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The differentiation within the genus *Chamaeleo* LAURENTI, 1768¹)

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CONTENTS

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¹) Thesis University of Amsterdam.

Conclusions

INTRODUCTION

Since long chameleons have been known as a curious and systematically difficult group.

The most common chameleons show rather little individual variation (for instance *Ch. chamaeleon* and *Ch. basiliscus*) and therefore can be distinguished as separate species by means of easily recognizable morphological characteristics.

As the most common chameleons were generally the first to be described as species, their distinguishing characters were used as "key characters" (for instance in the keys of BOULENGER (1887) and WERNER (1902, 1911). This situation has led taxonomists to consider these "key characters" as more or less constant for the whole group of chameleons, therefore valid as criteria for defining new species. Afterwards many descriptions of species have been based on the presence or absence of certain "key characters" in a few specimens only, sometimes even in one specimen.

This resulted in considerable taxonomic confusion, for there is increasing evidence, that the "keycharacters" are not constant in all species.

The main purpose of this study is the search for an explanation of this confusing individual and specific variation.

For this theoretical part of my study I required a survey of the species. Previous taxonomic work, e.g. that by WERNER (1902, 1911) and ANGEL (1942) proved very useful, but had to be extended by a personal examination and a critical taxonomical revision of many of the forms described.

I have treated the genus *Chamaeleo* LAURENTI, 1768 in the usual sense, as meant by BOULENGER (1887), WERNER (1911), ANGEL (1942), a.o.

I have divided the genus into groups of related species, aiming at a natural system. Even though WERNER's words (1902): „Die Chamäleons in vollständig natürlicher Weise zu gruppiren, scheint zur Zeit ein Ding der Unmöglichkeit" remain true, an attempt at such a system may be of great help to further investigations.

For practical reasons the chameleons of Madagascar were treated separately. Their connections with the species of the African continent are examined in section 11.

ACKNOWLEDGEMENTS

I am greatly indebted to the French Government, which provided a stipendium for a stay in Paris during two months, in order to study the greater part of the chameleons in the Muséum National d'Histoire Naturelle.

To DR. J. GUIBÉ, curator of the Herpetological Department of the Paris Museum I owe much gratitude for the kind way in which he received me and opened to me the rich collections of his department. It has been a pleasure to dedicate a new chameleon to him, as a token of my gratitude.

Thanks are also due to Professor Dr. ROBERT MERTENS of the Senckenberg Museum and Dr. L. D. BRONGERSMA of the Leyden Museum for the loan of valuable material, to Mr. J. G. J. KUIPER of the Institut Neérlandais in Paris, for his photographs, and to the Direction of the Congo Museum, Tervueren, of the hospitality which enabled me to

look at some of the rare Congo species. To Professor Dr. K. H. Voous I owe special thanks for his criticism and many valuable suggestions.

Finally, this study would not have been completed without the encouragement and direct help of my promotor Professor Dr. H. Engel. To him and Mrs Engel I am greatly indebted for the kindness and the patience with which they read and corrected my typescript at several stages.

Survey of the genus *Chamaeleo* Laurenti, 1768.

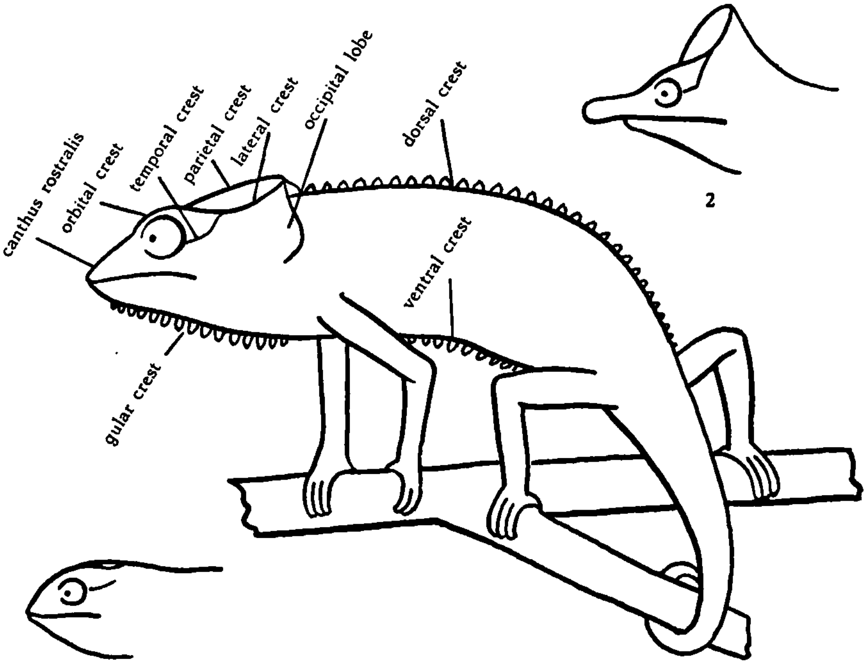
§ 1. CHARACTERS USED FOR THE DIAGNOSIS OF THE SPECIES.

The difficulty expressed by many authors of identifying a specimen of the genus *Chamaeleo*, is mostly due to the fact that WERNER'S „*Chamaeleontidae*" (1911) on which practically all later taxonomic work is based — including several faunae — assigns too large a diagnostic value to his "key" characters.

Especially in the systematics of the genus *Chamaeleo*, these "key" characters have acquired the meaning of principal criteria for distinguishing the species: absence or presence of one or more of these characters decides whether the specimen belongs to this or to that species. Several species and subspecies — the latter practically always without regard to locality — were described only because a specimen differed in one or two key characters from the species already known. As we will see in the following sections, practically none of the following characters — except oviparity and ovoviviparity — is constant in a species.

Here I give only a short list of the characters that are used. The variation and relative taxonomic value of these characters will be discussed in the following sections and summarized in § 19.

1. occipital lobes (see figs. 1 and 2) are dermal flaps connected with the posterior part of the casque. They may be reduced to almost invisible slits behind the head, they may be grown together or separated.
2. a dorsal crest of scales or cones (see fig. 1), sometimes extending over the tail.
3. a ventral crest of scales or cones (fig. 1).
4. a gular crest of scales, cones or scaled, dermal lobes (figs. 1, 6).
5. the squamation may vary from fine homogeneous (fig. 15) to coarsely heterogeneous (fig. 14); in the latter case horizontal rows of greater shields are often present.
6. axillary pits (fig. 7) are little pits in the axilla of the forelegs.
7. a finshaped dorsal crest may be found when the dorsal spines of the vertebrae are lengthened (fig. 16).
8. the casque may be elevated posteriorly (figs. 2, 12, 13, 17, 18), or in one line with the dorsal keel (fig. 3).
9. several crests may be present on the head, sometimes only as ridges, sometimes provided with spiny cones:
    canthus rostralis (figs. 1, 5, 18 and 19)
    orbital crest (fig. 1)
    parietal crest (fig. 1)
    lateral crest (fig. 1)
    temporal crest (fig. 1).
10. the casque may be roof-shaped, i.e. with the parietal crest higher than the lateral crests, or flat, i.e. with the parietal crest absent or on equal level with the lateral crests (fig. 4).
11. oviparity and ovoviviparity.
12. a white midventral line, broad or narrow.
13. the dorsal keel may be without regular series of scales, with a single row of scales or cones, or with a double row of scales (fig. 5).



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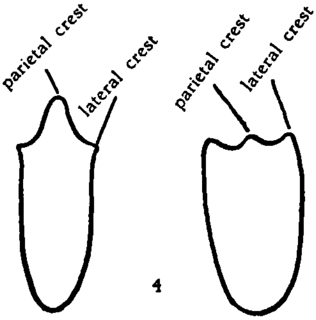

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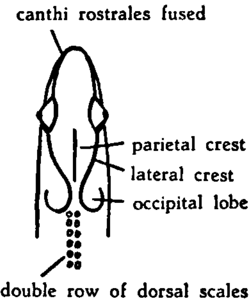

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10


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12


11

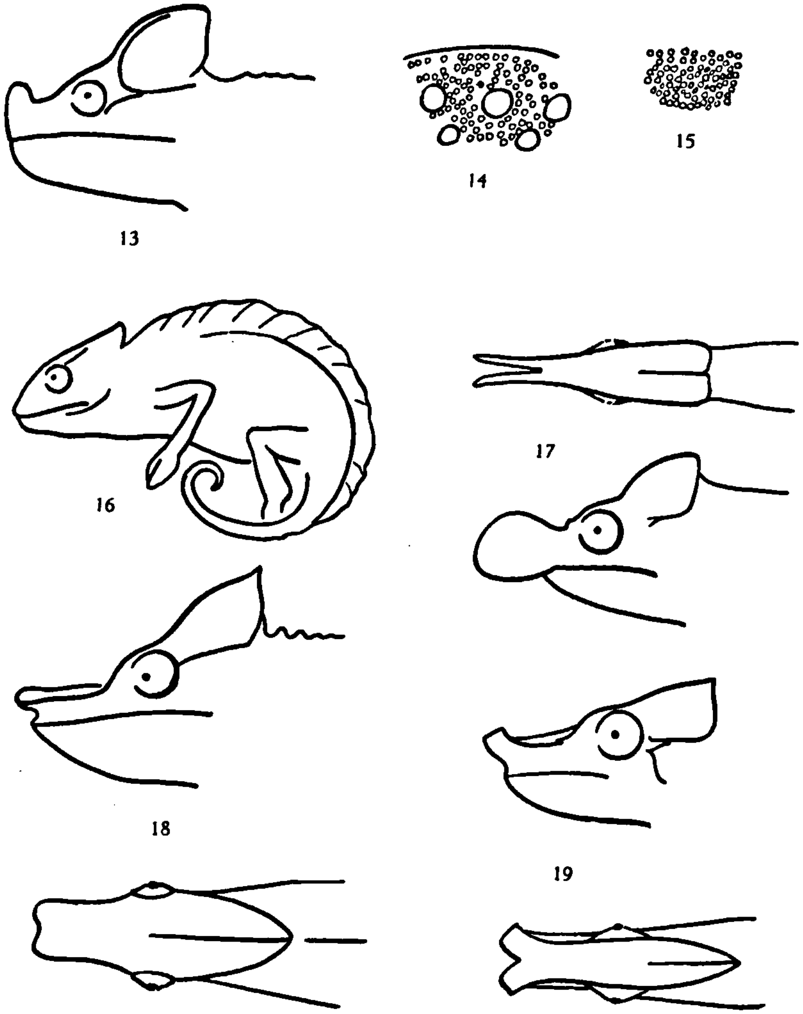

FIGURE 1—19. 1. *Chamaeleo.* The most common characters. 2. *Rhinoceratus*-nose (rigid), casque raised posteriorly. 3. Casque as in *Ch. laevigatus.* 4. Transverse section through roof-shaped casque (left) and flat casque (right). 5. Head from above. 6. Scaled gular lobes. 7. Axillary pit. 8. *Bifidus*-nose from above. 9. Cranial horns. 10. Tarsal spur. 11. *Nasutus*-nose (flexible). 12. *Melleri*-nose (rigid). 13. *Bitaeniatus*-nose. 14. Heterogeneous squamation. 15. Homogeneous squamation. 16. Fin-shaped dorsal keel. 17. *Xenorhinus*-nose from above and from the side. 18. Canthi rostrales fused and protuberant, from the side and from above. 19. Other variation of canthi rostrales fused and protuberant, from the side and from above.

14. on the hindfoot a tarsal spur may be present (fig. 10).
15. ringed horns may be present on the head, one, two, three or four (fig. 9).
16. several protuberances may be found on the snout as shown in figs. 8, 11, 12, 2, 13, 17, 18 and 19 ; I have named them after wellknown species in which they occur ; some of them, for instance those figured in fig. 18 and 19, and perhaps even those of figs. 2, 8, 17, may be taken together as variations of the canthi rostrales grown together.
17. the proportion of the length of the tail to the lenght of head and body may be of importance. The length of the tail is taken from the anus to the extremity of the tail. The length of the head and body is taken from the tip of the snout to the anus. In the following sections with tail index is meant the proportion of the length of the tail to that of the head and body: length of tail/length of head and body.

Part A. The chameleons of Madagascar.

§ 2. GROUP OF *Chamaeleo polleni*,

comprising *Chamaeleo polleni* PETERS, 1873; *Chamaeleo cephalolepis* (GÜNTHER, 1880).

Though the Comoro Archipelago is situated half-way between Madagascar and the African continent, ANGEL also dealt with the species from these islands in his "Lézards de Madagascar" (1942).

In the collections of the Paris and Leyden Museums I found 17 specimens of *Ch. polleni* in all, showing a remarkable variation in at least 9 characters which are generally considered constant in a given species and therefore are often used as characters for distinguishing the species. In the following sections it will be shown that this phenomenon is often found in species from Madagascar and sometimes in species from east Africa. They are, however, rather invariable in species from north and west Africa, Arabia and India. This is the reason why I treat *Ch. polleni* c.s., though not of pure Madagascar origin, in this first section of the chapter on Madagascar chameleons.

Ch. polleni and *Ch. cephalolepis* are both distinguished from the other species of the Madagascar area by the absence of any conspicuous character, such as protuberances on the snout, occipital lobes, strongly developed crests etc. The squamation is homogeneous.

Perhaps there is some relation between *Ch. polleni* and *Ch. pardalis* c.s. The form of the somewhat prominent rostral edge in males of *Ch. cephalolepis*, the shape of the casque in both groups and an occasional almost homogeneous squamation in the females of *Ch. guentheri* are suggestive of such a relationship.

In the collection of the Leyden Museum I found 6 specimens, collected by POLLEN, locality unknown, answering all more or less to the description of *Ch. polleni*. As to their provenance, the only indication, that they might be from the Madagascar region, is that POLLEN indeed visited this island and neighbouring islands. (Dr. L. D. BRONGERSMA in litteris). Therefore, it does not seem unlikely that these specimens were collected on Mayotte island, the territory of *Ch. polleni*.

TABLE A. Characters in *Ch. polleni* compared with those in *Ch. cephalolepis* showing the great variation in the first and the relative constancy in the latter.

		sex	casque elevated	parietal crest	lateral crest	head squamation	body squamation	dorsal crest	dorsal keel	ventral crest	gular crest	white midventral line	length head + body in mm	length tail in mm	axillary pits
Chamaeleo polleni	1	♂	±	±	±	a	b	a	1	±	y	—	100	113	—
	2	♂	+	+	+	a	b	a*	1	±	—	—	90	101	±
	3	♂	+	+	+	a	bc	a	1	+	—	—	87	107	+
	4	♂	±	±	±	a	a	a	1	+	y	+	71	83	±
	5	♀	—	±	+	a	a	b	1.2	—	—	+	58	62	+
	6	♀	—	—	+	a	c	b	1.2×	±	—	±	83	81	—
	7	♂	+	+	+	a	a	a	1	±	—	+	97	113	—
	8	♂	±	±	±	a	b	a	1	+	—	+	84	97	±
	9	♂	+	±	+	a	b	a	1	+	—	—	74	80	±
	10	♂	+	+	+	a	bc	a	1	+	—	+	73	88	±
	11	♂	+	+	+	a	b	a	1	+	—	+	71	81	±
	12	♀	—	+	+	a	b	b	1.×	+	—	+	60	68	±
	13	juv	—	±	±	a	b	a	1	±	—	—	37	40	—
	14	juv	—	±	±	a	a	b	1.2×	±	—	+	42	39	±
	15	juv	—	±	±	a	b	a	1	±	—	—	42	41	—
	16	juv	—	—	±	a	b	b	1.×	±—	—	±	28	26	±
	17	juv	—	—	±	a	b	a	1	+	—	±	28	31	±
Chamaeleo cephalolepis	18	♀	±	±	±	b	b	a	1	+	+	—	67	60	—
	19	♂	+	+	+	b	b	a	1	+	+	—	75	92	—
	20	♂	+	+	+	b	bc	a	1	+	+	—	75	93	—
	21	♂	+	+	+	b	bc	a	1	+	+	—	78	87	—
	22	♂	+	±	+	b	b	a	1	±	+	±	67	71	—

SYMBOLS USED: + = clearly developed; ± = feebly developed; y = a trace only; — = completely absent

Head squamation: a = mixed scales of irregular size; b = scales of the same size.

Body squamation: a = fine, granularly homogeneous; b = homogeneous, but scales arranged in rosettes, comparable with the structure in Ch. chamaeleon; c = moderately heterogeneous.

Dorsal crest: a = continuous from neck to tail; b = in neck region and anterior part of the back only (sometimes 10 isolated cones only).

Dorsal keel: 1 = a single row of scales from neck to tail; 1.2 = anterior part of the back with a single row of scales, followed by a double row of scales; × = irregularly placed scales, etc.

Chamaeleo polleni, nrs 1—6 (Leyden collection) locality unknown; nrs 7—10 and 14—17 (Paris collection: Ch. 54—84.463 and Ch. 54^1—84.467 respectively) from Mayotte, Humblot leg.; nrs 11—13 (Paris Ch. 54^2) Afrique, Koperhorn leg.

Chamaeleo cephalolepis, nrs 18—22 (Paris Ch. 17—85.466, 85.468, 85.469 and 87.78) from Grande Comore, Humblot leg.

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*) Probably. First part of the back is damaged.

These 6 specimens (nrs. 1—6 in table A) differ in many respects from the descriptions given by WERNER (1911) and ANGEL (1942). For instance nr. 6 may be described as follows: female with almost ripe eggs; a low casque, in silhouette an almost uninterrupted line with the dorsal keel; *parietal crest absent*; shields on the casque of irregular size; *squamation of the body moderately heterogeneous*; no continuous dorsal crest, but about 10 isolated little cones in the neck region and the foremost part of the back, *the rest of the dorsal keel partly showing a double row of scales, partly with irregularly placed scales; a ventral crest only faintly indicated*; a vague white midventral line; no gular crest; length of head and body 83 mm, length of tail 81 mm. (in italics the characters differing from the descriptions by WERNER (1911) and ANGEL (1942)).

As will be shown in the following sections, this kind of differences is often used as a base for the description of new species. But here all possible intermediates were found between the specimen described above and the descriptions given by WERNER (1911) and ANGEL (1942). Therefore I concluded that they probably belong to one species.

In table A the 6 specimens of the Leyden collection are compared with all the specimens of *Ch. polleni* and some of *Ch. cephalolepis* of the Paris collection.

As to the 17 specimens of *Ch. polleni* we found the following deviations from the official descriptions:

1. posterior part of the casque rather strongly elevated (10 specimens, all males),
2. poorly developed parietal crest (4 males, 1 female),
3. parietal crest absent (1 female, 2 juveniles),
4. poorly developed lateral crest (3 males),
5. moderately heterogeneous squamation (2 males, 1 female). The other specimens show all kinds of transitions between a fine, granular, homogeneous squamation and a squamation with the scales more or less arranged in rosettes as in *Ch. chamaeleon*,
6. 12 specimens (9 males, 3 juveniles) with a continuous crest of isolated low cones. One male possesses about 10 higher cones in the neck region,
7. 5 specimens (3 females, 2 juveniles) have a dorsal keel with partly a double row of scales, partly irregularly placed scales,
8. According to WERNER (1911), *Ch. polleni* possesses a clearly distinct ventral crest. In the key of ANGEL (1942) we read: "crête ventrale absente (parfois une trace chez les espèces *willsi, polleni, minor*)". I found a low, but clearly developed ventral crest in 8 specimens (6 males, 1 female, 1 juvenile), a poorly developed ventral crest in 7 specimens (3 males, 1 female, 3 juveniles), one juvenile specimen with only a slight indication of a ventral crest on the first quarter of the belly and one female completely lacking even an indication of a ventral crest.
9. 2 male specimens show a little trace of a gular crest. This is of importance as one of the major differences between *Ch. polleni* and *Ch. cephalolepis* is the presence of a gular crest in the latter species.
10. I found a white midventral line in 5 male specimens and in all 3 female specimens. ANGEL (1942) mentioned this character only in females.

As to the specimens of *Ch. cephalolepis*, they prove to be much less variable than the related *Ch. polleni*. Their differences with *Ch. polleni* are:

1. in male specimens a prominent rostral ridge formed by some cones on the junction of the canthi rostrales,
2. regular scales on the casque (irregular in *Ch. polleni*),
3. a well developed gular crest.

§ 3. GROUP OF *Chamaeleo rhinoceratus*,

comprising *Chamaeleo rhinoceratus* (GRAY, 1864); *Chamaeleo rhinoceratus* var. *lineatus* (METHUEN & HEWITT, 1913); *Chamaeleo labordi* GRANDIDIER, 1872; *Chamaeleo voeltzkowi* (BOETTGER, 1893); *Chamaeleo monoceras* (BOETTGER, 1913); *Chamaeleo barbouri* HEIKERTINGER, 1942.

A group of rare chameleons, distinguished from the other chameleons of Madagascar by the rigid, laterally compressed rostral appendix. The upper side of this appendix is formed by the canthi rostrales, grown together (differing, as to this respect, from the bony protuberance on the snout of *Ch. melleri* from the African continent).

The descriptions of the species and variety named above are compared in table B, only as far as they differ.

