay (Figure 2) could therefore not be considered as *prima facie* evidence for introgression. Furthermore, no signs of introgression outside the contact zone are observable in any of the other diagnostic characters of the melanistic form. With the information at hand it must be concluded that introgression in the vicinity of Jacobs Bay is of a very limited nature, supporting the view that Jacobs Bay represents a true contact zone and not an ecological gradient.

To the south of the Saldanha–Langebaan area, at Betjieskop and Rondeberg (Figure 2), Mouton (1987) noted that the subocular reaches the lip in a high number

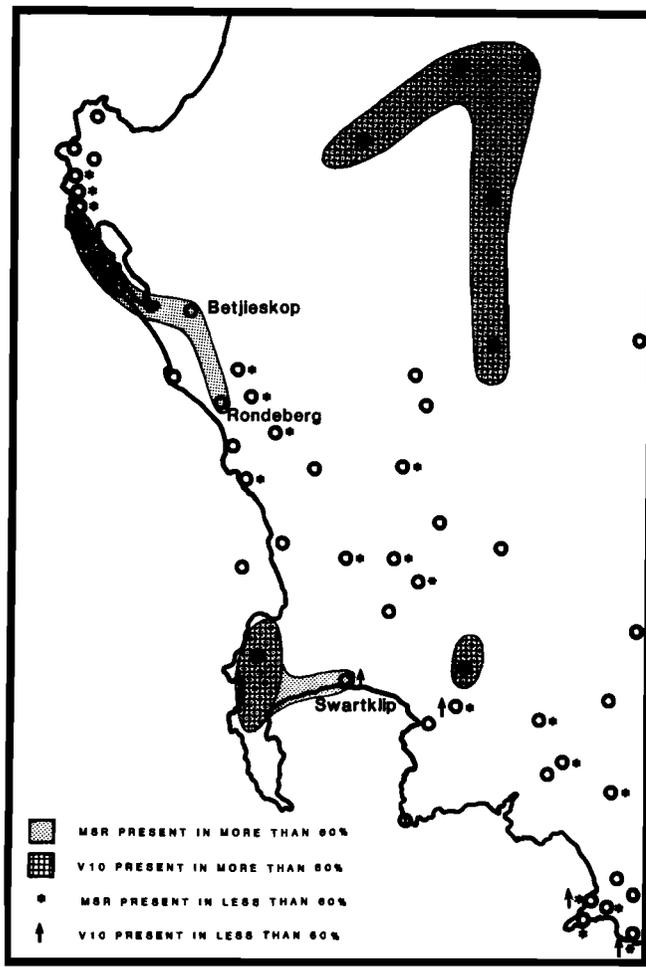


Figure 2 The geographic distribution of frequencies of occurrence of a subocular reaching the lip (MSr) and 10 rows of ventral scales (V10) higher than 60% (from Mouton 1987).

of individuals, in fact at a frequency of occurrence comparable to that noted for the melanistic populations, and he described these two populations as intermediate populations. Again it is only one character supporting introgression, but the fact cannot be ignored that these intermediate localities are located in close proximity to the melanistic population and that the frequency of a subocular reaching the lip is much higher than elsewhere for the typical form. These facts appear to suggest past interaction between the two morphotypes, lending support to the Mouton–Oelofsen hypothesis (1988) that small melanistic populations were swamped by an incoming typical form. It is, however, not clear why it is only the one character that shows signs of past swamping and not the whole set of diagnostic characters.

It can be reasoned that ecologically the melanistic form would not have been able to survive in the Betjieskop area owing to unfavourable warm climatic conditions in a changing environment and that it would have been easily replaced by the advancing typical form. Support for this statement comes from experiments conducted at our laboratories (Badenhorst, in prep.; Cronje, in prep.) where the activity periods of the melanistic forms were significantly impeded by high temperatures, in contrast to the typical form. It is,

however, obvious that in the Saldanha–Langebaan area the melanistic form fares exceptionally well along the coast and that melanism as well as possible other ecophysiological adaptations are responsible for species cohesion preventing the swamping action by the typical form. Since we are, in terms of climate, past the warmer part of the interglacial (Vogel 1985), chances are good that the melanistic form will survive the onslaught of the typical form and probably will also be able to extend its range with the climates becoming cooler and thus more suitable to its needs.