In the same table I have compared all the material of this group (7 specimens) from the Paris Museum, belonging to two species only (*Ch. rhinoceratus* and *Ch. labordi*) and one still unidentified specimen. This seems at first sight far too small a material for any conclusion. But taking into consideration that the total number of specimens, mentioned in literature, belonging to these 6 forms amounts to 13 only, it seems quite unreasonable to treat my 7 specimens as exceptions. The more so as the descriptions of *Ch. barbouri* (2 specimens), of *Ch. rhinoceratus* var. *lineatus* (1 specimen) and of *Ch. monoceras* (1 specimen) are extensive enough to be used for comparison. So that the data in my table B may be considered to be based on 11 specimens (against 13 in earlier literature).

It must be remarked that the measurements in the descriptions of *Ch. labordi* by ANGEL (1942) and WERNER (1911) do not agree with the measurements of the type specimen (Paris 5469) taken by myself.

In the original description GRANDIDIER gave the following measurements:

"largeur du corps 0,111 ; de la queue 0,122 ; de la tête 0,036"

This formulation suggests that with "largeur du corps" is meant the length of the body without that of the head.

Probably WERNER (1911) understood it that way, for he gives as the total length 269 mm (= 111 + 122 + 36 mm). In reality the total length is 233 mm, of which the tail takes 122 mm and the head 36 mm. The conclusion is that GRANDIDIER meant by "largeur du corps" the length of the body *plus* the length of the head. The misunderstanding by WERNER (1911), copied unchanged by ANGEL (1942), was confusing, as their descriptions suggested that the tail of *Ch. labordi* was shorter than head plus body, in contrast with the related species *Ch. rhinoceratus* and *Ch. voeltzkowi*.

(Table B)

	rhinoceratus	*labordi*	*voeltzkowi*	*monoceras*	PARIS collection							*rh. lineatus*	*barbouri*	
					1	2	3	4	5	6	7		*type*	*paratype*
squamation	b (—b)	a	b	b	b	±a	a	a	a	—b	—b	—b	—b	—b
lateral row of larger scales on the flank	— ?	—	+	+	+	—	—	—	—	+	+	+	?	?
dorsal crest	♂ a, ♀ b	♂ a, ♀ b & c	a	a	a	a	a	c	b	a	b	b	—	—
parietal crest	a ?	a	b	a?	a	a	a	a	a	a	a	a	a	a
rostral appendix	a & a b	♂ ab ♀ —a	a	+ b	a	b	ab	—a	—a	b	b	a	—a	—a
casque	ab	♂ a ♀ b	a	b	a	b	a	b	b	a	b	b	ab	ab
lateral crest	a	♂ b ♀ —b	—	a	a	a	b	—b	—b	—	a	—a	—	—
axillary pit	+ & —	+	+	+	—	+	+	+	±	+	+	?	+	+
whitish lateral line on the flank	+	♂ + ♀ —	+	+	±	±	+	—	—	+	+	±	—	—
tail index	<1 & > 1	♂ > 1 ♀ < 1	>1	<1	>1	<1	>1	<1	<1	>1	>1	< 1	>1	=1
colour under tail	?	+	+	—	—	—	±	+	+	±	—	+	+	+
gular + ventral crest	b	♂—a, ♀—a & —b	a	c	—b	—b	a	—b	—a	—b	—b	a	—	—
sex				♂	♂	♂	♂	♀	♀	♂	♂	♀?	♀	♀
locality				Betsako at Majunga N W. Madagascar			Belo					Tsivanoa	Morondava W. of Mahabo	

TABLE B. 7 specimens belonging to the group of *Ch. rhinoceratus* c.s. compared with the descriptions of *Ch. rhinoceratus, Ch. labordi, Ch. voeltzkowi, Ch. monoceras, Ch. rhinoceratus lineatus* and *Ch. barbouri.*

SYMBOLS USED : + = present; — = absent; —a = a feebly developed.
Squamation: a = homogeneous; b = heterogeneous.
Parietal crest: a = reaching the top of the casque; b = not reaching the top.
Dorsal crest: a = distinct from neck to tail; b = only distinct on the foremost part of the back; c = hardly distinct.
Rostral appendix: a = smaller than orbital diameter; b = larger than orbital diameter; ab = equal to orbital diameter.
Casque: a = elevated posteriorly; b = not elevated.
Lateral crest: a = reaching the top of the casque; b = not reaching the top.
Tail index: >1 = length of tail greater than length of head + body; <1 = length of tail smaller than length of head + body.
Colour under tail: absence (—) or presence (+) of white lines under the tail.

Gular + ventral crest: a = gular and ventral crest present unseparated; b = gular and ventral crest present separated; c = gular crest present.

For *Ch. rhinoceratus, labordi,* and *voeltzkowi* I used the descriptions of WERNER (1911), eventually as corrected by ANGEL (1942) and in the case of *Ch. labordi* corrected by myself after examination of the type specimen and of the two female specimens described by ANGEL (1942). The characters of *Ch. rhinoceratus lineatus* and *Ch. barbouri* are taken from the original publications. The specimens from the Paris Collection are catalogued as follows:

nr. 1 — Ch. 56.5467, type of *Ch. antimena*. Locality unknown. Determined as *Ch. rhinoceratus*.
nr. 2 — Ch. 56.38.156. Locality unknown. Det. as *Ch. rhinoceratus*.
nr. 3 — Ch. 39—99.312. Type of *Ch. labordi*. Belo.
nr. 4 — Ch. 39^1—5470. First described female of *Ch. labordi*. (ANGEL 1942). Locality unknown.
nr. 5 — Ch. 39^1—5470. First described female of *Ch. labordi* (ANGEL 1942). Locality unknown.
nr. 6 — Ch. 39^2—5469. Det. as *Ch. labordi*. Locality unknown.
nr. 7 — Locality unknown. Not registered.

Table B shows that the differences between *Ch. barbouri* and the females of *Ch. labordi* are negligeable. Obviously HEIKERTINGER (1942) had not yet read the descriptions of the females of *Ch. labordi*, published by ANGEL in the same year. So our first conclusion is that *Ch. barbouri* HEIKERTINGER, 1942 is a synonym of *Ch. labordi* GRANDIDIER, 1872.

The second conclusion to be drawn from table B is that, apart from the two specimens of *Ch. barbouri* (the data of which I abstracted from literature), every specimen differs from the others in one or more characters. Apart from the type specimen of course, none of the specimens answers completely to any description of a species.

For instance nr 7 (Paris Museum, not yet registered) corresponds
as to the squamation : mostly with *Ch. rhinoceratus,*
as to the lateral series of greater scales on the flank : with *Ch. monoceras,* somewhat with *Ch. voeltzkowi,*
as to the parietal crest : with *Ch. rhinoceratus, Ch. labordi* and *Ch. monoceras,*

as to the dorsal crest: with the females of *Ch. rhinoceratus* and of *Ch. labordi*,

as to the elevation of the casque: with *Ch. monoceras* and the females of *Ch. labordi*,

as to the lateral crest: with *Ch. rhinoceratus* and *Ch. monoceras*,

as to the axillary pit: with *Ch. rhinoceratus*, *Ch. labordi*, *Ch. voeltzkowi* and *Ch. monoceras*,

as to the whitish lateral line on the flank: with *Ch. rhinoceratus*, *Ch. voeltzkowi*, *Ch. monoceratus* and the male of *Ch. labordi*,

as to the tail in proportion to the length of head and body: with *Ch. rhinoceratus*, *Ch. labordi*, *Ch. voeltzkowi*,

as to the nature of the gular and ventral crest: with *Ch. rhinoceratus* and the females of *Ch. labordi*,

as to the relative length of the rostral appendix: with none of the species.

So this specimen has 8 characters in common with the description of *Ch. rhinoceratus*, 4 characters in common with the description of *Ch. voeltzkowi*, 7 characters in common with the description of *Ch. labordi* and 6 characters in common with the description of *Ch. monoceras*.

For the other specimens I made similar comparisons. In table C I have given the results: the number of characters that each of the specimens has in common with the descriptions of the species.

TABLE C. Conclusion of table B: numbers of characters which each of the specimens 1—7 (mentioned in table B) have in common with the descriptions of *Ch. rhinoceratus*, *Ch. labordi*, *Ch. voeltzkowi* and *Ch. monoceras*.

		rhinoceratus	*labordi*	*voeltzkowi*	*monoceras*
Specimen	1	10	5	7	6
	2	8	7	3	8
	3	7	12	6	4
	4	6	12	1	4
	5	5	12	1	4
	6	7	8	8	5
	7	8	7	4	6
	8	7	7	5	6
	9	5	7	4	2
	10	5	7	3	2
	11	7	6	3	12

The data of the specimens 8—11 were abstracted from the original descriptions of *Ch. rhinoceratus lineatus* (8), *Ch. barbouri* (9, 10) and *Ch. monoceras* (11).

It is difficult to decide to which species the specimens belong, apart from the specimens nr. 3, 4 and 5, which answer rather well to the description of *Ch. labordi* [not surprisingly, as nr. 3 is the type of this species and nr. 4 and 5 are the first females of it described by ANGEL, 1942 (though I had to make a slight correction in his description)].

Of course one might say that a specimen belongs to the species with which it has more in common than with any other. So then nr. 1 would belong to *Ch. rhinoceratus* and nr. 7, but with still less evidence, to the same species. But then the question arises to which species belong nr. 2 and nr. 6?

And what to think of the other specimens, with no more than 6 or 7 out of 12 characters in common with any of the described species?

As shown above, the total number of the specimens known in literature of the species *Ch. rhinoceratus. Ch. labordi, Ch. voeltzkowi* and *Ch. monoceras* amounts to 13 only. Considering I had to my disposal 7 specimens from the Paris collection and 4 quite sufficient descriptions from literature, I think I am quite justified in drawing the following conclusions: there is no sufficient reason to distinguish as separate species *Ch. rhinoceratus, Ch. labordi* and *Ch. voeltzkowi*. Therefore, as *Ch. rhinoceratus* is the first species described, I consider *Ch. labordi* and *Ch. voeltzkowi* to be synonyms of *Ch. rhinoceratus*. As to *Ch. monoceras*, I am not yet quite certain about its position. The type of *Ch. monoceras* differs in two characters from the specimens I reckon to be *Ch. rhinoceratus:* the much greater rostral appendix and the presence of the gular crest only. Considering that nr. 2, 6 and 7 have rostral appendices greater than mentioned in the descriptions of *Ch. rhinoceratus*, and that differences in gular and ventral crests seem less important for distinction especially in the species of Madagascar, the position of *Ch. monoceras* as a separate species is most doubtful. However, for the time being, before drawing further conclusions, I prefer waiting for more material.

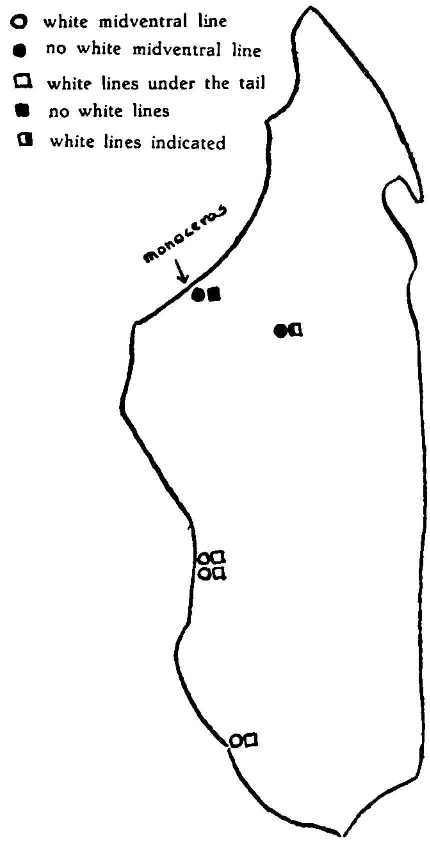
The variety *lineatus*, described after a single specimen, cannot be regarded as a subspecies. First, as the total number of all specimens known is so small and secondly, because the provenance of only a few specimens is known. Together with the type of *Ch. monoceras*, I have put all known specimens on map 1, with indications about the absence or presence of white midventral lines and white lines under the tail. Though the material is very little, the distribution of these characters coincides with the distribution of the characters "white lines under the tail" of *Ch. lateralis* (see p. 19).

Summarizing, *Ch. rhinoceratus* and *Ch. monoceras* are very rare species. The first shows a great variation in the squamation, absence or presence of a lateral line of larger scales on the flank, the dorsal crest, the length of the rostral appendix, absence or presence of a lateral crest, absence or presence of axillary pits, absence or presence of a white lateral line on the flank, the relative length of the tail, the gular and ventral crest. It may be that the white midventral line and the white lines under the tail show a tendency to be present in the north and to be absent in the south.

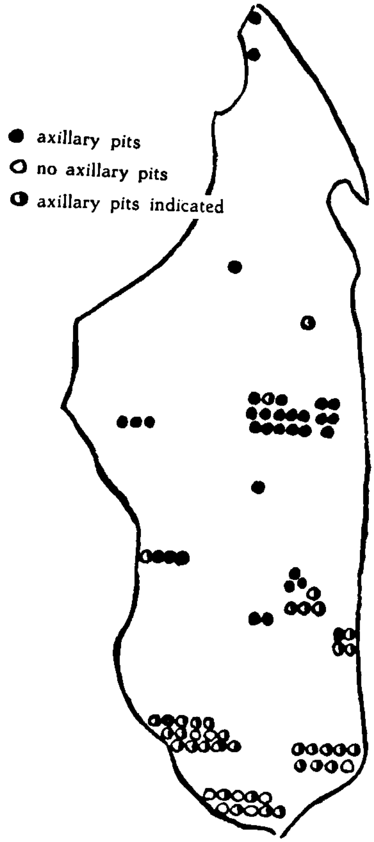
This great variability is not remarkable in this area. *Ch. polleni* (§ 1) and *Ch. lateralis* (§ 4) for instance, both show variations of mostly the same characters as *Ch. rhinoceratus*.

The rarity of *Ch. rhinoceratus*, combined with its great variability, is the cause of the many descriptions of separate species.

The nearest relative of *Ch. rhinoceratus* and *Ch. monoceras* is quite probably the East African *Ch. xenorhinus* (Boulenger, 1901). The only difference is found in the rostral appendix which in *Ch. rhinoceratus* and *Ch. monoceras* is unpaired, in *Ch. xenorhinus*, however, paired. There are indications that the rostral appendix of *Ch. rhinoceratus* also has a paired origin, as the edge of the appendix in some specimens clearly has a double row of scales. Moreover, the rostral appendix of *Ch. xenorhinus*, at least in the specimens I examined in the Museum of Tervueren (nr. 8949 Coll. BURGEON, Kalonge-Ruwenzori, Alt 2050 ... 9.VIII. 1932), does not consist of completely separated units. With the help of a needle it was possible to show that the double nature of this appendix only exists in its edges. Towards the centre the two halves are grown together.



MAP 1. Madagascar. Distribution of the characters "white midventral line" and "white lines under the tail" in *Ch. rhinoceratus* and *Ch. monoceras*.



MAP 2. Madagascar. Distribution of the character "axillary pits" in *Ch. lateralis*.

Ch. carpenteri PARKER, 1929 probably also belongs to the same group. I do not understand why LOVERIDGE (1957) regarded it as identical with *Ch. xenorhinus*. He gives no support for his statement, nor any reference.

§ 4. GROUP OF *Chamaeleo lateralis*,

comprising *Chamaeleo lateralis* GRAY, 1831; *Chamaeleo campani* GRANDIDIER, 1872 and *Chamaeleo lambertoni* (ANGEL, 1921).

This group is distinguished from the other chameleons of Madagascar by the double row of scales on the dorsal keel, the absence of occipital lobes and the presence of a white midventral line.

Doubting the validity of these species I made a close examination of the variation in the specimens of the collections of Paris, Leyden and Amsterdam, viz. 121 specimens of *Ch. lateralis*, 1 specimen of *Ch. lambertoni* (the type specimen) and 8 specimens of *Ch. campani* (see table D).

According to ANGEL (1921, 1942) *Ch. lambertoni* was distinguished from *Ch. lateralis* by the following characters:

a. absence of a gular crest.
b. very fine, homogeneous squamation.
c. 70 scales in a vertical row between the dorsal keel and the midventral line.
d. length of tail shorter than that of head and body together.

We found for *Ch. lateralis* (cf. table D):

a. 115 specimens with a gular crest, 6 with a slight indication of it, but none without gular crest.
b. every possible variation between a fine homogeneous (8 specimens), vaguely heterogeneous (48 specimens) and clearly heterogeneous squamation (65 specimens).
c. the number of scales on a vertical row between dorsal keel and midventral line varies from 54 to 85, with most specimens from 65 to 75.
d. out of 50 females (the type specimen of *Ch. lambertoni* is also a female) only 5 specimens had a tail longer than head and body together, in 2 specimens the length of the tail was equal to that of head and body together and in 43 specimens the tail was shorter (in the males those numbers were respectively 46,5 and 8, in the juvenile specimens 5, 1 and 6).

Moreover I found 19 specimens without the slightest indication of a ventral crest, as it is in *Ch. lambertoni*.

Thus the only difference between *Ch. lambertoni* and *Ch. lateralis* would be the total absence of a gular crest, *Ch. lateralis* having at least a vague indication of it. All the other characters of *Ch. lambertoni* fall within the normal variation of *Ch. lateralis*. Beside the type specimen, only one other specimen of *Ch. lambertoni* is known (ANGEL, 1950).

Therefore I consider *Ch. lambertoni* a synonym of *Ch. lateralis*.

Though *Ch. campani* is closely related to *Ch. lateralis* I can only conclude that both are valid species, as there are several constant differences

TABLE D. The type specimen of *Ch. lambertoni* compared with 121 specimens of *Ch. lateralis* and 8 specimens of *Ch. campani*, showing the lack of difference between *Ch. lambertoni* and *Ch. lateralis*.

	Ch. lateralis 121 specimens	*Ch. lambertoni* Paris Ch 41—21.269 1 specimen (type)	*Ch. campani* 8 specimens
squamation	8a, 48ab, 65b	1a	8c
number of scales on flank	54—85 (mostly 65—75)	75—78	47—66
gular crest	6±, 115+	1—	4±, 4—
ventral crest	102±, 19—	1—	2±, 6—
tail index	10 ♂a, 46 ♂ b 45 ♂ a, 5 ♂ b 10 juv. a, 5 juv. b	1 ♀ a	2♂ b, 1 ♂ a 5 ♀ a
axillary pits	71+, 42±, 8—	1+	8 +
colour	108+, 13—	1—	1±, 7x
colour of tail	32+, 38±, 51—	1±	2+, 5±, 1—

SYMBOLS USED:

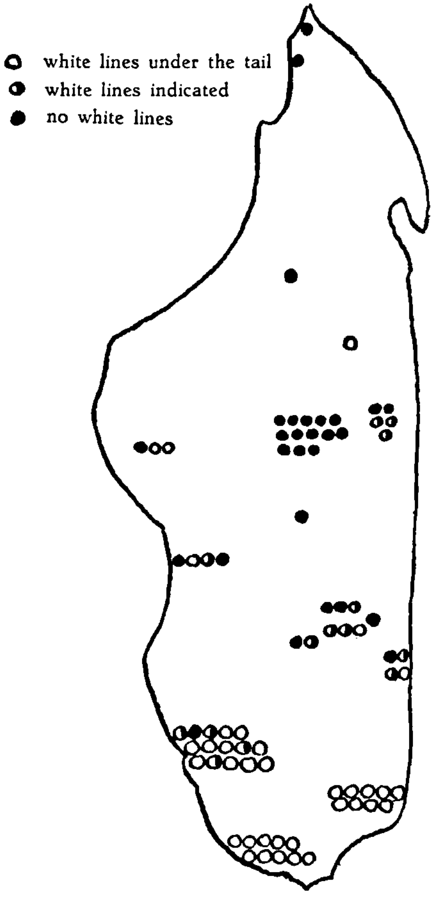
Squamation: a = homogeneous; b = heterogeneous; ab = slightly heterogeneous; c = as in *Ch. campani*, several horizontal rows of larger shields on the flank.
Number of scales on the flank is counted in a vertical row, about the middle of the body, from the dorsal keel to the midventral line.
Gular crest, ventral crest, axillary pits: + = present; — = absent; ± = hardly distinct.
Tail index: a = tail shorter than head + body; b = tail longer than head + body.
Colour: + = a horizontal white line on the flank; — = no such line; x = two or more white, horizontal lines on the flank.
Colour of tail: + = one or two white lines under the tail; — = no such lines; ± = white lines under the base of the tail only.

between them, while the distribution of *Ch. lateralis* overlaps that of *Ch. campani.*

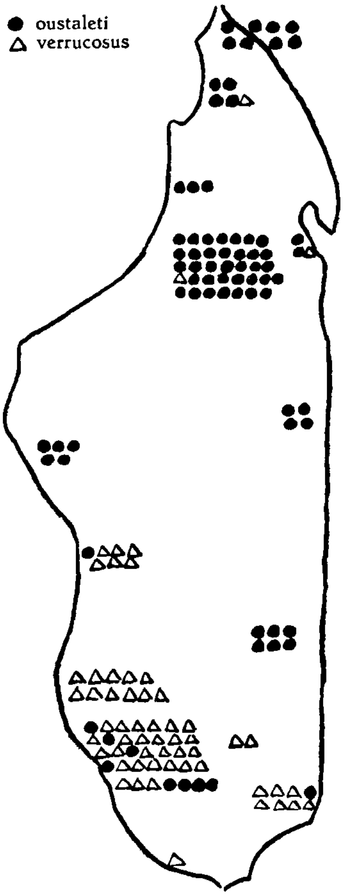
Ch. campani is distinguished from *Ch. lateralis* by the following characters :

1. about 6 horizontal rows of widely separated, larger scales on the flanks (*Ch. lateralis* sometimes has one row of larger scales, close together, always smaller than in *Ch. campani*).
2. usually 2 or more white lines on the flanks (*Ch. lateralis* has — not always — one white line on either flank).
3. the number of scales in a vertical row between dorsal keel and midventral line varies from 47 to 66 (in *Ch. lateralis* from 54 to 85, mostly from 65 to 75).