Moving to the Cape Peninsula, the intermediate population described by Mouton (1987) at Swartklip (Figure 2), not only occurs in close proximity to the Peninsula melanistic population, but displays two characters diagnostic of the melanistic form, namely a subocular reaching the lip as well as 10 longitudinal rows of ventral scales. The most plausible explanation likewise seems to be that this population represents the swamping of a melanistic population by the typical form in an area where the melanistic form could not manifest itself in a changing environment.

In summary, although there are signs of past interaction, as well as limited introgression at present, we are of opinion that the coastal melanistic form should receive specific status. It must be stressed that our view is a hypothesis based on our present interpretation of the available data. We consider a species-level hypothesis a more generalized hypothesis than a subspecies-level one. In the latter case the hypothesis would obviously be based on evidence implicating sister group relationship, but in our case no clear cut evidence is available in this regard. Rosen (1979) pointed out that the ability to interbreed may be a plesiomorphic character and that this ability cannot be considered *prima facie* evidence for sister group relationship. To use the vague signs of possible introgression as evidence for subspecific status would be irresponsible. What is needed is an in-depth analysis of the contact zone to determine the exact nature thereof. Eldredge & Cracraft (1980) point out that cases where only morphological intermediates are observed, with no concomitant breeding data, are incapable of decisive resolution. Under such conditions the phylogenetic criterion of species recognition (Eldredge & Cracraft 1980) becomes important. Unfortunately the relationship of the coastal melanistic form to other species, especially *Cordylus peersi*, is unresolved as will be discussed at a later stage. When such information becomes available one will be able to test the initial hypothesis of specific status for the coastal melanistic form. Although the status of the coastal melanistic form is clearly moot at this stage, we prefer the specific status hypothesis because of the very distinct pattern of geographic character variation, the nature of the contact zone as described earlier, as well as the high degree of concordancy among patterns of different species (Mouton & Oelofsen 1988). It is therefore proposed that specific status for the coastal melanistic morphotype, as was originally proposed by Cuvier (1829), be reinstated, namely *Cordylus niger*.

The range of this species includes the Cape Peninsula

(i.e. from the northern slopes of Table Mountain to Cape Point), the Langebaan Peninsula (with Churchhaven as the southernmost limit), Jutten Island, and Saldanha (from the Harbour northwards along the coast to Jacobs Bay where it is replaced by the nominate form).

Morphologically, *C. niger* is characterized by normally having 10 longitudinal rows of ventral scales, a median subocular scale bordering the lip, smooth head shields, occipitals rectangular in form, smooth and non-spinose, 9–10 femoral pores per side and the prefrontals often separated by a suture of the frontal and frontonasal. Glandular scales in front of femoral pores occur in males only. Individuals of this form are furthermore without exception melanistic in colour. The nominate form on the other hand is characterized by having 12 longitudinal rows of ventral scales, a median subocular scale not reaching the lip, occipitals irregular in form, rugose and slightly spinose, the prefrontals in contact and a lower number of femoral pores, normally 7–8 per side. Individuals of this form may vary in colour and may sometimes be very darkly coloured, but to date no completely black individuals have been found. For more detailed morphological data the reader is referred to the work of Mouton (1987).

Taxonomic status of the montane melanistic form

The montane melanistic morphotype described by Mouton (1987), is a new form and accordingly not taxonomically listed. This morphotype has several characters in common with *C. niger* and Mouton & Oelofsen (1988) consider them as sister taxa. If they are indeed sister

taxa, one is left with no other option than to describe this form as a distinct species as well. Although the two melanistic forms share several important characters they differ in so many other respects that subspecific status could not be considered without proof of reproductive compatibility between the two forms. To date no contact zone between the two melanistic forms has been found and there is no way of investigating the reproductive criterion.

The pattern of geographical character variation along the western borders of the Cape Fold Mountains is basically the same as along the coast, with isolated melanistic populations occurring here and there interspersed with populations of the typical form, while intermediate populations have also been identified (Figure 1) (Mouton 1987). The intermediate populations at Verkykerskop and Middelberg Pass (Figure 1) seemingly represent swamping of melanistic populations by the typical form and is accordingly considered as belonging to the greater gene pool of the typical form.

A formal description of the montane melanistic morphotype (Mouton 1987) as a new species of *Cordylus* is accordingly presented below.

Systematics

Cordylus oelofseni sp. nov. (Figures 3–6)

Type material examined: Two specimens collected at the type locality. Holotype: SAM-47388. Allotype: SAM-47389. These two specimens were deposited in the collection of the South African Museum, Cape Town.

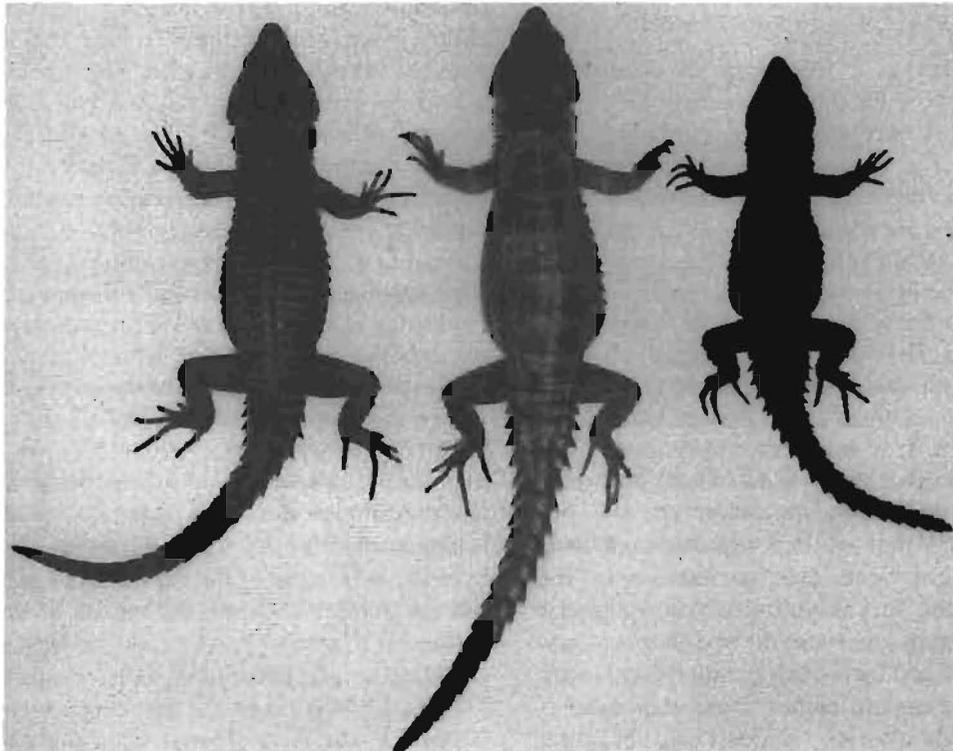


Figure 3 *Cordylus niger* (JEM-CR1203) (left), *Cordylus cordylus* (JEM-CR1510) (centre), and *Cordylus oelofseni* (holotype SAM-47388) (right).

Paratypes: 29 specimens collected at five localities in the south-western Cape. JEM-CR579-583 from Landdrooskop; JEM-CR970-975 and 977 from Obiekwa; JEM-CR63, 64, 585-587 and 1792 from Dasklip Pass; JEM-CR473-476 and 202-204 from the Piketberg Mountains; JEM-CR1217, 1218 and 1220-1222 from Piekenierskloof. All paratypes are in the collection of the J. Ellerman Museum, University of Stellenbosch.

Type locality: Dasklip Pass near Porterville, 32°42'S / 19°21'E, Cape Province, South Africa, at an altitude of 760 m.

Etymology: Named after Dr. B.W. Oelofsen, presently of the Directorate Sea Fisheries, South West Africa/Namibia, who, while employed at the University of Stellenbosch, acted as study leader for a project on the lizards of the fynbos region of which this study formed part. Dr. Oelofsen had a personal interest in the montane melanistic form having many years ago noted the existence of a melanistic *Cordylus* population at Landdrooskop in the Hottentots Holland Mountains.

Diagnosis: Melanistic in colour with adult body size not exceeding 70 mm. The median subocular normally reaches the lip and ten rows of ventral scales normally occur. The headshields are rugose and the occipitals are irregular in form and sometimes slightly spinose. Glandular scales in front of femoral pores absent in females. Although sometimes darkly coloured the typical form, *C. cordylus*, on the other hand, is nowhere completely black in colour, the adult body size normally exceeds 70 mm, the median subocular as a rule does not reach the lip, 12 longitudinal series of ventral scales normally occur, only the posterior head shields, from the prefrontals backwards, are rugose, but the occipitals are also irregular in form and spinose to some degree. Glandular scales in front of femoral pores may be present or absent in females. The coastal form, *C. niger*, is like the montane form, melanistic in colour, the median subocular reaches the lip, ten longitudinal rows of ventral scales occur and glandular scales in front of pore-bearing scales are absent in females, but unlike the latter, adult body size exceeds 70 mm, the head shields are smooth, and the occipitals are rectangular in form and smooth.