4. maximum length *Ch. campani*, male (Paris Ch 40^{12}—90.429).
head and body . . 6.4 cm
tail . . . . 6.7 cm
maximum length *Ch. campani*, female (Paris Ch. 16^{1}—91.391)
head and body . . 6.7 cm
tail . . . . 6.5 cm
maximum length *Ch. lateralis*, male (Paris Ch 40^{2}—91.330)
head and body . . 13.9 cm
tail . . . . 15.4 cm
maximum length *Ch. lateralis*, female (Paris without number)
head and body . . 11.0 cm
tail . . . . 11.8 cm



MAP 3. Madagascar. Distribution of the character "white lines under the tail" in *Ch. lateralis*.



MAP 4. Madagascar. Localities of *Ch. oustaleti* and *Ch. verrucosus*, according to the catalogue of the Paris Museum.

As *Ch. lateralis* is one of the commonest species, known from many places all over the island, I tried to find out, if there is any connection between the variations of the characters and their geographical distribution. First of all I found a remarkable correlation between the absence and presence of one or two white lines under the tail and the absence and presence of axillary pits, as is shown in table E. We find a tendency towards the combination of the characters "presence of axillary pits" and "absence of white lines under the tail" and a tendency contrariwise towards the combination of the characters "absence or only an indication of axillary pits" and "precence of white lines under the tail". These tendencies seem to be connected with the geographical distribution (see maps 2 and 3).

TABLE E. The relation of the characters "axillary pits" and "white lines under the tail", as found in 121 specimens of *Ch. lateralis.*

	axillary pits clearly developed	axillary pits absent or feebly developed
white lines under the tail, at least indicated	24	46
no white lines	47	4

With 39 specimens collected north of the line Tulear-Farafangana I found 32 with distinct axillary pits, 7 with an indication of these pits. Among these same specimens were 26 without white lines under the tail, 8 with an indication and 5 with clearly distinct white lines under the tail. With 38 specimens from Tulear and Farafangana and more southward, I found 8 without axillary pits, 28 with only an indication and 2 with distinct axillary pits. These same 38 specimens comprise 2 without white lines under the tail, 6 with indications and 30 with clearly distinct white lines under the tail.

The type of *Ch. lambertoni* (Paris Ch 41-21.269., provenance Sihanaka) fits quite well in this scheme of variation, as Sihanaka — according to ANGEL (1942) — lies north of the line Tulear-Farafangana and as this specimen possesses distinct axillary pits and only an indication of white lines under the tail. Approximately the same geographical distribution of axillary pits is found in the groups *Ch. verrucosus-Ch. oustaleti, Ch. nasutus* c.s. and *Ch. malthe* c.s. (see pages 23, 28 and 33).

As intermediate forms exist between animals with paired and unpaired rows of scales on the dorsal keel in *Ch. polleni* (see p. 10), it occurred to me that *Ch. lateralis* might occasionally show at least indications of unpaired scales on the dorsal keel. In most specimens I could not find even the slightest indication, in the Leyden collection only I found 10 specimens (LAM & MEEUSE, 19-XI-1938) 6 of which showed some unpaired scales in the neck (respectively 13, 5, 8, 7, 4 and 8 unpaired scales, the two last specimens showed some paired scales interrupting the unpaired ones). The same is found in *Ch. anchietae* (see p. 50).

I give here the description of a rather deviating specimen, which I provisionally consider to belong to *Ch. lateralis*:

Paris collection, without number. Male. Provenance Lac Tsimanampetsotsa. Dorsal keel irregular with paired and unpaired rows of scales. Rather high casque, with distinct parietal and lateral crests. Gular and ventral crest without interruption. White midventral line. A white lateral line on the flank. A little swelling above the nose, perhaps of accidental origin. Slightly heterogeneous squamation. No axillary pits (a vague indication under the right arm).

Length of head and body 10 cm, tail 13.7 cm.

§ 5. GROUP OF *Chamaeleo oustaleti*,

comprising *Chamaeleo oustaleti* (MOCQUARD, 1894); *Chamaeleo verrucosus* CUVIER, 1829; *Chamaeleo semicristatus* (BOETTGER, 1894); *Chamaeleo pardalis* CUVIER, 1829; *Chamaeleo guentheri* (BOULENGER, 1888).

This group is distinguished from the other chameleons of Madagascar by the coarse, heterogeneous squamation, the prominent parietal crest, the highly elevated casque, the absence of occipital lobes and by their large size (*Ch. oustaleti* is the biggest chameleon, maximum length 63 cm).

As table F shows, the differences between *Ch. oustaleti* and *Ch. verrucosus* are greater than those between *Ch. verrucosus* and *Ch. semicristatus*.

There seems to be one important difference only between *Ch. verrucosus* and *Ch. semicristatus*: the number of cones of the dorsal crest in *Ch. verrucosus* varies between 30 and 40, the dorsal crest covers the whole of the back, while in *Ch. semicristatus* the number of the dorsal cones varies between 5 and 20, situated on the anterior part of the back only. ANGEL (1942) recorded another difference between *Ch. verrucosus* and *Ch. semicristatus*; in the male of the latter the base of the tail is not swollen (in many species the males are distinguished by the swollen base of the tail). Both WERNER (1911) and ANGEL (1942) gave measurements only of males of *Ch. verrucosus* and only of females of *Ch. semicristatus*.

TABLE F. Comparison of *Ch. oustaleti*, *Ch. verrucosus* and *Ch. semicristatus* showing the relatively small difference between *Ch. verrucosus* and *Ch. semicristatus* whereas these two together are clearly distinguished from *Ch. oustaleti*.

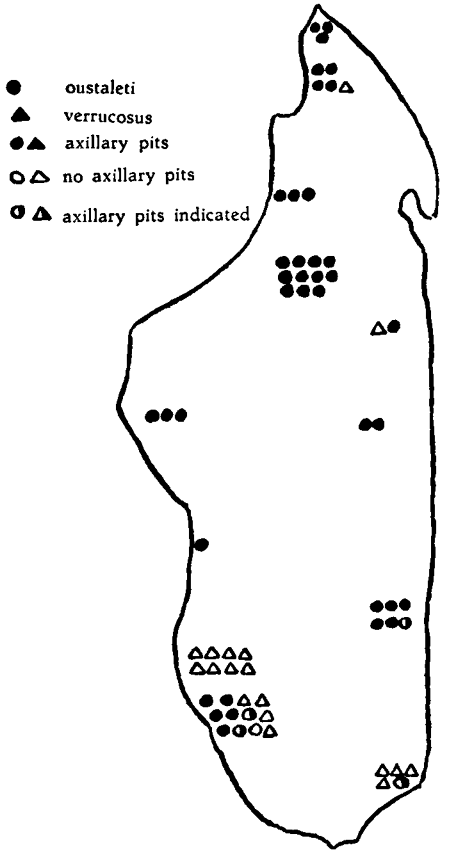
	Ch. oustaleti	*Ch. verrucosus*	*Ch. semicristatus*
large temporal shields	+ & —	+	+
a series of large lateral shields on the flank	—	+	+
number of dorsal cones	>45	30—40	5—20
axillary pits	+	—	—

In the collection of unidentified material of the Paris Museum I found 9 specimens of *Ch. verrucosus*, all males, and 5 specimens of *Ch. semicristatus*, all females.

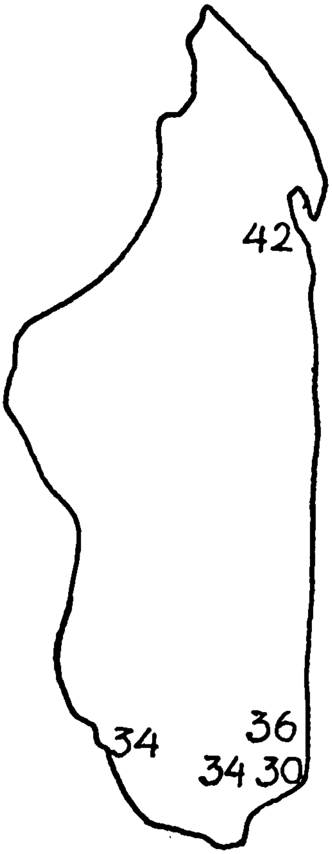
In the Paris Museum I examined the specimens recorded as females of *Ch. verrucosus* (only 12 out of the 14 catalogued were present); they all proved to be males (the base of tail and the belly in all these specimens were opened), 2 out of them belonged to *Ch. oustaleti*.

It seems clear to me that *Ch. semicristatus* (Boettger, 1894) is a synonym of *Ch. verrucosus* Cuvier, 1829. The original description of *Ch. verrucosus* is the description of a male specimen, that of *Ch. semicristatus* is of a female.

Ch. oustaleti and *Ch. verrucosus* both are recorded from throughout Madagascar (the latter also from some neighbouring islands). Kaudern (1922) thought that *Ch. verrucosus* was lacking in n.w. Madagascar, but Angel (1942) recorded some specimens from there.



Map 5. Madagascar. Distribution of the character "axillary pits" in *Ch. oustaleti* and *Ch. verrucosus*.



Map 6. Madagascar. Numbers of dorsal cones in *Ch. verrucosus*.

Mapping out all provenances of *Ch. verrucosus* and *Ch. oustaleti* (from the catalogue of the Paris Museum), we find that the centre of the distribution of *Ch. verrucosus* lies in the south and south west of Madagascar and that of *Ch. oustaleti* more to the north and east (see map 4).

It is remarkable that the northern species (*Ch. oustaleti*) possesses axillary pits and that the southern species (*Ch. verrucosus*) does not. Out of 25 specimens of *Ch. verrucosus* (+ *semicristatus*) 24 lack axillary pits, only one specimen, of unknown provenance, possesses an axillary pit (see p. 23).

The only specimens of *Ch. oustaleti* without a trace of an axillary pit came from Bas Fihérêna, Tulear (Paris Ch. 502-06.79 and 06.76), that is from pure *verrucosus* territory. Specimens lacking axillary pits on one side or with only an indication of axillary pits also came from this territory (see map 5).

So in these closely allied species we find a similar north-south pattern of distribution of the character axillary pits as in *Ch. nasutus* c.s., *Ch. lateralis* c.s. and as perhaps in *Ch. malthe* c.s.

Another north-south pattern of distribution can be found in the number of the cones of the dorsal crest, as is suggested already by the fact that the northern species (*Ch. oustaleti*) usually possesses more than 45 of these cones ant the southern species (*Ch. verrucosus*) less than 40. In 49 specimens of *Ch. oustaleti* I found an average of 55 dorsal cones, varying between 43 and 70. In 13 male specimens of *Ch. verrusus* I found an average of 37, varying between 30 and 48 (the female specimens, *Ch. semicristatus,* seldom have more than 15 cones).

Unfortunately *Ch. verrucosus* specimens from 5 localities only are available (see map 6). Such rare records would be of no value, if we had not found a clear tendency towards a greater number of dorsal cones from south to north in *Ch. oustaleti* (see map 7). The only northern specimen of *Ch. verrucosus* possesses 42 dorsal cones (the average is 37). The only specimen of *Ch. verrucosus* with traces of axillary pits (an indication for its northern provenance, which is unknown) possesses 44 dorsal cones.

Among the unregistered specimens of the Paris collection I found the following aberrant characters:

Ch. oustaleti:

—weak ventral crest in 5 specimens

—anterior part of the ventral crest present, posterior part absent in 3 specimens

—no ventral crest at all in 1 specimen (in the Amsterdam collection in 4 specimens)

—small numbers of dorsal cones : 47, 45—46, 44—45, 43, 45—46, 40—44 (if two figures are given, the latter comprises some little cones in the neck)

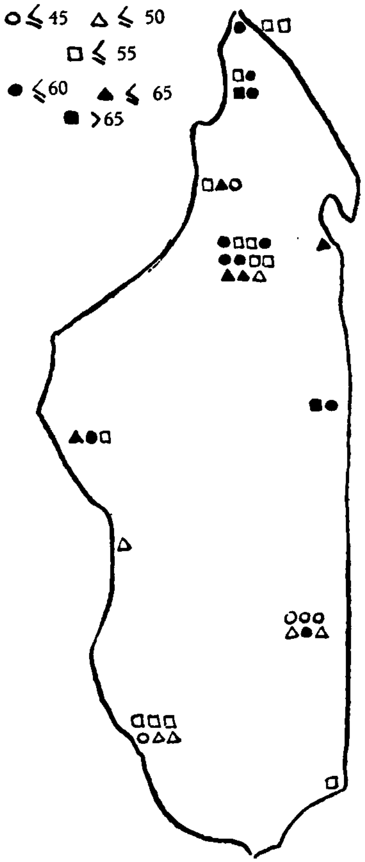
—indication of a lateral row of larger scales on the flank (as in *Ch. verrucosus*) in 7 specimens

—light midventral line in 1 specimen

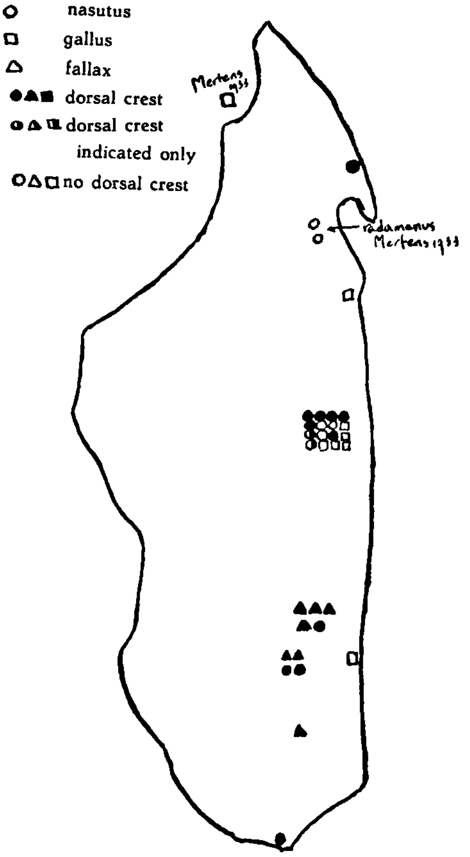
Ch. verrucosus :
—large numbers of dorsal cones: 41—42, 40—44, 42—48, 40—41, 40

The following provenances may be added to the range of *Ch. oustaleti* as given by ANGEL, 1942 (south west, west, north west, north, north east, central) : east, central south, south east, viz. 5 specimens from Ivohibe, 2 from Perinet, 1 from Fort Dauphin, 1 from Lac Alaotra.

The following provenances may be added to the range of *Ch. pardalis* as given by ANGEL, 1942 (east, north west, some islands): south east,



MAP 7. Madagascar. Numbers of dorsal cones in *Ch. oustaleti.*



MAP 8. Madagascar. Distribution of the character "dorsal crest" (in male specimens only) in *Ch. nasutus, Ch. gallus* and *Ch. fallax.* The localities of *Ch. radamanus* (= *Ch. nasutus*) are roughly indicated only (MERTENS, 1933: north-east Madagascar).

north, central east, west, viz. 1 specimen from Fort Dauphin, 3 specimens from Mont D'Ambre, 1 specimen from Mandraka and 1 from Ankarafantsika.

§ 6. GROUP OF *Chamaeleo nasutus,*

comprising *Chamaeleo nasutus* (DUMÉRIL & BIBRON, 1836); *Chamaeleo fallax* (MOCQUARD, 1900); *Chamaeleo gallus* (GÜNTHER, 1877); *Chamaeleo boettgeri* (BOULENGER, 1888); *Chamaeleo linotus* (MÜLLER, 1924); *Chamaeleo guibei* nov. spec.

This group is distinguished from the other chameleons of Madagascar by a flexible rostral appendix (absent only in the females of *Ch. linotus*). by the weak structure and elongated form of the scales of the dorsal crest (if present), by the absence of ventral and gular crest and most of all by their small size. These species are indeed the smallest known of the genus *Chamaeleo.*

At first sight *Ch. nasutus* and *Ch. fallax* have much in common. Both are small chameleons without occipital lobes and with a rather short rostral appendix (3 mm). Comparing them, however, (see table G) we find several clear differences.

In most specimens of *Ch. nasutus* the parietal crest is absent, the number of scales on the temple varies between 5 and 8 (average 5.8), the casque is not elevated, the squamation is fine, the canthus rostralis smooth.

In *Ch. fallax* we find (apart from the deviating specimens dealt with on p. 28) a parietal crest between 4 and 6 scales on the temple (average 4.8), casque in most cases elevated, squamation coarser than in *Ch. nasutus,* a knobby canthus rostralis.

ANGEL (1942) mentioned some other differences between *Ch. nasutus* and *Ch. fallax,* but apart from the larger scales on the temple and on the body of *Ch. fallax,* the variation in *Ch. nasutus* widely overlaps the characters of *Ch. fallax,* as is shown in table G.

Ch. gallus and *Ch. fallax,* both less variable than *Ch. nasutus,* are clearly distinguished species. *Ch. gallus* lacks a parietal crest, lacks a dorsal crest in both sexes, possesses a rostral appendix longer than the diameter of the eye ; the number of scales on the temple varies between 5 and 7 (average 5.7), it possesses axillary and inguinal pits. *Ch. fallax* possesses a parietal crest, all male specimens possess a dorsal crest (lacking in the females), it possesses a rostral appendix smaller than the diameter of the eye, the number of scales on the temple varies between 4 and 6 (average 4.8) and it lacks both axillary and inguinal pits.

The variations of the other characters overlap, but if greater numbers of specimens are available, we might find significant differences in the following characters, "dents de scie" (see fig. 20), relative length of the tail, elevation of the casque, squamation, structure of the canthus rostralis.

TABLE G. Comparison of the species around *Ch. nasutus.*

	Ch. nasutus	*Ch. gallus*	*Ch. fallax*	*Ch. boettgeri*	*Ch. guibei*
Number of species	53	14	17	10	3
parietal crest	50—, 3+	14—	2—, 5±, 10+	2—, 4±, 4+	3±
dorsal crest	25♀—, 4♀+ 9♂—, 11♂+ 2 juv.— 2 juv.+	14—	5♀, 0♀, 0♂—, 12♂+	10+	3—
dorsal cones spiniform	4♀—, 3♂—, 8♂+, 4 juv.—	/	12—	9—, 1+	/
number temporal scales	5—8 (5.84)	5—7 (5.68)	4—8 (4.82)	4—7 (5.7)	/
"dents de scie"	11—, 20±, 22+	4—, 2±, 8+	15—, 2±, 0+	6—, 2±, 2+	3+
rostral appendix	27a, 22b, 4c	14d	2a, 15b	10b	3a
axillary pit	25—, 17±, 11+	1±, 13+	15—, 1±, 1+	5—, 5±	3—
inguinal pit	22—, 25 ±, 6+	1—, 13+	16—, 1+	10—	3—
tail index	5a, 38b, 10c	8a, 6b	15a, 2b(c)	5a, 3a, 2c	/
temporal crest	11—, 12±, 30+	2—, 1±, 11+	4±, 13+	1—, 2±, 7+	3±
casque elevated posteriorly	53—	14—	5—, 8±, 6+	10—	3—
squamation	50—, 3±	14	3—, 8±, 6+	10—	3—
canthus rostralis	52—, 1±	14—	5—, 6±, 6+	10—	3—
occipital lobes	—	—	—	+ (grown together)	+ (seperately)

SYMBOLS USED: + = present; — = absent; ± = indicated only; 15a = 15 specimens show the character a.

Number of temporal scales: counted on the temporal ridge from the orbita to the end of the casque. The first two numbers are the extremes, average number in parentheses.

"Dents de scie": a character mentioned by ANGEL (1942), indicating the serrated line of the upper labials. See fig. 20.

Rostral appendix: a = hardly distinct; b = a little smaller than the diameter of the orbita; c = equal to the diameter of the orbita; d = much greater than the diameter of the orbita.

Tail index: a = tail longer than head + body; a = tail much longer than head + body; b = tail smaller than head + body; c = tail equal to head + body.

Squamation: — = fine homogeneous; + = somewhat heterogeneous.

Canthus rostralis: — = smooth ridges; + = knobby ridges.

FIGURE 20. The character "dents de scie".

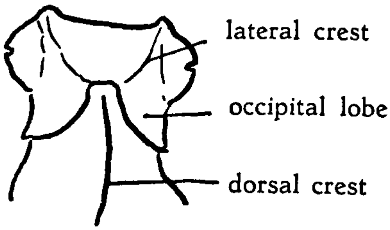


FIGURE 21. Aberrant specimen of *Ch. brevicornis* from Manjakatompo. Occiput seen from behind.

Ch. gallus and *Ch. nasutus*, though quite different at first sight, turn out to be closely allied. Apart from the larger rostral appendix of *Ch. gallus*, there are no constant differences between *Ch. gallus* and *Ch. nasutus*.