Description

Holotype. SAM-47388, adult female (Figures 3-6). Head-body length 66 mm, tail 68 mm. Head and body moderately depressed. Head triangular and longer than broad. Nostril pierced in lower posterior corner of a single nasal. Frontonasal subhexagonal, separated from rostral and frontal, but in good contact on sides with loreals (Figure 4). Prefrontals in contact mesially. Frontal six-sided, broader in front than behind and longer than broad. Four parietals, posterior pair slightly larger than anterior pair. Interparietal quadrangular in form. Six occipitals, irregular in form and some slightly

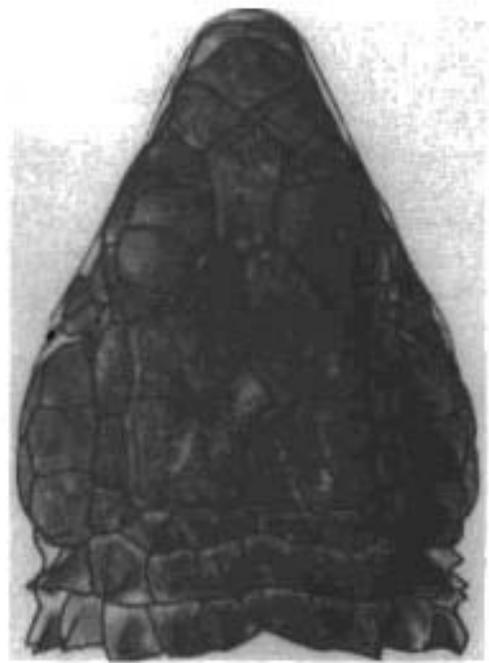


Figure 4 Dorsal view of the head of the holotype, SAM-47388.

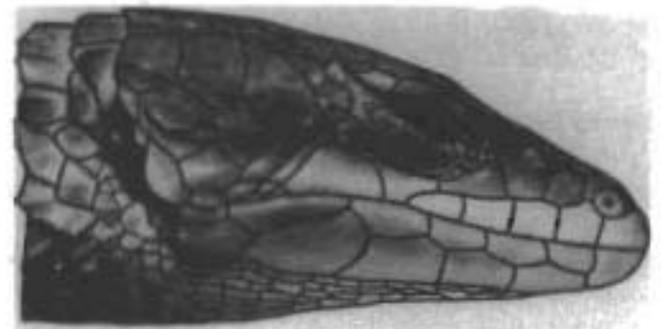


Figure 5 Lateral view of the head of the holotype, SAM-47388.

keeled and spinose (Figure 4). Upper head shields rugose.

The temporal scales slightly keeled. Four supraoculars and three supraciliaries (Figure 4). Loreal much smaller in size than preocular. Three suboculars, median one reaching lip (Figure 5). One postocular. Lower eyelid scaly.

Upper labials five, the last one the largest and strongly keeled. Five lower labials, the last strongly keeled. Five large sublabials bordering lower labials below; the fifth sublabial the smallest and strongly keeled.

Seven distinct chin shields (Figure 6). Sublingual scales polygonal to rounded anteriorly, but quadrangular and arranged in regular transverse rows posteriorly; two to three rows of sublinguals bordering sublabials three to five, smaller and much longer than broad. Scales on side of neck strongly keeled and spinose; gulars strongly imbricate; 16 gulars between the angles of the jaw.

Two vertebral rows of dorsal scales slightly enlarged, trapezoid and longitudinally keeled, other dorsals mucronate and also longitudinally keeled. Dorsals feebly