We might even suppose that *Ch. gallus* is but a mutant of *Ch. nasutus*, in a similar way as the peloric form of the snapdragons. An argument against this supposition is the great difference in variability of *Ch. nasutus* and *Ch. gallus*. If the longer rostral appendix were the effect of but one single mutation, occurring regularly in *Ch. nasutus*, we could expect approximately the same variation in the other characters in both species. This is not the case as is shown in table G. As the distribution of *Ch. nasutus* overlaps the distribution of *Ch. gallus*, we can only conclude that there is a reproductive barrier between the two forms and that *Ch. gallus*, therefore, is a valid species.

Though limited, the material of the Paris Museum suggests the following distributions :

Ch. fallax from central-east northward
Ch. gallus in the south-east
Ch. nasutus from the north to the south, completely overlapping the ranges of the other two species.

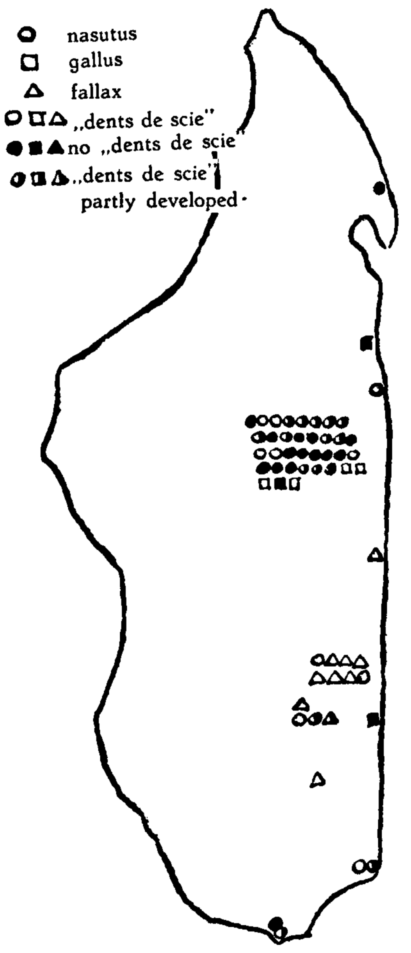
As shown in the maps 8, 9 and 10 we find the remarkable fact that specimens of *Ch. nasutus* obtained in the territory of *Ch. fallax* correspond with *Ch. fallax* as to the following characters : dorsal crest, "dents de scie", axillary and inguinal pits. On the other hand specimens of *Ch. nasutus* obtained in the territory of *Ch. gallus* correspond with *Ch. gallus* as to the same characters.

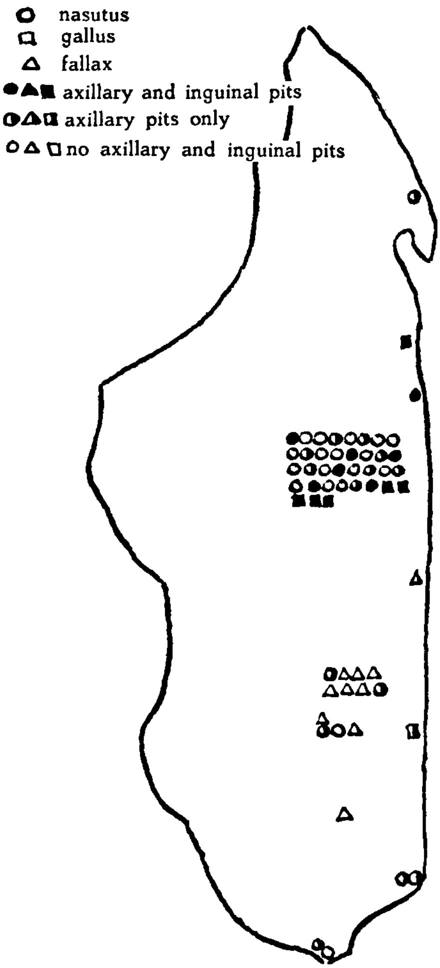
I suggest the following hypothesis :

Ch. gallus and *Ch. fallax* originated from *Ch. nasutus*, perhaps in the central east of Madagascar, the territory of *Ch. nasutus* being limited to that area. *Ch. fallax* went to the north, *Ch. gallus* went to the south. Reproductive barriers originated between the species which then differentiated independently.

Afterwards *Ch. nasutus* succeeded in enlarging its territory, until it widely overlapped the territories of *Ch. gallus* and of *Ch. fallax*. Sometimes hybridization might occur. This would be the reason why *Ch.*

nasutus in the territory of *Ch. gallus* resembles *Ch. gallus* and in the territory of *Ch. fallax* resembles *Ch. fallax*. Hybridization perhaps occurs, as may be shown, by the following specimens of *Ch. fallax* (*-nasutus*):
— Paris 88.24 almost indistinguishable parietal crest, fine squamation, almost smooth canthus rostralis (apart from the parietal crest, similar to *Ch. nasutus*).
— Paris 33.216 parietal crest absent, distinct axillary and inguinal pits, smooth canthus rostralis, but a coarser squamation (apart from the last character, similar to *Ch. nasutus*).
— Paris 02.96 parietal crest absent, fine squamation, smooth canthus rostralis (all similar to *Ch. nasutus*).





MAP 9. Madagascar. Distribution of the character "dents de scie" (see fig. 20) in *Ch. nasutus, Ch. gallus* and *Ch. fallax*.

MAP 10. Madagascar. Distribution of the characters "axillary pits" and "inguinal pits" in *Ch. nasutus, Ch. gallus* and *Ch. fallax*.

Ch. boettgeri, Ch. linotus and *Ch. guibei* are all three distinguished from the above-mentioned species by the presence of occipital lobes. There are also differences in the variation of characters in both groups, as is shown in table G.

Ch. linotus is closely allied to *Ch. boettgeri.* The only important distinguishing characters of *Ch. linotus* are the lack of a dorsal crest and in the female the lack of a rostral appendix (MERTENS 1933).

In the collection of the Paris Museum I found 3 specimens registered under the name of *Ch. boettgeri* (nr. Ch. 11^2—50.354), which I consider to belong to a new species. I dedicate this species to Dr. J. GUIBÉ, curator of herpetology of the Musée d'Histoire Naturelle of Paris, thanks to whom I could examine the greater part of the material used for this study.

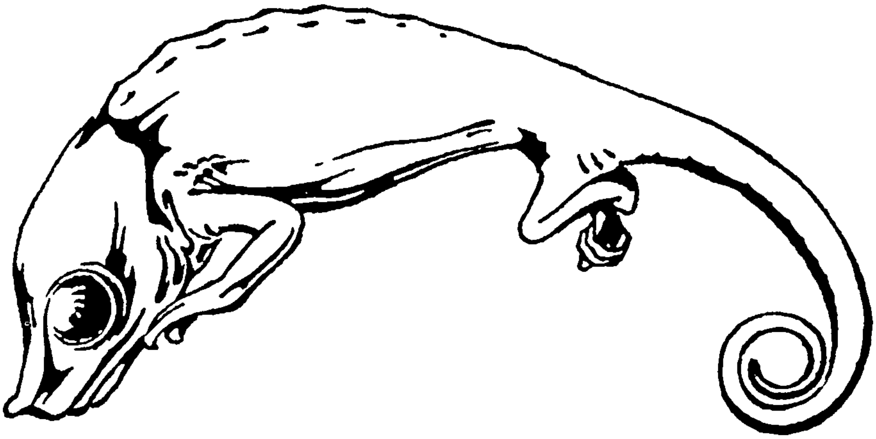


FIGURE 22. *Chamaeleo guibei* nov. spec. Type specimen

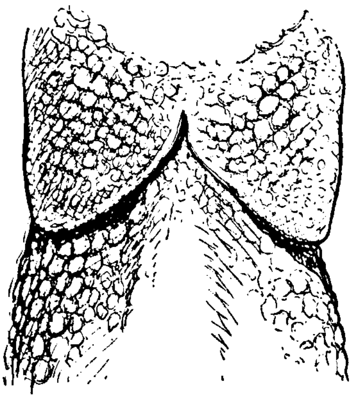


FIGURE 23. *Chamaeleo guibei* nov. spec. Neck region seen from above. Occipital lobes completely separated.

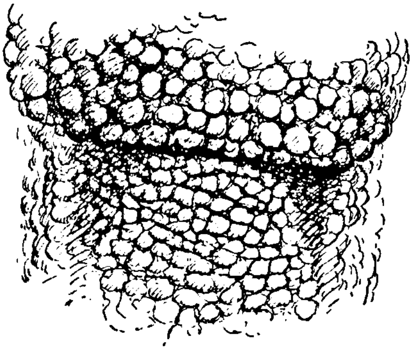


FIGURE 24. *Chamaeleo boettgeri.* Neck region seen from above. Occipital lobes completely fused, no suture visible.

Chamaeleo guibei nov. spec. (figs. 22, 23, 24)

Related to *Ch. boettgeri* and *Ch. linotus*, but easily distinguished by the total separation of the occipital lobes, by the lack of a dorsal crest (as in *Ch. linotus*) and by the very short rostral appendices.

Type specimen : juv.? Coll. Musée d'Histoire Naturelle de Paris, nr. Ch. 11^2—50.354. The type specimen has the label attached to it (registered as *Ch. boettgeri*). Collected by Paulian. Terra typica : Mt. Tsaratanana, mountains in the N.E. of Madagascar, 1800 m.

Description of the type specimen : Canthus rostralis, temporal and parietal crest present, but weak and without prominent cones. Casque not elevated and on the same level as the dorsal keel. Distance between corner of the mouth and tip of the snout a little longer than the distance between corner of the mouth and the tip of the casque. A flexible, scaled, rostral appendix, rounded off at the end. The length of this appendix clearly shorter than half the diameter of the orbit. Rather large occipital lobes, touching each other behind the casque, but totally separated (just as in the non-related *Ch. dilepsis* or *Ch. brevicornis*). Scales of casque and occipital lobes approximately of the same size, both greater than the scales of the body. Squamation of the body rather fine, a little heterogeneous, comparable with the squamation in *Ch. boettgeri*. Scales 47—48 on a vertical line between the middle of the back and the middle of the belly. (In *Ch. boettgeri* I found 55—56 and 45—47). The scales on the limbs are greater than those on the body (just as in *Ch. boettgeri*), less flat. The character "dents de scie", described by ANGEL, 1942 in *Ch. nasutus*, is more or less present. More than one row of scales between the nasale and the supra-labialia. No trace of a dorsal crest. No gular and ventral crest. No axillary or inguinal pits. Colour in alcohol light greyish, head and limbs darker, the belly whitish.

Length of head and body 35 mm, length of tail 33 mm. Length of rostral appendix ± 1 mm.

Cotypes : Collected together with the type, registered with the same number two juvenile specimens. No important differences from the type.

Specimen a : length of head and body 35 mm, tail 35 mm, rostral appendix ¾ mm

Specimen b : length of head and body 29 mm, tail 30 mm, rostral appendix ½ mm.

(I compared the rostral appendix with that in a juvenile specimen of *Ch. boettgeri* Paris 93.178 :

length of head and body 29 mm, tail 30 mm, rostral appendix 2,5 mm.)

§ 7. GROUP OF *Chamaeleo cucullatus*,

comprising *Chamaeleo cucullatus* GRAY, 1831; *Chamaeleo malthe* (GÜNTHER, 1879); *Chamaeleo brevicornis* (GÜNTHER, 1879)

A group of related chameleons distinguished from the other chameleons of Madagascar by the large occipital lobes and — in the male specimens — by small, more or less paired protuberances on the snout, on the junction of the canthi rostrales. The occipital lobes somewhat resemble those of *Ch. boettgeri* and especially of *Ch. guibei* which species

TABLE H. Comparison of the species around *Ch. cucullatus.*

	brevicornis	*malthe*	*cucullatus*	*brevicornis* deviating
number of specimens	41	12	6	4
occipital lobes	11b, 18c, 12d	11a, 1b	6a	4e
occipital lobe scales	26a, 13ab, 1b, 1bc	2a, 1ab, 4bc, 5c	3b, 3bc	3b, 1a
body squamation	15b, 26c	1a, 10b, 1c	6b	4c
axillary pits	3+, 15±, 23—	2+, 2±, 8—	6+	1±, 3—
gular crest	21+, 20±	9+, 2±, 1—	6—	3+, 1±
ventral crest	25a, 11b, 5c	6a, 6c	2a, 4c	4c
parietal crest	14+, 25±, 2—	6+, 6±	4+, 2±	3±, 1—
height of occiput	9a, 17b, 15c	8a, 2b, 2c	3b, 3c	4a
occipital spine	1±, 40—	1±, 11—	6+	4—
tail index	♂ 1.10—1.60 (1.38) ♀ 1.01—1.55 (1.29) juv. 1.12—1.33 (1.21)	♂ 1.11—1.41 (1.22) ♀ 1.05—1.32 (1.15) juv. 1.00—1.12 (1.04)	♂ 0.97—1.04 (1.01) ♀ 1.00—1.05 (1.02)	0.96—1.16 (1.04)

SYMBOLS USED: + = present; — = absent; ± = feebly developed.

Occipital lobes: a = fused completely, no suture visible; b = fusion not more than ± 3 mm; c = a trace only of a fusion; d = completely separated but touching; e = separated by a little distance, not touching.

Occipital lobe scales: a = larger than elsewhere on the body; b = equal to the larger scales on the head; c = smaller than the larger scales on the head.

Body squamation: a = homogeneous; b = slightly heterogeneous; c = distinctly heterogeneous.

Ventral crest: a = transverse rows of cones; b = normal ventral crest; c = no crest.

Height of the occiput: a = distance from the top of the casque to the angle of the the mouth smaller than the length of the mouthcleft; b = these distances are equal; c = distance from the top of the casque to the angle of the mouth larger than the length of the moutcleft.

Tail index: the numbers in parentheses are the average tail indexes.

both in size and general appearance are clearly different from *Ch. cucullatus* c.s.

The posterior part of the casque of *Ch. cucullatus* has a spine-like extension connected on both sides with the occipital lobes, wich character distinguishes the species from the other two. According to WERNER (1911) and ANGEL (1942) the other two species differ in the following respects :

Ch. brevicornis	*Ch. malthe*
occipital lobes not fused	occipital lobes fused, no suture visible
scales on the occipital lobes larger than elsewhere on head and body	scales on the occipital lobes small
tubercular lateral crest	?
heterogeneous squamation	slightly heterogeneous squamation
sometimes transverse rows of cones on throat and belly	isolated cones on throat and belly
parietal crest rather distinct	parietal crest only poorly developed

distance from the angle of the mouth to the occiput equal to the distance to the snout	distance from the angle of the mouth to the occiput smaller than the distance to the snout.
tail much longer than head and body together	tail only somewhat longer than head and body together

In the Paris Museum I had the opportunity of comparing 45 specimens of *Ch. brevicornis*, 12 specimens of *Ch. malthe* and 6 specimens of *Ch. cucullatus*. In table H are shown the results (4 specimens, rather deviating from the descriptions of *Ch. brevicornis*, are treated in a separate column). The specimens of *Ch. cucullatus* prove to be quite different indeed from the other species, but the differences between *Ch. brevicornis* and *Ch. malthe* are much less marked than might be concluded from the descriptions by WERNER (1911) and ANGEL (1942). The most important differences (though not absolute) are:

- the occipital lobes are seldom fused for more than 3 mm in *Ch. brevicornis*, whereas *Ch. malthe* in most cases possesses completely fused occipital lobes, without any visible suture
- the scales on the occipital lobes are in most cases relatively larger in *Ch. brevicornis* than in *Ch. malthe*
- (not mentioned in the table because the nuances are difficult to express in figures:) the cranial crests of *Ch. brevicornis* are formed by more or less pointed cones, whereas these crests in *Ch. malthe* are more rounded.

According to WERNER (1911) and ANGEL (1942) the rostral protuberances of the males of *Ch. brevicornis* are rather different from those found in *Ch. malthe*. I found no essential differences as to this character in the specimens I examined. With 10 out of 15 females of *Ch. brevicornis* I found a trace of rostral protuberances. I found the same with 4 out of 5 females of *Ch. malthe*. All females of *Ch. cucullatus* lack even the slightest indication of protuberances.

The variation of some characters is correlated with the geographical distribution (see maps 11 & 12). The absence or presence of axillary pits shows a pattern of distribution entirely in line with those of the same character in *Ch. nasutus* c.s., *Ch. lateralis*, and *Ch. oustaleti* c.s.

Some of the most aberrant specimens are described here:

1) Cf. *Ch. malthe*, male, Paris Ch. 42^{2}—50.355, Tsaratanana, 8 specimens, of which only this and the following specimen are aberrant. Length of head and body 6.8 cm, length of tail 9.6 cm, tail index = 1.41.

The larger scales on the occipital lobes are larger than elsewhere on the head or body. The squamation is distinctly heterogeneous. Gular crest present.

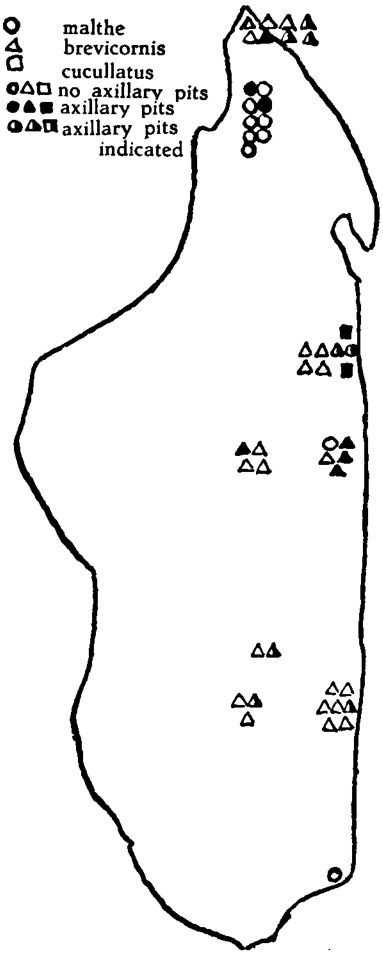
2) Cf. *Ch. malthe* (see nr. 1) female, length of head and body together 6.3 cm, length of tail 8 cm, tail index 1.14. The larger scales on the occipital lobes are larger than elsewhere on body or head. Gular crest present. Transverse rows of cones on the belly indicated.

3) Cf. *Ch. malthe* (Paris Ch. 42-35.142, Isaka, Ivondro, 700 m) female, length of head and body together 10.3 cm, length of tail 13.6 cm., tail index 1.32. Only a small part of the occipital lobes is fused. Larger scales on the occipital lobes only somewhat larger than elsewhere on

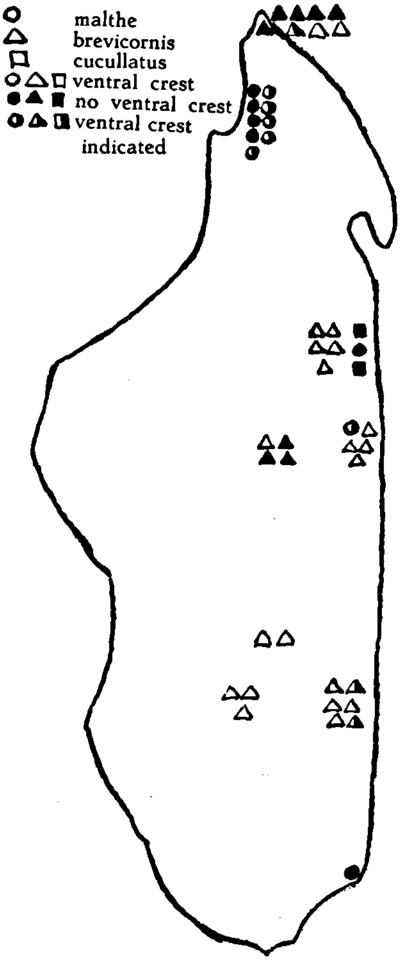
head and body. Distance from the angle of the mouth to the occiput equal to the distance to the snout.

Of the eight distinguishing characters mentioned on p. 31, 32, specimen 1) has five characters in common with *Ch. malthe* and three with *Ch. brevicornis*; specimen 2) has six characters in common with *Ch. malthe* and two with *Ch. brevicornis*; specimen 3) has four characters in common with *Ch. malthe* and four with *Ch. brevicornis*. Perhaps these intermediate forms originate from hybridization.

4) Cf. *Ch. brevicornis* (Paris collection, not yet catalogued, Manjakatompo, XII-1950) juvenile. Length of head and body together 5.7 cm, length of tail 5.8, tail index 1.02. The occipital lobes do not touch each other but are separated by a little interval caused by the abnormal shape of the posterior part of the casque (see fig. 21). This structure is more



Map 11. Madagascar. Distribution of the character "axillary pits" in *Ch. cucullatus* c.s.



Map 12. Madagascar. Distribution of the character "ventral crest" in *Ch. cucullatus* c.s.

or less comparable with that in *Ch. parsoni* c.s. Ventral crest absent. Gular and ventral crest poorly developed. On the tail some isolated cones only. Distance from the angle of the mouth to the occiput smaller than the distance to the snout. The larger scales on the occipital lobes are equal to the larger scales on head or body. No parietal crest.

5) Cf. *Ch. brevicornis* (Provenance see nr. 4) juvenile. Length of head and body together 5.9 cm, length of tail 5.7 cm, tail index 0.96. Casque and occipital lobes aberrant in the same way as in nr. 4. No ventral crest. Poorly developed gular crest. Dorsal crest and crest on the tail still less developed than in nr. 4. Distance from the angle of the mouth to the occiput smaller than the distance to the snout. Larger scales on the occipital lobes equal to the larger scales on head or body. No parietal crest.

6) Cf. *Ch. brevicornis* (Paris Ch. 12^5—88.23, provenance unknown). Length of head and body together 7.0 cm, length of tail 8.1 cm, tail index 1.16. Apart from a trace of a parietal crest, this specimen corresponds with the aberrant specimens 4 and 5.

7) Cf. *Ch. brevicornis* (Paris Ch. 126—39.52, Manjakatompo), female with eggs. Length of head and body together 5.7 cm. length of tail 5.8 cm, tail index 1.02. Apart from the fact that the larger scales on the occipital lobes are somewhat larger than elsewhere on head or body and the presence of a poorly developed parietal crest this specimen corresponds with the specimens nr. 4 and 5.

Specimen nr 7) was found in 1939. This means that the same strikingly aberrant form was found in the same place after an interval of more than 10 years. This might suggest the existence of a distinct subspecies. From the same provenance, however, a specimen is known which quite answers to the description of *Ch. brevicornis*. The only difference from the descriptions by WERNER (1911) and ANGEL (1942) is : distance from the angle of the mouth to the occiput smaller than the distance to the snout. But as table H shows, this can no longer be regarded as a distinguishing character.

Perhaps, when more material will be available from this area, this population will prove to be subspecifically different from the typical *Ch. brevicornis*.

§ 8 GROUP OF *Chamaeleo parsonii*,

comprising *Chamaeleo parsonii* CUVIER, 1824; *Chamaeleo globifer* (GÜNTHER, 1879); *Chamaeleo oshaughnessyi* (GÜNTHER, 1881).

This group of closely related species is distinguished from the other chameleons of Madagascar by the broad, flat casque (parietal crest absent or only poorly developed, never higher than the lateral crests), gular and ventral crests absent, no white line(s) on the belly and under the tail. The male specimens possess a pair of laterally compressed, rigid rostral protuberances, comparable with those in *Ch. bifidus* c.s., but much shorter.

In table I I compare 21 specimens of *Ch. parsonii*, 5 specimens of *Ch. globifer*, 6 specimens of *Ch. oshaughnessyi* and 2 aberrant specimens from Sihanaka (Paris collection, registered as *Ch. globifer*, Ch. 32-21. 261). This table shows that the variations of several characters overlap.

TABLE I. Comparison of the species around *Ch. parsonii.*

	parsonii	*globifer*	*oshaughnessyi*	specimens from Sihanaka
number of specimens	21	5	6	2
gular squamation	21b	5a	6a	2b
dorsal crest	4a, 6ac, 11c	2a, 3d	6d	1a, 1ac
dorsal keel	9a, 12 b	2a, 3c	1b, 5c	2a
parietal crest	19a, 2b	2a, 3b	6a	2b
body squamation	21a	5c	6b	2a
legs squamation	21a	5b	6b	2a
"sillons verticaux"	21+	5+	5—, 1+	2+
occipital lobes	21a	5b	6a	1a, 1ab
temporal scales	10b, 11 c	4a, 1b	1a, 5b	2b
extremity of casque	20a, 1b	5b	6b	2b

SYMBOLS USED

Gular squamation: a = scales on the middle of the throat smaller than the surrounding scales; b = scales on the middle of the throat equal to the surrounding scales.
Dorsal crest: a = distinct crest of dorsal cones; b, c, d = no crest developed; b = a single row of scales on the dorsal keel; c = a double row of scales on the dorsal keel; d = scales irregularly placed on the dorsal keel.
Dorsal keel: a = round in cross-section; b = more or less elevated above the dorsal spines; c = normal (as in *Ch. chamaeleon* for instance).
Parietal crest: a = indicated; b = absent.
Body squamation: a = homogeneous; b = heterogeneous; c = only foremost part of the body with heterogeneous squamation.
Legs squamation: a = homogeneous; b = heterogeneous.
"Sillons verticaux": + = present; — = absent.
Occipital lobes: a = feebly developed; b = rudimentary.
Temporal scales: a = coarse, warty cones; b = less coarse cones; c = smooth scales.
Extremity of casque: a = extended; b = not extended.

There remains, however, a number of constant differences between these forms, which, together with the overlapping of their ranges suggest that they are to be considered separate species.

Ch. parsonii and *Ch. globifer* show differences in gular squamation, squamation of the body, development of the occipital lobes, temporal scales, the extension of the extremity of the casque, the squamation on the legs, as also more or less, in the absence or presence of a dorsal crest.

Ch. parsonii and *Ch. oshaughnessyi* show differences in gular squamation, absence or presence of a dorsal crest, the form of the dorsal keel, squamation of the body and of the legs, absence or presence of "sillons verticaux" and the extension of the casque.

Ch. globifer and *Ch. oshaughnessyi* show differences in squamation of the body, absence or presence of "sillons verticaux", development of occipital lobes and the structure of the temporal scales.

The specimens of Sihanaka have many characters in common with *Ch. globifer;* at the same time they correspond with *Ch. parsonii* at all critical points except in the extension of the casque ; this may be due to both specimens being juveniles.

§ 9. GROUP OF *Chamaeleo bifidus*

comprising *Chamaeleo bifidus* BRONGNIART, 1800; *Chamaeleo minor* (GÜNTHER, 1879); *Chamaeleo willsi* (GÜNTHER, 1890).

This group of closely related species is distinguished from the other chameleons of Madagascar by the following characters; a flat casque (parietal crest absent, or if present only slightly higher than lateral crests), absence of occipital lobes, in many cases an indication of a gular and ventral crest (except in *Ch. minor*), groups of scales forming rosettes, in many cases a paired or single midventral white line and a single or paired white line under the tail. The male specimens possess a pair of laterally compressed rigid rostral protuberances, which in the female are lacking, or only slightly indicated. This last feature connects it with the group of species around *Ch. parsonii* (as does the flat casque) but *Ch. parsonii* c.s. possess occipital lobes and always lack gular and ventral crests, as also white lines on the belly and under the tail. Moreover the rostral protuberances are always shorter in *Ch. parsonii* c.s.

In table J a number of specimens of *Ch. bifidus*, *Ch. minor* and *Ch. willsi* are compared as also some specimens of the closely related continental African *Ch. fischeri* (REICHENOW, 1887) and an aberrant male specimen not yet catalogued, of the Paris collection, from Ankarafantsika.

Table J accentuates the close relationship among the four species, but it also shows that they are to be considered separate species.

In *Ch. bifidus* the parietal crest is absent or only slightly indicated, squamation rather heterogeneous with groups of scales in form of rosettes, gular and ventral crest absent in most cases, sometimes an indication of a ventral crest, in most cases on either flank a low lateral white band, seldom one or two white lines on the belly, sometimes a single white line under the tail, rostral protuberances more or less blunt at the end and parallel, sometimes axillary pits, the number of scales on the flank, counted on a vertical line from middorsal to midventral, varies between 54 and 58 (average 55.75), the number of scales between parietal crest and lateral crest varies between 5 and 9 (average 7.1).

In *Ch. minor* the parietal crest is mostly indicated, squamation homogeneous without groups of scales in form of rosettes, gular crest sometimes combined with ventral crest, both poorly developed, no lateral white bands, a single midventral white line, sometimes a pair of white lines under the tail, rostral protuberances blunt at the end and parallel, sometimes axillary pits, no crest on the tail, the number of scales on the flank, counted on a vertical line from middorsal to midventral, varies between 50 and 58 (average 53.6), the number of scales between parietal crest and lateral crest varies between 3 and 7 (average 5.14).

Ch. willsi in most cases has an indication of a parietal crest, squamation slightly heterogeneous with groups of scales more or less arranged in rosettes, especially just behind the forelegs, ventral crest sometimes combined with a gular crest, both poorly developed, no lateral white bands, a single midventral white line, a pair of white lines under the tail, rostral protuberances pointed at the end, parallel or divergent,

Table J. Comparison of the species around *Ch. bifidus*.

	bifidus	*minor*	*willsi*	*fischeri*	*willsi* Ankarafantsika
number of specimens	12	4	5	6	1
parietal crest	6±, 7—	1+, 2±, 1—	4±, 1—	4+, 2±	—
rosettes	13+	4—	5±	6+	±
squamation	1a, 7b, 5c	4a	5b	6b	—b
dorsal crest	4bc, 9bd	2bc*, 2bd	4bd, 1d	1—a, 5bd**	bd
gular and ventral crest	4—b, 9d	2a, 2—c	2—a, 3—b	6d	d
midventral line(s)	1a, 3b, 9c	4b	5b	2a, 4c	b
line(s) under the tail	7b, 6c	3a, 1c	5a	2—a, 4c	—a
rostral protuberances end	3—a, 9b, 1—	2b, 2—	4a, 1—	5b, 1—	a
rostral protuberances direction	1a, 11b, 1—	2b, 2—	2a, 2b, 1—	5b, 1—	—a
axillary pits	+ & —	2±, 2—	5—	6—	—
crest on tail	2±, 11—	4—	5—	6+	—
scales on flank	54—58(55.75)	50—58 (53.6)	44—50 (46.2)	47—60 (53.6)	50—51
scales between parietal and lateral crest	5—9 (7.1)	3—7 (5.14)	5—7 (6.17)	2—3 (2.75)	6—7

Symbols used: + = present; — = absent; ± feebly developed; — a = a feebly developed. By rosettes are meant groups of scales arranged in form of rosettes.

Squamation: a = homogeneous; b = slightly heterogeneous; c = clearly heterogeneous.

Dorsal crest: a = from neck to tail; b = on the foremost part of the back only; c = a single row of scales on the dorsal keel; d = scales irregularly placed on the back; bd = a crest on the foremost part of the back, followed by irregularly placed scales.

* one specimen has a double row of scales behind the crest.

** two specimens have a double row of scales behind the crest.

Gular and ventral crest: a = both present; b = ventral crest only; c = gular crest only; d = both crests absent.

Midventral line(s): a = paired white lines on the belly; b = a single white line on the belly; c = white lines absent.

Line(s) under the tail: a = paired white lines under the tail; b = a single white line under the tail; c = white lines absent.

Rostral protuberances, end: a = pointed; b = blunt.

Rostral protuberances, direction: a = divergent; b = parallel.

Scales on flank: counted on a vertical line from midventral to middorsal. The first two numbers are the extremes, average number in parentheses.

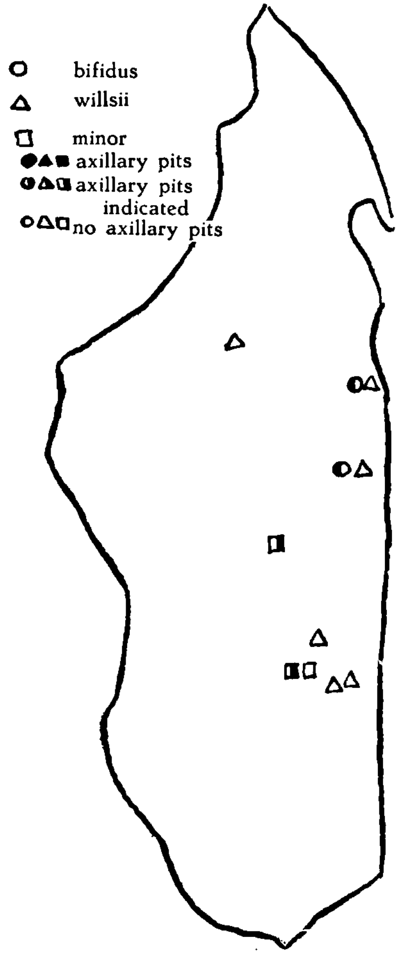
Scales between parietal and lateral crest: counted on a transverse line between these crests. The first two numbers are the extremes, average number in parentheses.

willsi, Ankarafantsika is an aberrant specimen probably belonging to *Ch. willsi*, captured in Ankarafantsika.

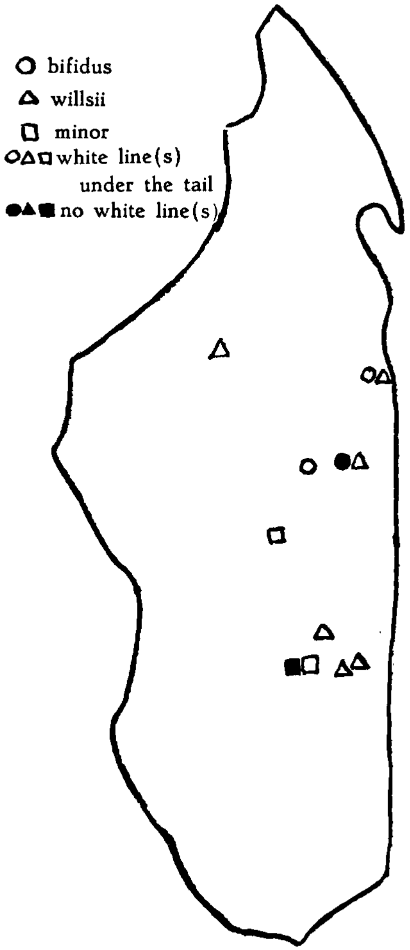
no axillary pits, no crest on the tail, the number of scales on the flank, counted on a vertical line from middorsal to midventral, varies between 44 and 50 (average 46.2) the number of scales between parietal crest and lateral crest varies between 5 and 7 (average 6.17).

In *Ch. fischeri* the parietal crest is distinct in most cases, squamation rather heterogeneous with groups of scales arranged in rosettes, gular and ventral crest absent, sometimes a paired white line on the belly and under the tail, rostral protuberances blunt at the end, parallel, no axillary pits, crest on the tail, the number of scales on the flank, counted on a vertical line from middorsal to midventral, varies between 47 and 60 (average 53.6), the number of scales between parietal crest and lateral crest varies between 2 and 3 (average 2.75).

Apart from the absence of a gular and ventral crest (as in *Ch. bifidus*) the specimen from Ankarafantsika (Paris collection, not yet catalogued) has most characters in common with *Ch. willsi* (form and divergence of the rostral protuberances). This means a new locality for this species. ANGEL (1942) mentions central and central east of Madagascar only; Ankarafantsika lies in the western part of the island.



MAP 13. Madagascar. Distribution of the character "axillary pits" in *Ch. bifidus* c.s.



MAP 14. Madagascar. Distribution of the character "white line(s) under the tail" in *Ch. bifidus* c.s.

As maps 13 and 14 show, there is no particular geographical pattern of distribution of the characters "axillary pits" and "one or two white lines under the tail" in this species, in contrast to *Ch. lateralis, Ch. nasutus* c.s., *Ch. rhinoceratus, Ch. oustaleti* c.s. and *Ch. brevicornis* c.s. But perhaps the result would be different if more material were available.

§ 10. *Chamaeleo furcifer and Chamaeleo gastrotaenia*

Chamaeleo furcifer Vaillant & Grandidier, 1880; *Chamaeleo gastrotaenia* (Boulenger, 1888).

Two closely related species, distinguished from the other chameleons of Madagascar by the fine, homogeneous squamation, the absence of gular and ventral crests and especially by the very poorly developed occipital lobes, only indicated by a small slit just behind the casque.

Contrary to Werner, 1911 and Angel, 1942, I found a dorsal crest though poorly developed (in one specimen only 5 dorsal cones) with 3 specimens out of 7 of *Ch. gastrotaenia*. This accentuates its relationship to *Ch. furcifer*. All specimens investigated of *Ch. gastrotaenia* and *Ch. furcifer* possess axillary pits.

The only clear differences between *Ch. gastrotaenia* and *Ch. furcifer* are the still smaller occipital slits of *Ch. furcifer* (hardly visible in the type specimen), the rostral appendix of *Ch. furcifer* and the number of scales on a vertical row between middorsal and midventral: in *Ch. gastrotaenia* varying between 43 and 49 (average 46.5) whilst in *Ch. furcifer* varying between 63 and 65 (average 64.5).

§ 11. CHAMELEONS OF MADAGASCAR. GENERAL.

Out of the 69 species of the genus *Chamaeleo*, distributed throughout Africa, Arabia and neighbouring countries, 27 are found in Madagascar. So nearly 40% of all species inhabit a relatively small area. This suggests Madagascar to be the centre of distribution of the genus. A closer examination, however, shows (as will be more extensively explained in the last part of this paper) that east Africa (Kenya and Tanganyika) is to be regarded as such. The main reason for this assumption is that all characters distinguishable in chameleons of Madagascar are also found on the continent and not vice versa. The following characters occur in continental chameleons whilst absent in those of Madagascar: ovoviviparity, cranial horns, tarsal spurs and scaled gular lobes.

All these characters are found in many divergent habitats and most of them have a wide distribution on the continent. Therefore, it is improbable that their absence in Madagascar should have been caused by selection. It is more probable that they never reached the island.

One character, viz. axillary (occasionally inguinal) pits, which occur in many Madagascar species, is not found in the descriptions of any continental species. However, Sternfeld (1913) reports this character in a specimen of *Ch. gracilis* from central Africa. Moreover, these pits occur in several species of the related genus *Brookesia* from east Africa (a.o. Loveridge, 1951).

Then probably the most important reason for the flourishing condition of the genus *Chamaeleo* on Madagascar is the absence of higher predators as well as the absence of competitors. For the same reason lemurs, iguanas and boas survive in Madagascar ,whereas they are extinct on the continent.

Several Madagascar species show such a close relationship to continental ones, that they may be regarded as belonging to the same groups. The Madagascar *Ch. rhinoceratus* is closely related to the continental *Ch. xenorhinus* and *Ch. carpenteri*. The Madagascar *Ch. nasutus* c.s. is probably closely related to the continental *Ch. tenuis* and perhaps *Ch. spinosus* (I have not had the opportunity of examining specimens of the latter species). The Madagascar *Ch. bifidus* c.s. is undoubtedly closely related to the continental *Ch. fischeri* and *Ch. tavetensis*.

The other 16 species of *Chamaeleo* of Madagascar do not show a striking, nearer resemblance to any of the species of the continent.

These facts suggest that two main periods of immigration may be assumed: a first period, so long ago that the species that have evolved from it have lost any close resemblance to continental species and a second, more recent period, in which at least three different groups came to Madagascar, viz. *rhinoceratus*-like specimens, *nasutus*-like specimens and *bifidus*-like specimens.

Perhaps a later emigration in the opposite direction, from Madagascar to east Africa should be assumed to have taken place. The *Ch. nasutus* group in Madagascar shows the following three possibilities of variation : occipital lobes fused, occipital lobes separated, occipital lobes absent. On the continent the related *Ch. tenuis* and *Ch. spinosus* both lack occipital lobes, so only one variation of the character is present on the continent.

In the last section of our paper our conclusion will be that the ancestral chameleon probably already possessed occipital lobes, which means that fused occipital lobes or absence of occipital lobes both are characters that arose later on. In this case it means that probably the Madagascar *Ch. guibei* bears closest resemblance to the common ancestor of the species of the *nasutus* group, while *Ch. boettgeri* and *Ch. linotus* on the one hand, on the other *Ch. nasutus, Ch. fallax, Ch. gallus* all from Madagascar, as well as the continental *Ch. spinosus* and *Ch. tenuis* show later developments. Therefore it is probable that *Ch. spinosus* and *Ch. tenuis* both evolved from an emigrant from Madagascar to the continent, which had already lost its occipital lobes.

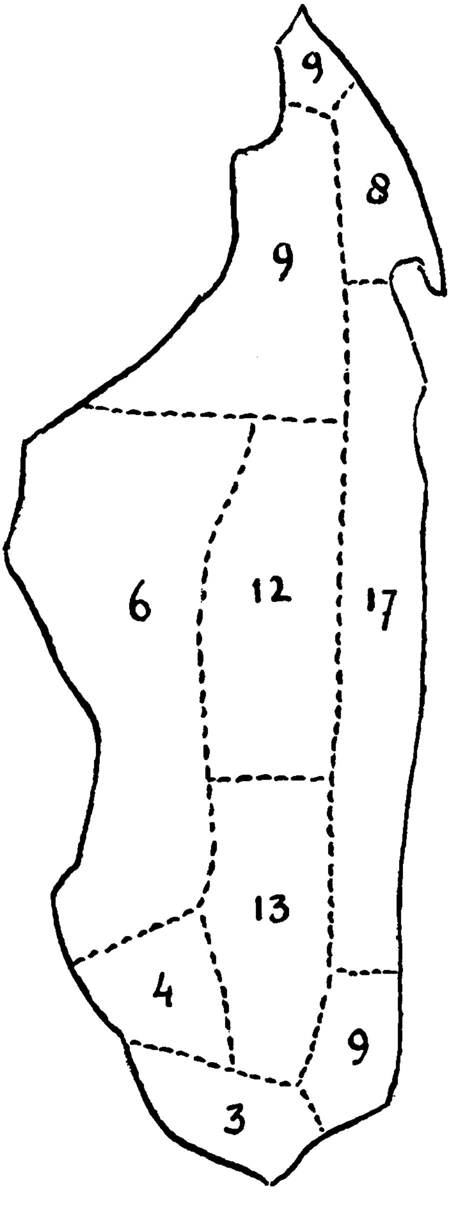
Mapping out the numbers of species pro district (as ANGEL, 1942, did) we find most species in the eastern part (see map 15). This is probably caused by the concentration of woods in this part of Madagascar. (A lesser reason is that, the larger cities being situated in the eastern part of the island, most of the collecting has been done from these centres, whilst the western part has been relatively neglected in this respect).