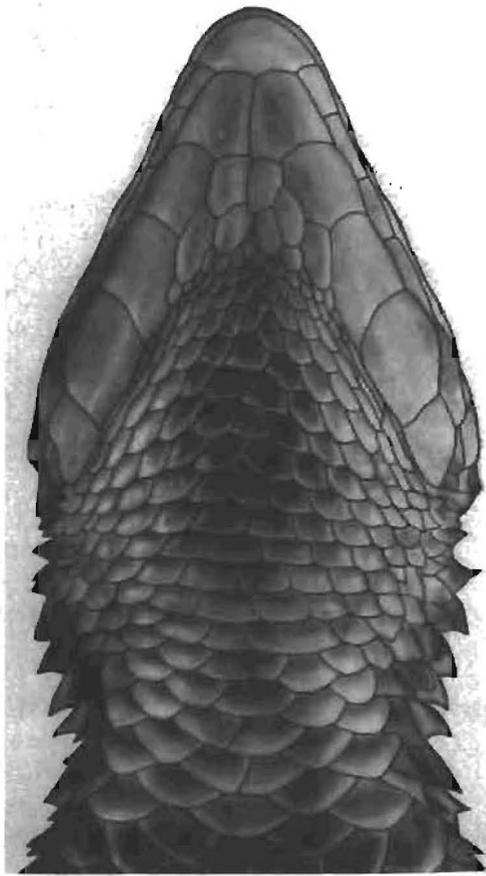


Figure 6 Ventral view of the head of the holotype, SAM-47388.

serrated to smooth posteriorly. Dorsals and laterals arranged in 27 transverse and 28 longitudinal rows. Lateral scales subequal in size to dorsal scales. Ventral scales smooth, quadrangular, broader than long except the outer row of which the scales are longer than broad; arranged in 10 longitudinal and 24 transverse series. A pair of enlarged preanal plates present.

Scales on limbs above large, imbricate, strongly keeled and sharply spinose. Scales under fourth toe 15,

and 13 under fourth finger. Five active femoral pores (with secretion) plus two non-active pores (without secretion) on each side, no glandular scales in front of pore-bearing scales. Tail with whorls of elongate, strongly keeled and sharply spinose scales.

Limbs, head, body and tail black above with a faint broken white vertebral line from behind head to hind limbs; body and limbs below a pencil grey. Two faint light brown lines along side of neck from ear opening to front limbs.

Allotype. SAM-47389, adult male. Head-body length 58 mm, tail 56 mm. Occipitals six, irregular in form. Anterior sublinguals much larger than posterior scales, but no sharp transition. Dorsals arranged in 28 transverse series and 18 longitudinal series. Ventrals arranged in 22 transverse and 10 longitudinal series. Femoral pores seven on one side and eight on other side. Two rows of glandular scales in front of pore-bearing scales. In other characters similar to holotype.

Paratypes: Variation in meristic and morphometric characters an additional 29 individuals from five localities are listed in Table 1. At the Piketberg locality (Figure 1) the prefrontals are separated in JEM-CR473 and 474, while in JEM-CR476 the median subocular does not reach the lip. Glandular scales in front of pore-bearing scales absent in all females, but present in all males. In all other respects similar to holotype.

Field notes

Like *C. cordylus* this is a rupicolous form, but occurring only at higher altitudes along the Cape Fold Mountains. Individuals of this new form prefer shallow cracks on the surface of boulders where they wedge themselves in tightly. Never were two individuals found sharing the same crack. Two to three young are born during late summer to early autumn.

Distribution

Cordylus oelofseni sp. nov. is distributed along the

Table 1 Variation in meristic and morphometric characters among the 29 paratypes of *C. oelofseni* sp. nov. from five localities

	Landdros- kop	Obiekwa	Dasklip Pass	Piketberg	Piekeniers- kloof
	(n = 5)	(n = 7)	(n = 5)	(n = 7)	(n = 5)
Transverse series of dorsals	23-25	24-26	24-26	24-26	24-26
Longitudinal series of dorsals	18-20	19-22	17-21	18-20	18
Transverse series of ventrals	19-23	20-22	20-24	21-23	19-22
Longitudinal series of ventrals	10	10	10	10	10
Upper labials	5	5	5-6	4-5	5
Lower labials	4-7	5	5-6	4-6	5
Scales under 4th toe	14-17	13-14	13-14	13-14	12-14
Scales under 4th finger	11-14	10-12	11-12	11-13	10-13
Femoral pores	7-9	7-9	7-8	6-8	6-8
Occipitals	6	5-6	6	6-8	4-7
Head/body length (maximum)	66	69	65	65	68
Tail length (maximum)	72	69	65	69	65

western borders of the western section of the Cape Fold Mountains (Figure 1). This species has been collected at the following localities:

1. Landdroskop: 340248S;185938E, 3418 BB Somerset West.
2. Obiekwa: 331616S;190352E, 3319 AC Tulbagh.
3. Dasklip Pass: 325425S;190214E, 3219 CC Keerom.
4. Perdekop: 324757S;183809E, 3218DC Moravia.
5. Koggelmanderokop: 324808S;184237E, 3218 DC Moravia.
6. Piekenierskloof: 323721S;185733E, 3218 DB Eendekuil.
7. Platberg: 324024S;182707E, 3218 CA & CB Aurora.

Discussion

It must be understood that the taxonomic status of the melanistic forms is certainly not fully resolved. At present there is certain information lacking which could, once it becomes available, affect the taxonomic status of these forms.

Firstly, although the very distinct pattern of geographical character variation in *C. cordylus* complex in the south-western Cape, with the coastal melanistic populations only occurring in insular and peninsular situations and the montane melanistic populations only occurring along the extreme western borders of the Cape Fold Mountains, as well as information on melanism in general, strongly suggests that melanism is associated with adverse climatic conditions, the history of present day melanistic populations has not been satisfactorily resolved. Mouton & Oelofsen (1988) present good arguments against the melanistic populations being local adaptations to adverse climatic conditions, but their proposal that the melanistic populations are relict, genealogically related populations and not local adaptations to similar environmental conditions, urgently needs to be substantiated. Electrophoretic techniques could establish whether the populations constituting the two melanistic species are genealogically related respectively. In other words confirmation is needed whether *C. niger* and *C. oelofseni* sp. nov. represent monophyletic assemblages. It stands to reason that if the melanistic populations are not genealogically related, but local adaptations, the taxonomic status of these two species would have to be reconsidered.

Secondly, and perhaps the most crucial information lacking at present, is a corroborated statement of monophyly regarding the three species, *C. cordylus*, *C. niger* and *C. oelofseni* sp. nov. Any discussion of genealogical relationships among forms must include all taxa at the specific hierarchical level, in other words the group under question must be monophyletic. Any taxonomic analysis is based on the acceptance of a hypothesis of monophyly at a higher level as a starting point (Eldredge & Cracraft 1980). To Mouton (1987) and Mouton & Oelofsen (1988) this starting hypothesis was that *C. niger* and *C. cordylus* are sister taxa (Rose 1926; Loveridge 1944), if not one and the same taxon (FitzSimons 1943). Thus the key question was not whether the two taxa constitute a monophyletic group,

but in fact whether *C. niger* was 'different enough' from *C. cordylus* to warrant formal taxonomic description. Having now established that the two forms, as well as the newly described montane form, differ consistently (Mouton 1987) and are worthy of formal taxonomic description, the question of monophyly becomes important.

Mouton & Oelofsen (1988) in their scenario of the evolution of the three morphotypes under question, accepted that the three forms constitute a monophyletic group. This was based on the observed intergrading at the contact zones, as well as the existence of intermediate populations. This evidence may sound convincing enough, but there is no proof that, for example, *C. peersi* from Little Namaqualand, which has some important characters in common with the two melanistic morphotypes (Visser 1971), is reproductively isolated from *C. cordylus*, *C. niger* and *C. oelofseni* sp. nov. In other words there is no proof that *C. peersi*, or for that matter any other taxon, should not have been included in the group for it to be monophyletic. At present, hypotheses on the interspecific relationships within the genus *Cordylus* are virtually non-existent which makes it difficult to discuss notions of monophyly at a specific level within the genus. It is nevertheless imperative that the relationship of the two melanistic morphotypes to other members of the genus be investigated as such information may affect the taxonomic status of the two melanistic forms.

In summary, with the information at hand at present, the most logical thing to do, would be to consider the two melanistic forms as species closely related to *C. cordylus*. There are, however, two areas of uncertainty which call for further investigation and which might change their status in the future. These are uncertainty as to whether the two melanistic forms are monophyletic, respectively, and secondly uncertainty as to whether the three morphotypes of Mouton (1987) form a monophyletic group.

If, however, one accepts *C. cordylus*, *C. niger* and *C. oelofseni* sp. nov. as constituting a monophyletic group, the question of interspecific relationships comes to the fore. According to the model of Mouton & Oelofsen (1988) the two melanistic taxa are sister taxa, having originated through vicariance of an ancestral species to the west of the western section of the Cape Fold Mountains. Their model advocates that this ancestral form came under severe climatic pressure along the western coastal lowlands during the last glacial maximum (16 000 BP), to such a degree that a drastic decrease in population size followed which allowed the rapid spreading of favourable mutations throughout the entire population. According to their model, melanism was one of these adaptive traits that evolved during this time, in other words melanism can be considered a synapomorphy suggesting close relationship between the two melanistic morphotypes.