Several different groups of species show a common geographical pattern in the presence or absence of the character axillary pits. This character is distinctly present in the north of Madagascar, whereas in the south it is less distinct or absent. This is shown in *Ch. lateralis*, *Ch. oustaleti* c.s., *Ch. nasutus* c.s. and *Ch. cucullatus* c.s.

These analogous distribution patterns probably mean that the conditions in the north are favourable to the development of the character axillary pits. Since, however, the function of these pits is unknown, nothing sure can be stated.

Other patterns of distribution, more or less comparable to that of the axillary pits, are shown by the numbers of dorsal cones in *Ch. oustaleti* c.s., white lines under the tail in *Ch. lateralis*, ventral crests in *Ch. cucullatus* c.s. and "dents de scie" in *Ch. nasutus* c.s.

More extensive general conclusions are given in sections 19, 20 and 21.



MAP 15. Madagascar. Numbers of species per district (districts after ANGEL, 1942).

Part B The chameleons outside Madagascar.

§ 12. GROUP OF *Chamaeleo chamaeleon*,

comprising *Chamaeleo chamaeleon* (LINNAEUS, 1758); *Chamaeleo calcarifer* PETERS, 1852; *Chamaeleo zeylanicus* LAURENTI, 1768; *Chamaeleo calyptratus* DUMÉRIL, 1851; *Chamaeleo basiliscus* COPE, 1868; *Chamaeleo laevigatus* GRAY, 1863; *Chamaeleo senegalensis* (DAUDIN, 1802); *Chamaeleo gracilis* HALLOWELL, 1842; *Chamaeleo etiennei* (SCHMIDT, 1919); *Chamaeleo dilepis* LEACH, 1819; *Chamaeleo angusticoronatus* (BARBOUR, 1903).

This closely related group of chameleons (see table K) is first of all distinguished by the absence of any conspicuous characters such as horns or other cranial protuberances, fin shaped dorsal keels etc. These species all possess a homogeneous squamation, a white midventral line, in most cases a dorsal crest, at least on the anterior part of the back a single

TABLE K. Comparison of the species around *Ch. chamaeleon*, showing the great homogeneity of the group.

	chamaeleon	*calcarifer*	*zeylanicus*	*calyptratus*	*basiliscus*	*laevigatus*	*senegalensis*	*gracilis*	*etiennei*	*dilepis*	*angusticoronatus*
casque	a	a	a	a	a	c	b	b	b	b	a
casque elevation	c	b	b	+a	b	c	bc	±b	b	a—c	
lateral crest	$^1/_2$	+	$^1/_2$	$^1/_2$	$^1/_2$	$^1/_2$	+?	+?	$^1/_2$	+	$^1/_2$
occipital lobes	d	c	d	d	e	e	e	d	d	b—d	
squamation	a	a	a	ab	a	a	a	a	a	a	a
dorsal crest	c	a	a	a	c	±a	a	a	?	a	
gular crest	—a	a	+a	+a	a	a	a	a	a	a	a
ventral crest	c	a	+a	a	±a	a	a	a	a	a	
tarsal spur	—	♂ + ♀ —	♂ + ♀ ±	♂ + ♀ ±	♂ + ♀ —	—	—	♂ + ♀ —	—	♂ + ♀ —	
white midventral line	+	+	+	+	+	+	+	+	+	+	+

SYMBOLS USED:

Casque: a = roof-shaped (parietal crest higher than the lateral crests); b = flat (parietal crest absent or on the same level as the lateral crests); c = parietal crest and dorsal crest in one continuous line, not clearly separated.

Casque elevation, a = distance from the angle of the mouth to the occiput greater than the distance to the snout; b = these distances equal; c = distance from the angle of the mouth to the occiput smaller than the distance to the snout.

Lateral crest: + = continuous to the extremity of the casque; ½ = stopping behind the temporal region.

Occipital lobes: a = fused; b = large; c = just movable; d = only slightly indicated; e = absent.

Squamation: a = homogeneous; b = heterogeneous.

Dorsal crest: a = present; b = no crest, but a single row of scales on the dorsal keel; c = a single row of scales on the foremost part of the back only, the rest with irregularly placed scales; d = irregularly placed scales from neck to tail.

Gular and ventral crest: a = present; b = no crest, but scales on the midgular or midventral line are somewhat greater than the surrounding scales; c = absent.

Tarsal spurs: + = present; — = absent; ± = feebly developed.

Midventral white line: + = present; — = absent.

Mainly after the descriptions of WERNER (1911). It is shown in the text that several details cannot be correct.

row of scales and in most cases a gular and a ventral crest. Though not occurrung in all species, a tarsal spur is typical for this group. Temporal crests are absent.

The first four species (*Ch. chamaeleon, Ch. calcarifer, Ch. zeylanicus* and *Ch. calyptratus*) may be considered apart, being more related between them than to the other species : the combination of a roofshaped casque (parietal crest higher than the lateral crests) and occipital lobes is characteristic for them.

The relation between Ch. chamaeleon and Ch. calcarifer.

PARKER's description of the subspecies *Ch. chamaeleon orientalis* (1938) mentions one single difference from the description of *Ch. calcarifer* only, viz. the absence of tarsal spurs. On the other hand, this description of *Ch. chamaeleon orientalis* has much in common with the description of *Ch. chamaeleon musae* (STEINDACHNER, 1900). This corresponds with the geographical range of *Ch. chamaeleon orientalis* lying between that of *Ch. chamaeleon musae* and *Ch. calcarifer* (Suez, southern Hedjaz and south Arabia respectively). In order to clarify this I examined all the specimens, of the Paris collection, from the periphery of the range of *Ch. chamaeleon* (from Cyprus ,Egypt, Syria, perhaps Persia, Oran ;

TABLE L. The variation of characters in specimens of *Ch. chamaeleon*, collected mainly in the periphery of the distribution of this species. All specimens belong to the collection of the Paris Museum. Symbols see table K.

	Ch. 18—2212, Cyprus	Ch. 18^{1}—2541, Béit-Méri (Siban), Syria	Ch. 18^{1}—2572, Lekkiyé? Syria	Ch. 18^{1}—2542, Rég. de Djéroud, Syria	Ch. 18^{1}—6375, Harem, Syria	Ch. 18^{2}—6629, Egypte	Ch. 18^{5}—1506, Suez	Ch. 18^{10}—2477, loc. unknown	Ch. 18^{10}—6630, Egypte	Ch. 18^{10}—2211, Oran	Ch. 18^{10}—621, Tripoli	Ch. 18^{10}—2210, Perse ?
casque	a	a	a	a	a	a	a	a	a	a	a	a
casque elevation	±b	c	b	c	b	b	c	b	b	c	b	b
occipital lobes	d	d	d	d	d	cd	bc	d	d	d	d	d
squamation	a	a	a	a	a	a	a	a	a	a	a	a
dorsal crest	c	c	c	c	c	c	c	c	c	c	c	c
gular crest	—a	—a	a	a	—a	a	—a	a	a	a	a	—a
ventral crest	b	—a	—a	—a	—b	—a	c	b	—a	c	—a	—a
tarsal spur	±	—	±	—	±	±	±	—	±	—	±	—
sex	♂	♀	♂	♀	♂	♂	♀	♀	♂	♀	♂	♀

see table L). The first striking point is that out of 12 specimens, 2 only (from Oran and Suez) are lacking a ventral crest (which lacking, according to **Werner**, 1911, is characteristic for *Ch. chamaeleon*), the other specimens possess a more or less distinct ventral crest.

In two specimens the occipital lobes are somewhat greater than normal in *Ch. chamaeleon*, i.e. resembling *Ch. calcarifer*. The same specimens (Paris—6629 from Egypt and Paris—1506 from Suez) possess rather straight parietal crests.

Most remarkably, all the male specimens (6) possess indications of tarsal spurs, which is in contrast to the normal *Ch. chamaeleon*. Even a female from Suez (Paris—1506) possesses a slight indication of a tarsal spur.

Parker (1938) summarized the differences between *Ch. chamaeleon orientalis* and *Ch. chamaeleon musae* as follows:

C. c. orientalis	*C. c. musæ*
(1) Distance from the tip of the snout to the commissure of the mouth equal to the distance from the latter point to the extremity of the casque in the very young, but distinctly shorter in the adult.	(1) Length of the mouth greater than the distance from its commissure to the extremity of the casque in juveniles, equal in adults.
(2) Distance between the supra-orbital ridges at the centre of the eyes 3 to 4 times in the length from the snout to the extremity of the casque.	(2) Distance between the supra-orbital ridges 3 to 3.3 times in the same distance.
(3) Parietal crest strongly arched.	(3) Parietal crest only slightly arched.
(4) Scales on the occipital lobes flat, larger than those on the casque.	(4) Scales on the occipital lobes granular: not larger than those on the casque.
(5) Granules on the middle line of the belly transversely enlarged in all except one specimen.	(5) Granules of the middle line not enlarged.

These same 5 points were compared in the above mentioned specimens from Egypt and Suez, as well as in 3 specimens of *Ch. calcarifer*. The results are as follows :

Ch. chamaeleon (Paris Ch. 18^{5}—1506, Suez):
in point (1) corresponding with *orientalis* more or less
,, ,, (2) ,, with *orientalis* and *musae*
,, ,, (3) ,, with *musae*
,, ,, (4) ,, with *orientalis*
,, ,, (5) ,, with *orientalis*

Ch. chamaeleon (Paris Ch. 18^{2}—6629, Egypt):
in point (1) corresponding with *orientalis* and *musae*
,, ,, (2) neither corresponding with *orientalis* nor with *musae*, as the distance between the supra-orbital ridges at the centre of the eyes contained 2.75 times only in the length from the snout to the extremity of the casque.
in point (3) corresponding with *musae*
,, ,, (4) ,, with *musae*
,, ,, (5) ,, with *orientalis* more or less

Ch. calcarifer (Paris Ch. 14—95.41, Arabia):
in point (1) corresponding with *orientalis*
„ „ (2) „ with *orientalis*
„ „ (3) „ with *orientalis*
„ „ (4) „ with *musae* more or less
„ „ (5) „ with *orientalis*

Ch. calcarifer (Paris Ch. 14^1—02.110, south Arabia):
in point (1) corresponding with *orientalis*
„ „ (2) „ with *orientalis* and *musae*
„ „ (3) „ with *musae*
„ „ (4) „ with *musae*
„ „ (5) „ with *orientalis*

Ch. calcarifer (Paris Ch. 18^2—5861, Aden):
in point (1) corresponding with *orientalis*
„ „ (2) „ with *orientalis* more or less
„ „ (3) „ with *musae*
„ „ (4) „ with *musae*
„ „ (5) „ with *orientalis*

Resuming we have the following points:

1. Going from North Africa via Suez and the Hedjaz to southern Arabia, we find the following species and subspecies in adjacent ranges *Ch. chamaeleon chamaeleon, Ch. chamaeleon musae, Ch. chamaeleon orientalis* and *Ch. calcarifer* respectively.
2. The characters of the subspecies *musae* and *orientalis* are a mixture of the characters of *Ch. chamaeleon chamaeleon* and of *Ch. calcarifer.*
3. Specimens found between the ranges of *Ch. chamaeleon chamaeleon* and *Ch. calcarifer,* not referable to one of the known species or subspecies, possessing ventral crests, tarsal spurs and sometimes somewhat greater occipital lobes than normal *Ch. chamaeleon chamaeleon,* may be regarded as intermediate forms between *Ch. chamaeleon chamaeleon* and *Ch. calcarifer.*

This means that the closely related forms *Ch. chamaeleon chamaeleon* and *Ch. calcarifer* live in neighbouring ranges, which are not overlapping, while in the zone between them intermediate forms only are found. In my opinion, we have sufficient reason to conclude that *Ch. calcarifer* is a subspecies of *Ch. chamaeleon* : *Chamaeleo chamaeleon calcarifer* Peters, 1852.

The subspecies *Ch. chamaeleon saharicus* Müller, 1887 is not valid in my opinion, as the only distinguishing character, the presence of a separate interorbital part of the parietal crest may occur throughout the whole range of the species *Ch. chamaeleon* (for instance in Oran, Tripolis, Suez, Cyprus.

The relation between Ch. chamaeleon and Ch. zeylanicus.

According to table K the Indian *Ch. zeylanicus* is distinguished from *Ch. chamaeleon* by the following characters :

1. a higher casque,
2. a dorsal crest from neck to tail,
3. a more developed gular crest,
4. presence of a ventral crest,
5. male specimens and sometimes female specimens posses a tarsal spur.

In table L it is shown that the presence of a ventral crest and tarsal spurs, even in females, are not so very important as distinguishing characters between *Ch. chamaeleon* and *Ch. zeylanicus*, especially not when we regard *calcarifer* as a subspecies of *Ch. chamaeleon*.

As to the height of the casque, in the Paris collection I found 2 specimens in which the distance from the extremity of the casque to the commissure of the mouth is much greater than the distance from the latter point to the tip of the snout ; in 3 specimens the mouth is only slightly shorter than the distance from its commissure to the extremity of the casque; 1 specimen (though juvenile) corresponds in this respect more or less with *Ch. chamaeleon*.

In the dorsal crest I did not find any difference between *Ch. zeylanicus* and *Ch. chamaeleon* : 4 specimens lack a dorsal crest, the foremost part of the dorsal keel has a single row of scales followed by irregularly placed scales ; 2 other specimens have a single row of scales on the dorsal keel from neck to tail, one of these has a number of higher cones in the form of a real crest on the foremost part of the back.

Contrary to WERNER (1911) I have found in all 6 specimens that the lateral crests extend as far as the extremity of the casque. So we find only a few, gradual differences between *Ch. chamaeleon* and *Ch. zeylanicus*.

Considering their geographic position I think it justified to regard *Ch. zeylanicus* as the Indian subspecies of *Ch. chamaeleon* : *Chamaeleo chamaeleon zeylanicus* LAURENTI, 1768.

Ch. chamaeleon calcarifer should not be regarded as an intermediate subspecies between *Ch. chamaeleon chamaeleon* and *Ch. chamaeleon zeylanicus*. The main reason for this is that the pure *calcarifer*-form is found in south Arabia and the pure *zeylanicus*-form in India and Ceylon. I assume that *Ch. chamaeleon calcarifer* and *Ch. chamaeleon zeylanicus* developed independently from the original *Ch. chamaeleon chamaeleon*.

The relation between Ch. chamaeleon calcarifer and Ch. calyptratus.

SCHMIDT (1953) draws the following conclusion about *Ch. calyptratus* : "Fifty-four specimens, all from Ta'izz. With this large series at hand, ANDERSON's suggestion that *calcarifer* PETERS is a synonym of *calyptratus* DUM. & DUM. seems to be amply confirmed".

ANDERSON (1898) wrote : "I am, however, not quite satisfied that, with larger materials, the differences that now are supposed to separate *C. calcarifer* from *C. calyptratus* may not eventually break down. If however, they should not, then the two, as now, must be regarded as very closely allied species."

In other words, the material available to ANDERSON offered no sufficient reason for uniting *Ch. chamaeleon calcarifer* and *Ch. calyptratus*. The material I have seen does not justify this conclusion either. It must be regretted therefore that SCHMIDT (1953) does not give any support for his conclusion.

The type specimens of *Ch. calyptratus* (Paris Ch. 15^{1}—6634 and 15^{2}—6522) are clearly distinguishable from all the specimens of *Ch. chamaeleon calcarifer* I have seen, viz. by a gular crest of very long cones (comparable more or less with the crest of *Ch. chamaeleon zeylanicus*), by the smaller size of the occipital lobes and especially by the very high, laterally compressed casque, different from the casque in any other species.

According to Werner (1911) *Ch. calyptratus* has a disjunct distribution : "Oberer Nil (?); Yemen". I do not know why Werner put a question mark, as the label on the three type specimens clearly indicates their provenance: "Région du Nil Botta". If both provenances are right, *Ch. calyptratus* would be the only chamaeleon having a disjunct distribution.

According to the label two other specimens of *Ch. calyptratus* were captured in Yemen and in Aden (Paris Ch. 15^{3}—87.224 and Ch. 15^{5}—59.70 respectively). The latter corresponds with *Ch. chamaeleon calcarifer* as to the gular crest, the occipital lobes and the shape of the casque. This specimen may be eliminated from our consideration, obviously being wrongly identified. The other specimen, with the provenance "Yemen" distinctly belonged to *Ch. calyptratus*, though the occipital lobes were somewhat greater.

Anderson (1898) also mentions a specimen from Yemen and according to the beautiful picture he gives of this specimen, it belongs to *Ch. calyptratus* indeed. But in the same publication Anderson also mentions Socotra and Abessynia as provenances. Both are most probably wrong, and indeed are never taken seriously in literature. That means that Yemen is not very reliable as a provenance either.

As shown in the previous discussion, *Ch. chamaeleon calcarifer* is connected with *Ch. chamaeleon chamaeleon* by intermediate forms from the neighbourhood of Suez and the southern Hedjaz. This suggests that *Ch. chamaeleon calcarifer* probably invaded Arabia from the north, i.e. from the direction of Suez and not directly by a casual passage over the Red Sea in the neighbourhood of Aden. As far as I know, no such connections can be found between the assumed *Ch. calyptratus* from Yemen with the *Ch. calyptratus* from the Nile region, nor do we find intermediate forms between the *Ch. calyptratus* from Yemen and *Ch. chamaeleon calcarifer*. This, together with the unreliability of Anderson's information on provenances, suggests that we may neglect Yemen as a provenance for *Ch. calyptratus*. It also means that there is not sufficient reason for uniting *Ch. calyptratus* with *Ch. chamaeleon calcarifer*.

Now we have to find an explanation for Schmidt's conclusion. He examined 42 specimens which according to him were intermediate between *Ch. calyptratus* and *Ch. chamaeleon calcarifer*. I suppose that these specimens correspond more or less with the specimens I mentioned above, intermediate between *Ch. chamaeleon chamaeleon* and *Ch. chamaeleon orientalis*. Schmidt has perhaps been misled by the fact that *Ch. calyptratus* is the only species mentioned from Yemen. So my conclusion is :

1. *Ch. calyptratus* is still a valid species
2. Schmidt's considering synonymous *Ch. calyptratus* and *Ch. chamaeleon calcarifer* is due to wrong identification

3. the provenance Yemen is false. The only provenance we can give is just as global as BOULENGER's (1887): "Nile".

The other chameleons of this group : *Ch. basiliscus, Ch. laevigatus, Ch. senegalensis, Ch. gracilis, Ch. etiennei, Ch. dilepis* and *Ch. angusticoronatus* are all more or less closely allied with *Ch. chamaeleon*. As table K shows we often find a single difference only between these species. Therefore it is probable that in future several of these species will prove to be subspecies or synonyms. As it is I can only give some miscellaneous notes on some of them.

Ch. laevigatus.

The squamation of *Ch. laevigatus* is said to be fine, homogeneous (see WERNER, 1911), but I found in several specimens rather large scales. One specimen of the Paris collection (Ch. 2^4—04.41, Camp de Guem, pays des Soudanais. Chouli. 1220 m. Haute Nil ?) possesses 54—55 scales counted on a vertical line between the dorsal crest and the ventral crest (the average in chameleons is 65—70). Contrary to the description of WERNER (1911) are also: feebly developed tarsal spurs, parietal crest non-forked.

In the Amsterdam collection I found a specimen with 58—59 scales on the flank, also a feebly developed tarsal spur and a hardly visible, non-forked parietal crest.

A specimen of the Paris collection (Ch. 69—95. 308 Haut Oubanghi) answers more to the official description, my count amounting to 82—83 scales on the flank between dorsal and ventral crest, tarsal spurs being absent and the parietal crest being clearly forked.

TABLE M. Specimens of *Ch. laevigatus* (in the last column 7 specimens of doubtful position) compared with the probably most related species *Ch. senegalensis* and *Ch. basiliscus.*

	senegalensis	*laevigatus*			*basiliscus*	*laevigatus* ?
		Paris		A'dam	Paris 92—271	Paris 58^5 32.156 & 32.157
		69 05.308	2^4 04.41	Uganda		
number of specimens	8	1	1	1	12	7
number of scales on the flank	69—84	82—83	54—55	58—59	65—70	
casque	8b	bc	ac	bc	12a	7bc
casque elevation	8c	—c	—c	b	1a, 5b, 6c	7c
lateral crest	8+	½	½	½	12 ½	7+
occipital lobes	8e	e	e	e	12e	3d, 4e
dorsal crest	8c	b	b	b	12c	6c, 1d
gular crest	8a	a	a	a	12a	7a
ventral crest	8a	a	a	a	12a	6a, 1b
tarsal spur	3±, 5—	—	±	±	1+, 10±, 1—	5+, 2±
forked parietal crest	8—	+	—	—	12—	—

SYMBOLS USED:

Number of scales on the flank: counted on a ventral line between dorsal and ventral crest.

Forked parietal crest: + = forked; — = non-forked.

Other symbols see table K.

In table M I also compare 7 juvenile specimens from Gao, Soudan (Paris collection Ch. 58^{5}—32.156 and 32.157), because of some deviations from known species. All 7 specimens possess a casque more or less in the shape of the casque of *Ch. laevigatus*. Three specimens possess feebly developed occipital lobes. There is no dorsal crest, 6 specimens have a single row of scales on the foremost part of the back, followed by irregularly placed scales from neck to tail. Most deviating are 5 specimens possessing clearly developed tarsal spurs, while 2 specimens possess at least an indication of these spurs.