The identification of synapomorphies remains the primary goal of systematics and in most cases the most practical method of determining transformation direction is by outgroup comparison. The lack of knowledge

on intrageneric relationships within *Cordylus* as well as a suspected high incidence of convergencies in the genus, render it difficult to select an outgroup in the case under discussion. If *C. peersi* is selected as outgroup, melanism, 10 rows of ventral scales, a median subocular reaching the lip, as well as separated prefrontals must be considered plesiomorphic character states as these states are also characteristic of *C. peersi*. The possession of these states by both the melanistic forms therefore is not an indication that they are sister species. In fact, with *C. peersi* as an outgroup, not a single one of the character states used by Mouton (1987) to discriminate between the three forms, can be considered a synapomorphy and this makes it impossible to resolve the relationships among the three taxa. If another species, for example *C. mclachlani*, is taken as outgroup, a completely different picture is obtained. A subocular scale reaching the lip, 10 rows of ventral scales, melanism, and separated prefrontals now all become synapomorphies claiming *C. niger* and *C. oelofseni* as sister forms, thus in line with the notions of Mouton & Oelofsen (1988). To obtain a clearer perspective of possible relationships between *C. cordylus*, *C. niger* and *C. oelofseni* a corroborated hypothesis on intrageneric relationships within *Cordylus* is necessary. This would also mean that a clearer perspective of the extent of convergent evolution within the genus is needed.

Acknowledgements

The authors would like to thank Dr B.W. Oelofsen of the Directorate Sea Fisheries, Southwest Africa, Dr M.H.C. Visser of the Department of Zoology, University of Stellenbosch, and Dr J. Gauthier of the California Academy of Sciences for valuable discussions. This study is a product of the Cordylidae Research Group of the University of Stellenbosch.

References

- BRANCH, W.R. 1981. An annotated checklist of the lizards of the Cape Province, South Africa. *Ann. Cape Prov. Mus. (Nat. hist.)* 13(11): 141–167.
- CUVIER, G.L.C.F.D. 1829. Le Règne Animal distribué d'Après son organisation pour servir de base à l'Histoire naturelle des Animaux et d'introduction à l'Anatomie Comparée. 2. Les Reptiles. Paris Ed.2: 1–406.
- DE WAAL, S.W.P. 1978. The Squamata (Reptilia) of the Orange Free State, South Africa. *Mem. Nat. Mus. Bloemfontein* 1: 1–160.
- ELDREDGE, N. & CRACRAFT, J. 1980. Phylogenetic patterns and the evolutionary process. Columbia Univ. Press, New York.
- ESSEX, R. 1927. Studies on reptilian regeneration. *Proc. Zool. Soc. London* 2: 879–945.
- FITZSIMONS, V.F.M. 1943. The lizards of South Africa. *Transv. Mus. Mem.* 1: 1–528.
- LOVERIDGE, A. 1944. Revision of the African lizards of the family Cordylidae. *Bull. Mus. Comp. Zool. Harv.* 95: 1–118.
- MOUTON, P.le F.N. 1987. Phenotypic variation among populations of *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape Province, South Africa. *S. Afr. J. Zool.* 22: 119–129.
- MOUTON, P.le F.N. & OELOFSEN, B.W. 1988. A model explaining patterns of geographic character variation in *Cordylus cordylus* (Reptilia: Cordylidae) in the south-western Cape, South Africa. *S. Afr. J. Zool.* 23: 20–31.
- POWER, J.H. 1930. On the South African species of the genus *Zonurus*. *Ann. Tvl Mus.* 14: 11–19.
- ROSE, W. 1926. Some notes on the lizards of the Cape Peninsula. *Ann. S. Afr. Mus.* 6: 491–494.
- ROSEN, D.E. 1979. Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative biogeography. *Syst. Zool.* 27: 159–188.
- VISSER, J. 1971. *Cordylus cordylus* and its races in the Cape Province — a general discussion. *J. Herp. Assoc. Afr.* 7: 18–20.
- VOGEL, J.C. 1985. Southern Africa at 18 000 years B.P. *S. Afr. J. Sci.* 81: 250–251.
- WILEY, E.O. 1981. Phylogenetics: The theory and practice of phylogenetic systematics. John Wiley and Sons, New York.