Ch. dilepis.

The literature about *Ch. dilepis* and its subspecies is extensive and very confusing. The subspecies of *Ch. dilepis* are characterized bij larger or smaller occipital lobes, by larger or smaller scales on the occipital lobes, by the absence or presence of tarsal spurs etc. These characters are clearly visible but the difficulty is that the geographical ranges of the subspecies are not sufficiently known. According to literature the ranges of several subspecies overlap over thousands of kilometers, which does not correspond with the modern concept of subspecies.

Loveridge (1929) mentions 17 males from Tanganyika, of which 2 specimens with tarsal spurs, 5 with an indication of tarsal spurs and 10 specimens completely lacking tarsal spurs. The latter 10 specimens answer to the description of the subspecies *Ch. dilepis roperi*. In the same publication Loveridge records that in ample material he found many intermediate forms between the subspecies *isabellinus* and typical *dilepis*. He also found all kinds of intermediate forms between *Ch. angusticoronatus* and *Ch. dilepis* among specimens from Zanzibar.

According to Schmidt (1919), *Ch. angusticoronatus* is still "specifically distinct", "although *C. dilepis* has also been recorded from Zanzibar". To modern standards the latter can hardly count as an objection, on the contrary it is an argument to regard *Ch. angusticoronatus* and *Ch. dilepis* as separate species. In the same publication Schmidt remarks : "the distinction of the subspecies *quilensis* appears to be doubtful" and "*roperi* and *isabellinus* are not different in ranges from *dilepis*".

Already in 1913, Sternfeld stated : „Ein triftiger Grund, *Ch. gracilis* von der folgenden Art (*dilepis*) zu trennen, liegt meines Erachtens nicht vor". In ample material of *Ch. dilepis* he found all sorts of intermediate forms, specimens hardly distinguishable from *Ch. gracilis* as well as specimens with large occipital lobes. *Ch. dilepis roperi* shows relations to both extremes : „denn es kommt sowohl ein fast völliges Schwinden der Kopflappen vor („nur angedeutet" Kibwezi), und zwar am gleichen Fundorte mit Exemplaren, die noch ganz deutlich als typische *roperi* erkennbar sind, wie ein Auswachsen jener häutlichen Anhängsel zum Gröszenmaximum bei gleichzeitig völliger Trennung".

To my opinion these remarks suffice for regarding the status of the subspecies of *Ch. dilepis* at least as doubtful. But in the publication of Loveridge (1942) we meet again with practically all the subspecies of *Ch. dilepis*, even a new one being added (*idjiwiensis*) distinguished by combining characters of *Ch. dilepis roperi* and *Ch. dilepis dilepis* !

Though the differences between *Ch. angusticoronatus* and *Ch. dilepis* seem to be negligeable, these differences (practically the shape of the casque only) prove to be fairly constant. In the collection of the Paris Museum I found 4 female specimens (Ch. 22^4—10.38, Zanzibar) as to the shape of the casque all answering to the description of *Ch. angusticoronatus*. Perhaps it wil turn out that *angusticoronatus* is one of the few justifiable subspecies of *Ch. dilepis*, as it is distinguished by a rather constant, though minor character and bound to a limited, well defined range (the island of Zanzibar).

In the Paris collection I also found 2 male specimens from Angola (Ch. 23—1285) with occipital lobes so small that it is not clear whether they belong to *Ch. gracilis* or to the *roperi* form of *Ch. dilepis*.

As a rather negative conclusion of these notes on *Ch. dilepis* I may quote Mertens (1955): „Da die Frage nach den Rassen von *Chamaeleo dilepis* noch immer nicht im Zusammenhange bearbeitet worden ist, wurde hier auf die Festlegung der Subspecies verzichtet".

Ch. gracilis.

Ch. etiennei is distinguished from *Ch. gracilis* only by the lack of tarsal spurs in the male specimens. As far as I know, *Ch. gracilis* has not been recorded from the range of *Ch. etiennei*, in other words no male specimens possessing tarsal spurs have been found there. This means that we may regard *etiennei* as a subspecies of *Ch. gracilis*, characterized by the absence of tarsal spurs in both sexes and by a well defined area: "hills near Banana".

§ 13. Species more or less related to *Chamaeleo chamaeleon* c.s.

1) *Chamaeleo anchietae* Bocage, 1872. Apart from the double row of scales on the dorsal keel this species is only little different from *Ch. laevigatus*. The characters of 9 specimens of the collection of the Leyden Museum (coll. Van der Kellen, West Afrika) are: casque resembling that of *Ch. laevigatus*, though the parietal crest is somewhat higher, no temporal crest, the squamation is fine, granular homogeneous, number of scales counted on a vertical line between the dorsal keel and the ventral crest varies between 77 and 84, the lateral crest stops just behind the temporal region, a feebly developed but quite distinct ventral and gular crest, no tarsal spur, a white midventral line from chin to anus. As the double row of scales on the dorsal keel is the only striking difference from *Ch. laevigatus*, I paid special attention to this character. Out of these nine specimens, seven possess 5 to 10 unpaired cones in the neck region just behind the parietal crest.

The subspecies are distinguished by Laurent (1952) as follows:

[The last column added after data of Werner (1911 and Laurent (1952).]

	vinckei	*marunguensis*	*mertensi*	*anchietae*
„Longueur de la queue dans la distance museau-anus	1.45—1.49	?	1.23	1.66?
idem	1.65—1.88	1.19—1.51	1.35	
"Longueur de la tête dans la distance museau-anus	3.5 —3.6	3.2 —3.3	2.9 —3.4	4.23
"Espace séparant les crêtes susorbitaires au niveau du centre de l'oeil dans la longueur de la tête	2.9	3 —3.1	... 3.4—3.5	?
"Distance de la commissure à la narine dans la distance de la commissure à l'occiput	1.20—1.23	1.20—1.24	1.17—1.20	1.00

Trying to identify the 9 specimens mentioned above with this key I took the measurements given in table N.

TABLE N. Measurements in mm. of 9 specimens of *Ch. anchietae.*

specimen nr.	1	2	3	4	5	6	7	8	9
length of head and body	98	105	105	56	90	103	82	90	85
length of tail	64	77	67	41	58	56	63	64	47
length of head	23	26	22	15	22	32	19	20	19
distance between the supraorbital ridges at the centre of the eyes	10.5	10.5	10	7	11	11	9	10	8.5
distance commissure mouth-nostril	16	18	15	10	15	15	12	12	12.5
distance commissure mouth-extremity of casque	17.5	21	18.5	10.5	18	19	15	15	15

Herefrom I got the following result:

(Explanation : a, b, c, & d indicate in sequence the diagnostic characters of LAURENT's table.
a. *mertensi* means that in the character indicated by a. the specimen corresponds with *Ch. anchietae mertensi* etc.)

specimen 1 :	a. *vinckei*	b. *anchietae*	c. ?	d. *mertensi/anchietae*
2 :	a. *mertensi*	b. cf. *anchietae*	c. ?	d. *mertensi*
3 :	a. *vinckei*	b. cf. *anchietae*	c. ?	d. *vinckei/marunguensis*
4 :	a. *marunguensis*	b. cf. *vinckei*	c. ?	d. cf. *anchietae*
5 :	a. *vinckei*	b. cf. *anchietae*	c. ?	d. *vinckei/marunguensis/mertensi*
6 :	a. *vinckei*	b. *marunguensis/mertensi*	c. *vinckei*	d. cf. *vinckei/marunguensis*
7 :	a. *marunguensis*	b. cf. *anchietae*	c. ?	d. cf. *marunguensis*
8 :	a. *marunguensis*	b. cf. *anchietae*	c. ?	d. cf. *marunguensis*
9 :	a. *vinckei*	b. ?	c. ?	d. *vinckei/marunguensis/mertensi*

The subspecies differ only to a small degree and have been described after only a few specimens (3 specimens of *Ch. anchietae mertensi*, 2 specimens of *Ch. marunguensis*). This combined with my table provides sufficient reason for regarding *Ch. anchietae vinckei, Ch. anchietae mertensi* and *Ch. marunguensis* as synonyms of *Chamaeleo anchietae* BOCAGE, 1872.

FIGURE 25. Dorsal knobs of *Ch. namaquensis.*

FIGURE 26. Dorsal knobs of *Ch. wiedersheimi.*

2) *Chamaeleo namaquensis* SMITH, 1831. This species is usually regarded as very isolated, not closely related to any of the known species. However, in my opinion it shows relations more or less to the *Ch. chamaeleon* group because of the following characters: homogeneous squamation, sometimes with scales arranged in rosette-shaped groups, no temporal crest, casque resembling that of *Ch. basiliscus* (roof-shaped, parietal crest distinctly higher than lateral crests, elevated posteriorly, lateral crest stopping just after the temporal region, no occipital lobes). A dorsal crest of 16—17 knob-like groups of scales, each group situated above a spine of a dorsal vertebra (see fig. 25). We meet a similar structure in *Ch. wiedersheimi* (see fig. 26). The only difference is that between the dorsal knobs we find a double row of scales in *Ch. wiedersheimi,* whereas in *Ch. namaquensis* the dorsal scales between the knobs are irregularly placed.

A female specimen of *Ch. namaquensis* from Namaqua (Coll. Paris) possesses a white midventral line.

3) *Chamaeleo monachus* (GRAY, 1864). I examined 3 specimens (Paris Ch. 45) corresponding with the *Ch. chamaeleon* group in the following characters:

a) shape of the casque (especially corresponding to specimens of *Ch. dilepis angusticoronatus* from Zanzibar)
b) apart from the fusion, the occipital lobes agree with those of *Ch. dilepis*
c) a white midventral line
d) a tarsal spur in male specimens
e) no temporal crest
f) (contrary to WERNER, 1911) the dorsal crest is only distinct on the foremost part of the back, followed by irregularly placed scales.

The only striking differences from members of the *Ch. chamaeleon* group are:

a) heterogeneous squamation
b) occipital lobes fused.

The geographical distribution of this species (Socotra) confirms my view that *Ch. monachus* should be included in the *Ch. chamaeleon* group.

Contrary to WERNER's description, 1911, I found a poorly developed, but clearly distinct ventral crest in all specimens of the Paris Collection. One female specimen (Paris Ch. 45—6656, with probably false provenance: Madagascar) possesses rudimentary tarsal spurs.

4) *Chamaeleo melleri* (GRAY) 1864. This species stands more isolated than the previous species. I examined one specimen, probably male (Paris Ch. 43—56, 576, Ugami, East Africa). It corresponds with *Ch. monachus*

in the following characters, and via this species with the *Ch. chamaeleon* group :

a) squamation more or less
b) an indication of a tarsal spur
c) occipital lobes somewhat less fused than in *Ch. monachus.*

Quite different, however, are the rostral processes (see fig. 12) and the more or less fin-shaped dorsal keel. This keel shows 17—18 waves, each situated above the spine of a dorsal vertebra. There is a double row of scales on the dorsal keel.

§ 14. GROUP OF *Chamaeleo oweni*,

comprising *Chamaeleo oweni* GRAY, 1831; *Chamaeleo unicornis* (MOCQUARD, 1906); *Chamaeleo michelli* (MÜLLER, 1913).

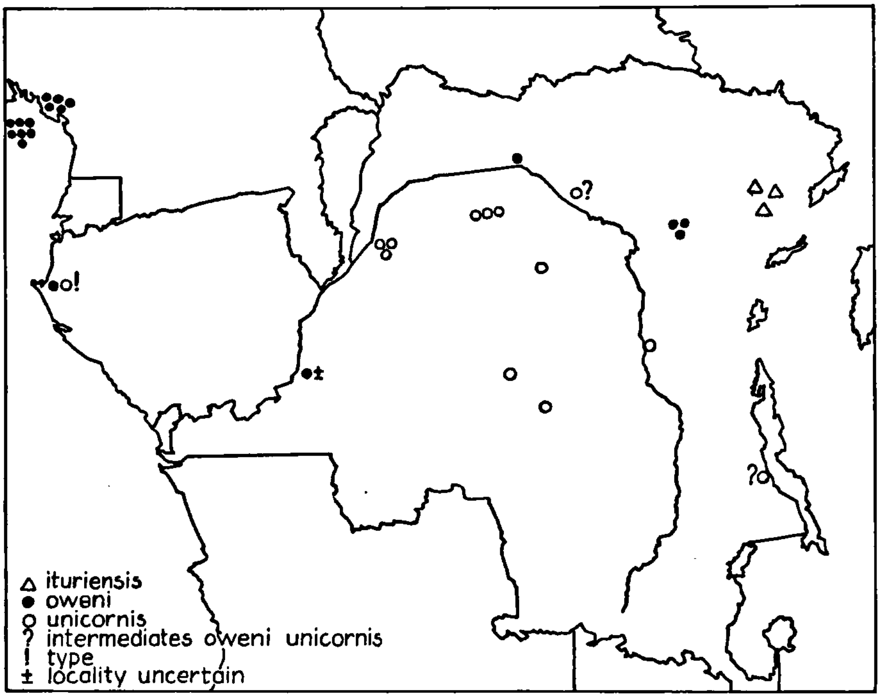
These are closely allied chameleons, distinguished from other chameleons by small occipital lobes (4—5 mm or less), by homogeneous or slightly heterogeneous squamation, by a double row of scales on the dorsal keel (sometimes a few, small, unpaired cones in the neck region), while the male specimens possess one or three cranial horns, and the tail is much longer than head and body together.

SCHMIDT (1919) concluded already that *Ch. mi*(*t*)*chelli* does not considerably differ from *Ch. oweni* and that therefore *Ch. mi*(*t*)*chelli* should be considered a synonym of *Ch. oweni.*

Contrary to WERNER's description of *Ch. oweni* (1911) are the following characters (some already mentioned above) found in 14 specimens from the collections of Paris, Amsterdam and Leyden:

all specimens possess a double row of scales on the dorsal keel, 8 of them show a few, small, unpaired cones in the neck region, 9 specimens possess a more or less distinct midventral white line, the squamation of 8 specimens is slightly heterogeneous (agreeing with STERNFELD 1912) and 7 specimens show a trace of a ventral crest.

According to WERNER (1911), the only differences between *Ch. oweni* and *Ch. unicornis* are the absence of praeorbital horns in males of the latter and the shape of the occipital lobes, which (*Ch. unicornis*) „mit dem Hinterrande des Helmes in einer queren, in der Mitte schwach concaven Linie liegen sollen, während sie bei *Ch. oweni* stark nach hinten vorspringen und demgemäsz einen tiefen winkligen Einschnitt zwischen sich erkennen lassen". In the above-mentioned specimens of *Ch. oweni* I found all sorts of intermediates between the forms which WERNER attributed to *Ch. oweni* and *Ch. unicornis.* The size of the occipital lobes varied between less than 1 mm to about 5 mm. In the Congo Museum, Tervueren, Brussels I had the opportunity of examining 15 specimens of *Ch. unicornis.* I did not find any essential differences from *Ch. oweni* as to the variation in shape and size of the occipital lobes. The only character that remains is the lacking of praeorbital horns in the males of *Ch. unicornis.* Indeed all the 15 ♂ specimens of *Ch. unicornis* mentioned above do not show even the slightest trace of these horns. Curiously enough, the type of *Ch. unicornis* (Paris Ch. 63—06.173. Gabon : Haug. Ngome. Bas-Ogooché) clearly shows distinct traces of praeorbital horns, very small on the left side, on the right side about 1 mm).



MAP 16. Congo region. Localities of *Ch. oweni* and *Ch. unicornis.*

Therefore, it is difficult to decide whether the following species belong to *Ch. oweni* or to *Ch. unicornis* :

1) Tervueren 16528. Bokuma 1952 : in every detail corresponding with the previously mentioned specimens of *Ch. unicornis* except for the possession of two little praeorbital horns (about 3 and 4 mm long, frontal horn 10 mm)

2) Tervueren 19792. Bomanya 1955 : in every detail corresponding with the preceding specimen. The praeorbital horns are 2 and 3 mm long, the frontal horn about 9 mm.

So we found that the above-mentioned specimens of *Ch. unicornis* had the following characters in common with *Ch. oweni*: a double row of scales on the dorsal keel, sometimes 5—8 unpaired cones in the neck region, a white midventral line, the squamation homogeneous or slightly heterogeneous, the tail much longer than head and body together, the same shape and size of the occipital lobes.

Though exact localities are scarcely known (as shown on map 16), we may add that BOULENGER (1887) mentioned a specimen of *Ch. oweni* from the Cameroons and WERNER (1902) two specimens of *Ch. oweni* from the Cameroons too. This indicates that the ranges of the closely related forms *oweni* and *unicornis* do not overlap, but are adjoining. Therefore I conclude that *oweni* and *unicornis* have to be regarded as the northern and southern subspecies respectively of *Chamaeleo oweni.*

§ 15. *Chamaeleo johnstoni*

Chamaeleo johnstoni (Boulenger, 1901).

This species is probably closely allied with *Ch. oweni,* from which, according to Werner (1911) it differs in the following characters:

Ch. oweni	*Ch. johnstoni*
1. small occipital lobes	occipital lobes completely absent
2. homogeneous squamation	heterogeneous squamation
3. tail much longer than head and body together	tail only a little longer or shorter than head and body
4. a double row of scales on the dorsal keel, sometimes with a few, small, unpaired cones in the neck (Werner does not mention this character, but all specimens I examined show it)	according to Werner's key (p. 7): „Rückenschneide von einer einzigen unpaaren Schuppenreihe gebildet......"
5. cranial crests indistinct	lateral crest tubercular

In the other characters the species are quite similar: in the shape of the casque, in the absence or indistinctness of the canthus rostralis, in the absence of dorsal, gular and ventral crests, while the males have 3 horns, the females none. Trying to put the above mentioned differences to the test, we find:

ad 1. Of 14 specimens of *Ch. johnstoni* (Paris Ch. 37^1 Kiseny, Belgian Congo) all showed an indication of occipital lobes, not much less than in some specimens of *Ch. gracilis*. *Ch. ituriensis* (Schmidt, 1919) must be considered as very closely allied to *Ch. johnstoni* (Loveridge, 1942 regarded it as a subspecies of *Ch. johnstoni,* hornless in both sexes and possessing clearly developed canthi rostrales, which are lacking in *Ch. johnstoni*). Now *Ch. ituriensis* possesses at least a trace of occipital lobes. A female specimen of *Ch. oweni* (Leyden coll. provenance unknown) possesses occipital lobes so rudimentary that only a small row of prominent cones remains, quite agreeing in this respect with *Ch. ituriensis.* We may conclude that absence or precence of occipital lobes cannot be considered as an essential difference in these species.

ad 2. It is known for a long time (see previous section) that the squamation of *Ch. oweni* is not always homogeneous. There are specimens of *Ch. johnstoni* which are hardly heterogeneous (see end of this section).

ad 3. As to the relative length of the tail I did not find intermediates between *Ch. oweni* and *Ch. johnstoni* (*Ch. ituriensis* entirely corresponds with *Ch. johnstoni* in this character).

ad 4. All specimens of *Ch. johnstoni* I examined have a double row of scales (contrary to Werner, 1911).

ad. 5. Tubercular lateral crests may be found in *Ch. oweni* too.

The difference in relative length of the tail and slight, gradual differences in the shape and size of the occipital lobes remain the only distinguishing characters. Considering the geographical ranges of *Ch. oweni, Ch. ituriensis* and *Ch. johnstoni*, which do not overlap, but are adjoining, it might be suggested that these 3 forms are subspecies of one species, *Ch. oweni*. Yet, I prefer to postpone this conclusion, till it can be proved by more material, from more provenances.

The subspecies *Ch. johnstoni graueri* (STEINDACHNER, 1911) is distinguished by the absence of a parietal crest and the presence of a feebly developed ventral crest. 12 specimens out of 16 from Kiseny, Belgian Congo, show a feebly developed ventral crest, all specimens, however, possess a parietal crest too. The same characters are combined in a specimen (Paris 33.176) from Babandana, Lac Kivu, Belgian Congo.

The character "vertebral line more or less compressed, wavy in outline from the side" as mentioned in *Ch. ituriensis* by SCHMIDT (1919), sometimes distinct in *Ch. johnstoni* too (LAURENT, 1951), may perhaps be regarded as an indication of relationship with the greater, fin-shaped dorsal keels in *Ch. montium* a.o. The little waves in the outline are each situated above a spine of a dorsal vertebra.

The character "midventral white line", present in many specimens of *Ch. oweni*, present in all specimens (15) of *Ch. ituriensis* (examined in the Museum of Tervueren), is absent in all specimens (15) of *Ch. johnstoni* I have seen.

Finally I give a short description of a specimen of *Ch. johnstoni* (Amsterdam coll. Tanganyika, 1914, don. STEINDACHNER): dorsal keel wavy in outline above the spines of the dorsal vertebrae; a double row of scales on the dorsal keel; clearly distinct ventral crest; lateral crests just as tubercular as in specimens of *Ch. oweni* (Amsterdam coll., Lagos Nigeria (?!) male and female); hardly heterogeneous squamation ; length of head and body together 60 mm, length of tail 56 mm ; 3 horns of about 2 mm.

§ 16. THE OVOVIVIPAROUS CHAMELEONS I: GROUP OF *Chamaeleo pumilus*,

comprising *Chamaeleo pumilus* DAUDIN, 1802; *Chamaeleo melanocephalus* (GRAY, 1864); *Chamaeleo gutturalis* A. SMITH, 1849; *Chamaeleo taeniobronchus* A. SMITH, 1831; *Chamaeleo ventralis* GRAY, 1845; *Chamaeleo damaranus* (BOULENGER, 1887), *Chamaeleo caffer* (BOETTGER, 1889).

The ovoviviparous chamelons form a rather homogeneous group. Apart from the ovoviviparity, they have in common the coarse, heterogeneous squamation, the small to moderate size and, in most cases, the absence of a ventral crest. The group of species around *Ch. pumilus*, which will be dealt with in this section, are only found in South Africa. They are distinguished from the ovoviviparous species around *Ch. bitaeniatus* (§ 17) by the following characters :

1. the parietal crest is not forked, the lateral crest is clearly distinct (see fig. 6),
2. in most cases gular lobes or scaled tubercles are found on the gular crest (the sometimes smooth gular cones of *Ch. melanocephalus* are comparable with those in *Ch. bitaeniatus*),

TABLE O. Comparison of the forms around *Ch. pumilus*.

	1. *pumilus pumilus*	2. *pumilus transvaalensis*	3. *melanocephalus*	4. *gutturalis*	5. *ventralis ventralis*	6. *ventralis occidentalis*	7. *ventralis karrooicus*	8. *damaranus*	9. *caffer*	10. *taeniobronchus*
casque elevation	±	+	—	±?	+&±	?	—	+	±	—
casque breadth	b	b	b	b ?	b	ab(b)	(a)b	b	b	b
distance commissure mouth-extremity of casque	a&b	b&c	a	a&b	b&c	?	?	c	c	a&b
cranial crests	±	+	±	+	+&±	+	±	±	—	—
lateral rows of larger scales on the flank	+	+(—)	—&+	+	+	+	+	+	—(±)	—(+)
gular lobes scaled	a	a	c(a)	c&b	a	a	a	a	a	a&b
gular lobes compressed	+	+	—	—	+	+	—	+	+	—
gular lobes overlapping	—	—&+	—	—&+	+	+	—	+	+	—
gular lobes large or small	±	+	±	±	+	+(—)	+	+	—	—
gular lobes long or broad	a	a&b	a	a	ab	b(a)	a	c	c	a
dorsal cones isolated	±	+	+(—)	+	±	±	—	±	±	+&—
tail index	♂ c ♀ a	♂ c ♀ c	♂ c ♀ a	a	a	a	a	c	♂ c ♀ a&b	♀ a

SYMBOLS USED:
Casque elevation: + = high; — = low.
Casque breadth: a = broad; b = narrow.
Distance commissure mouth — extremity of casque: a = shorter than the mouthcleft; b = equal to the mouthcleft; c = greater than the mouthcleft.
Cranial crests: + = prominent and denticulated; — = weakly developed.
Lateral rows of larger scales on the flank: + = present; — = absent.
Gular lobes scaled: a = completely scaled; b = partially scaled; c = not scaled at all.
Gular lobes compressed: + = compressed; — not compressed.
Gular lobes overlapping: + = overlapping; — = not overlapping.
Gular lobes large or small: + large; — = small.
Gular lobes long or broad: a = longer than broad; b = broader than long; c = the anterior lobes only are broader than long.
Dorsal cones isolated: + = isolated; — = not isolated, in a more or less continuous row.
Tail index: a = length of tail shorter than length of head and body; b = length of tail equal to length of head and body; c = length of tail greater than length of head and body.

3. the dorsal crest is formed by more or less equal cones or tubercles,
4. no rostral appendages present,
5. no occipital lobes present.

TABLE P. Conclusion of table O : the numbers of characters that the descriptions of species and subspecies around *Ch. pumilus* have in common with each other. All descriptions according to WERNER, 1911 and FITZSIMONS, 1943.

	1. *p. pumilus*	2. *pumilus transvaal.*	3. *melanocephalus*	4. *gutturalis*	5. *v. ventralis*	6. *ventralis occident.*	7. *ventralis karr.*	8. *damaranus*	9. *caffer*	10. *taeniobronchus*
1. *p. pumilus*	12	8	10	8	7	9	7	7	7	8
2. *pumilus transvaal.*	8	12	7	6	11	10	7	9	8	6
3. *melanocephalus*	10	7	12	10	6	9	11	6	5	11
4. *gutturalis*	8	6	10	12	8	10	9	4	6	9
5. *v. ventralis*	7	11	6	8	12	12	7	10	8	6
6. *ventralis occident.*	9	10	9	10	12	12	8	9	9	9
7. *ventralis karrooicus*	7	7	11	9	7	8	12	6	4	11
8. *damaranus*	7	9	6	4	10	9	6	12	10	5
9. *caffer*	7	8	5	6	8	9	4	10	12	7
10. *taeniobronchus*	8	6	11	9	6	9	11	5	7	12

The descriptions of the species and subspecies around *Ch. pumilus* mention many clearly distinct differences, so that it seems quite easy to determine each specimen.

There are indeed specimens which answer in every detail to the descriptions. But the number of exceptions and of intermediate forms is so great, that we must doubt the validity of all these species and subspecies.

In table O I have made an attempt to analyse the differences between the species and subspecies, according to WERNER's descriptions, 1911, if necessary corrected according to those by FITZSIMONS, 1943, in order to get comparable data. There are 12 characters, which in several combinations are characteristic for the species and subspecies.

In table P I have noted the numbers of these characters that each species or subspecies has in common with each of the other species. The result is astonishing : *Ch. p. pumilus* has more characters in common with *Ch. melanocephalus* than with its subspecies *Ch. pumilus transvaalensis.* The subspecies *Ch. pumilus transvaalensis* has more in common with *Ch. v. ventralis, Ch. ventralis occidentalis* and *Ch. damaranus* than with *Ch. p. pumilus.* This agrees with FITZSIMONS' remark in the original description of (the species) *Ch. transvaalensis :* "The above species falls between *C. ventralis* and *C. damaranus*".

Table Q is but another arrangement of the conclusions of table O. It shows the degree of affinity indicated by the number of characters that each species has in common with the other species or subspecies.

Ch. v. ventralis has less in common with its subspecies *Ch. ventralis karrooicus* than with 5 other species and subspecies.

TABLE Q. The relationship of the forms around *Ch. pumilus*, measured with the number of characters they have in common.

	numbers of characters in common			
	12	11	10	9
p. pumilus	*p. pumilus*		*melanoceph.*	*v. occident.*
pumilus transvaal.	*p. transv.*	*ventralis*	*ventr. occid.*	*damaranus*
melanocephalus	*melanoceph.*	*v. karrooicus* *taeniobronch.*	*p. pumilus* *gutturalis*	*ventr. occident.*
gutturalis	*gutturalis*		*melanoceph.* *v. occident.*	*v. karrooicus* *taeniobronchus*
v. ventralis	*v. ventralis* *v. occident.*	*p. transv.*	*damaranus*	
ventr. occident.	*v. occident.* *v. ventralis*		*p. transv.* *gutturalis*	*p. pumilus* *melanoceph.* *damaranus* *caffer* *taeniobronchus*
ventr. karrooicus	*v. karrooicus*	*melanoceph.* *taeniobronch.*		*gutturalis*
damaranus	*damaranus*		*v. ventralis* *caffer*	*p. transv.* *v. occident.*
caffer	*caffer*		*damaranus*	*v. occident.*
taeniobronchus	*taeniobr.*	*melanoceph.* *v. karrooicus*		*gutturalis* *v. occident.*

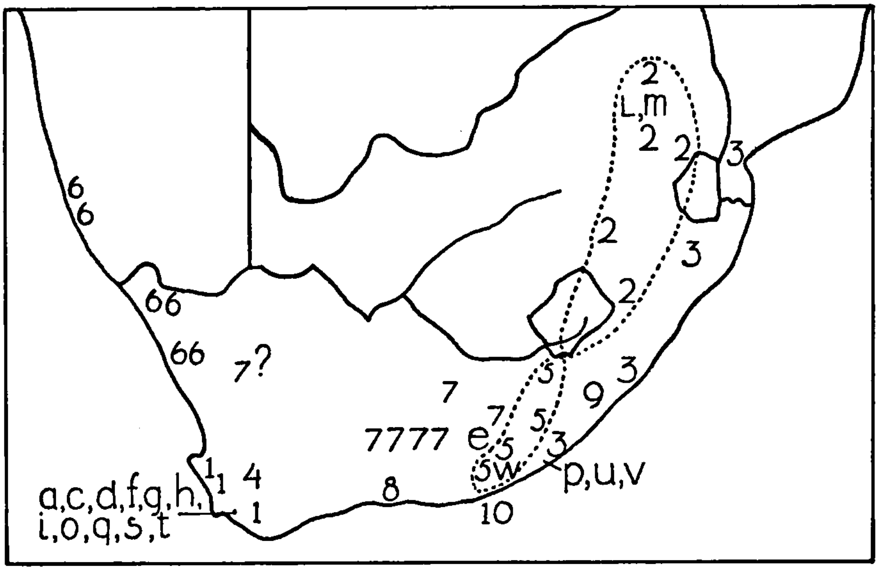
If we consider the species and subspecies from the geographical view-point, as is done in map 17, it is difficult to understand why some forms are regarded as subspecies of other forms from which they are separated not only by many characters, but also by large areas occupied by other forms.

For instance, *Ch. p. pumilus* has not only less in common (8 characters) with its subspecies *Ch. pumilis transvaalensis* than with the species *Ch. melanocephalus* (10 characters) and *Ch. ventralis occidentalis* (9 characters), but also *Ch. p. pumilus* and *Ch. pumilus transvaalensis* are separated by a wide geographical gap, whereas the ranges of the more related *Ch. p. pumilus* and *Ch. ventralis occidentalis* are adjoining.

Other conclusions from the combination of table Q and map 17 are:

Ch. pumilus transvaalensis has much (11 characters) in common with the adjacent *Ch. v. ventralis*. *Ch. v. ventralis* has much in common with *Ch. v. occidentalis*, indeed the variations of all 12 characters of either species are overlapping. Though the geographical distance is large, there are no other forms to be found between these two forms. *Ch. v. ventralis* has also many characters (10) in common with the adjacent *Ch. damaranus*. So we find a rather close connection, geographically and taxonomically: *Ch. pumilus transvaalensis* ←→ *Ch. v. ventralis* ←→ *Ch. ventralis occidentalis*, with side-branches *Ch. v. ventralis* ←→ *Ch. damaranus* and *Ch. v. ventralis* ←→ *Ch. caffer*.

On the other hand, we find that *Ch. pumilus transvaalensis* and *Ch. melanocephalus*, whose ranges border on each other on a line of hundreds



MAP 17. South Africa. Distribution of the forms around *Ch. pumilus*. Ciphers see table P, letters see table R.

of kilometers, have relatively few (7) characters in common. As their distributions are more or less coinciding with the distribution of highland and lowland, it seems quite plausible that these forms are separated as highland and lowland forms. This view is confirmed by the affinity of the assumed lowland form *Ch. melanocephalus* with *Ch. taeniobronchus* and with *Ch. ventralis karrooicus*. Though the Karroo is not lowland, it is not a mountain area either. Perhaps we had better distinguish between flat land and mountains instead. If we compare our map 17 with a physical map of South Africa, we find that the area of *melanocephalus-taeniobronchus-ventralis karrooicus* crosses the area of *pumilus transvaalensis-v. ventralis-damaranus* (*ventralis occidentalis*), which coincides with the crossing of the flat coastal area continuing into the valley of the Sunday River and the Great Karroo, with the mountainous areas of the Drakensberg range continuing into the Swartberg range.

Ch. ventralis occidentalis, as shown closely related with *Ch. v. ventralis*, has also connections with the adjacent species *Ch. gutturalis* (10 characters in common) and *Ch. p. pumilus* (9 characters in common). (The taxonomic affinities of the latter with *Ch. melanocephalus*, at first sight geographically uncomprehensible, will be dealt with later on.)

Map 17 shows that the ranges of these forms are in many cases adjacent, but never overlapping. As these forms are closely related, differing in a few characters only, we have sufficient reasons to call this whole group of forms one single species, with several geographically bound subspecies.

This picture is based on the literature compiled by WERNER (1911) and FITZSIMONS (1943) only. I have not been able to take into account the publication of POWER, 1932, as I cannot reconcile his statements and those of WERNER, 1911, and FITZSIMONS, 1943. For instance, POWER gives a map of the geographical distribution of the forms around *Ch. pumilus,* which in many essential points differs from map 17, composed by me after the publications of WERNER, 1911, and FITZSIMONS, 1943. According to POWER *Ch. taeniobronchus* lives from Algoa Bay to north Transvaal. FITZSIMONS, though mentioning POWER, gives as the distribution of this chameleon : "Apparently confined to the neighbourhood of Algoa Bay, Cape Province."

The only conclusion can be that POWER has given other names to the same material known to FITZSIMONS. As he did not motivate his determinations, I cannot "translate" his names into those used by me (after WERNER and FITZSIMONS). I only want to mention a series of 7 specimens from North Transvaal, which, according to POWER, who had the opportunity of examining the type specimen of *Ch. taeniobronchus,* "gives a complete range of variation between *pumilus* (sensu stricto) and the type of *taeniobroncha*".

In the collections of Paris, Leyden and Amsterdam I found several specimens more or less deviating from the descriptions, or from other provenances than those given in literature.

In a casual group of 9 specimens from the Paris collection, registered as *Ch. pumilus,* only 6 answer to any description by WERNER, 1911 or FITZSIMONS, 1943, viz. to that of *Ch. p. pumilus.* Apart from 2 specimens without recorded provenance, only 2 specimens came from the known range of *Ch. p. pumilus.* The remaining 2 specimens came from East-London, that is from the range of *Ch. melanocephalus* and *Ch. v. ventralis.* At first sight this seems uncomprehensible, as the recorded ranges of these species are so wide apart. But table P and Q show that *Ch. p. pumilus* has much in common indeed with *Ch. melanocephalus* (10 characters), more than with any other species. The 2 specimens of *Ch. p. pumilus* of East-London, in combination with the close taxonomical relationship of the species *Ch. p. pumilus* and *Ch. melanocephalus* suggest a closer geographical relationship too. Considering map 17, which has been drawn after the data of FITZSIMONS, 1943, we find a few records only from the area between the ranges of *Ch. p. pumilus* and of *Ch. melanocephalus.* Indeed, it is possible that more specimens varying between *Ch. p. pumilus* and *Ch. melanocephalus* will be found in this area.

This view is supported by the analysis of other specimens given in tables R, S and T, which run parallel with the tables O, P and Q. For instance, we find in the range of *Ch. p. pumilus* the specimens a, c, d, and s, which fit in fairly well with the description of *Ch. p. pumilus,* but also the specimens f, g, h, i, o and t, which do not answer to any description, but which are more or less connected with *Ch. gutturalis* (adjacent species), *Ch. melanocephalus* (connection mentioned above), *Ch. taeniobronchus* (significant if we consider the lines *melanocephalus-taeniobronchus* and *melanocephalus-p. pumilus*).

All these aberrant specimens have been put on map 17.

These aberrant specimens complete the picture derived from WERNER, 1911 and FITZSIMONS, 1943. They firstly show the homogeneity of the group of forms around *Ch. pumilus,* and secondly they accentuate the forms as geographically bound.

TABLE R. The characters of some aberrant specimens belonging to the group around *Ch. pumilus*. Symbols see table O.

	a	b	c	d	e	f	g	h	i	j	k	l	m	o	t	v	w
sex	♀	♂	♂	♂	♀	♂	♂	juv.	juv.	♀	♂	♂	♂	♂	♂	♂	?
casque elevation	±	+	±	±	±	±	±	—	—	±	±	+	+	±	±	±	±
casque breadth	b	b	b	b	b	b	ab	ab	a	ab	b	ab	ab	b	b	b	b
distance commissure mouth-extremity of casque	b	a	a	a	b	a	a	a	a	c	a	c	a	b	a	a	c
cranial crests	±	±	±	±	±	±	±	—	—	+	+	±	—	±	±	±	±
lateral rows of larger scales on the flank	+	+	+	+	—	+	+	+	+	±	+	+	+	+	+	+	+
gular lobes scaled	a	a	a	a	a	±b	a	c	a	b	b	b	a	b	a	a	a
gular lobes compressed	+	+	+	+	+	—	—	—	±	±&—	+&—	+&—	+	±	—	—	+
gular lobes overlapping	—	—	—	—	±	—	—	—	—	+	+	—	—	—	—	—	+
gular lobes large or small	±	±	±	+	—	±	±	±	±	±	±	—	—	±	+	±	+
gular lobes long or broad	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b(a)
dorsal cones isolated	±	±	+	±	+	—	±	+	+	+	+	+	+	±	±	±	±
tail index	b	c	c	c	a	a	a	a	a	a	a	c	c	c	c	a	a

Localities of the specimens: a — Capetown, leg. Thors 1950, coll. Amsterdam. b — loc. unknown, coll. Leyden. c, d — Dieprivier, Kaapkolonie, leg. M. Weber 1894, coll. Amsterdam. e — Bedford, leg. G. Theiler, July 1938, coll. Leyden. f, g, h, i — Kaapstad, 6 Sept. 1938, coll. Leyden. j, k — loc. unknown. l, m — Pretoria District, leg. Breyer, coll. Amsterdam. The other specimens belong to the Paris Museum. The specimens n, p, q, r, s, u are not treated in table R, as they quite answer to the descriptions of *Ch. p. pumilus* as given by WERNER, 1911 and FITZSIMONS, 1943. The localities of the specimens n and r have not been recorded. The specimens o, q, s, t come from Capetown. The specimens p, u, v come from East-London, w comes from Grahamstown.

TABLE S. The numbers of characters that the specimens mentioned in table R have in common with the descriptions of the forms around *Ch. pumilus,* according to WERNER, 1911, and FITZSIMONS, 1943.

	1. *p. pumilus*	2. *pumilus transvaal.*	3. *melanocephalus*	4. *gutturalis*	5. *v. ventralis*	6. *ventralis occident.*	7. *ventralis karrooicus*	8. *damaranus*	9. *caffer*	10. *taeniobronchus*
a	12	9	9	8	7	5	6	6	7	8
b	11	9	8	7	7	6	5	8	6	7
c	12	9	8	8	8	6	6	7	7	7
d	12	8	10	8	8	6	8	7	6	8
e	9	8	7	8	9	7	6	6	9	9
f	8	4	9	10	5	3	8	3	3	9
g	9	5	10	9	6	6	9	4	4	9
h	7	5	10	9	3	4	7	2	4	9
i	9	7	10	8	5	6	8	4	6	10
j	6	7	6	9	7	8	5	4	6	5
k	7	8	7	10	8	7	5	4	5	7
l	7	8	7	6	7	6	7	7	7	8
m	9	8	8	5	6	6	6	7	7	7
o	10	7	9	9	5	4	6	5	5	8
t	11	8	11	9	7	4	8	6	6	9
v	11	8	11	10	8	5	9	5	6	10
w	9	10	6	7	12	10	7	10	10	7

Therefore, I conclude that all these forms belong to one species, viz. *Ch. pumilus* DAUDIN, 1802 (the first described form)and that all the remaining forms should be regarded as subspecies of this. Their names have to be (in sequence of the ciphers on map 17, the same as in the tables O, P and S):

1. *Chamaeleo pumilus pumilus* DAUDIN, 1802
2. *Chamaeleo pumilus transvaalensis* (FITZSIMONS, 1930)
3. *Chamaeleo pumilus melanocephalus* (GRAY, 1864)
4. *Chamaeleo pumilus gutturalis* A. SMITH, 1849
5. *Chamaeleo pumilus ventralis* GRAY, 1845
6. *Chamaeleo pumilus occidentalis* (HEWITT, 1935)
7. *Chamaeleo pumilus karrooicus* (METTHUEN and HEWITT, 1914)
8. *Chamaeleo pumilus damaranus* (BOULENGER, 1887)
9. *Chamaeleo pumilus caffer* (BOETTGER, 1880)
10. *Chamaeleo pumilus taeniobronchus* A. SMITH, 1831

The arguments given by METTHUEN and HEWITT, 1915; POWER, 1932 and others for a re-establishment of a separate genus *Lophosaura* or *Microsaura* (both by GRAY, 1864), are not consistent. The differences in skull and lungs between *Ch. pumilus* and *Ch. dilepis* seem quite

TABLE T. The relationship of the specimens mentioned in table R, measured with the number of characters each has in common with the descriptions of the forms around *Ch. pumilus*.

	12	11	10	9
a	*p. pumilus*			*pumilus transv.* *melanocephalus*
b		*p. pumilus*		*pumilus transv.*
c	*p. pumilus*			*pumilus transv.*
d	*p. pumilus*		*melanocephalus*	
e				*p. pumilus* *v. ventralis* *caffer* *taeniobronchus*
f			*gutturalis*	*melanocephalus* *taeniobronchus*
g			*melanocephalus*	*p. pumilus* *gutturalis* *ventralis karr.* *taeniobronchus*
h			*melanocephalus*	*gutturalis* *taeniobronchus*
i			*melanocephalus* *taeniobronchus*	*p. pumilus*
j				*gutturalis*
k			*gutturalis*	
l	(8 characters in common with *Ch. pumilus transv.* and *Ch. taeniobronchus*)			
m			*p. pumilus* *pumilus transv.*	
o			*p. pumilus*	*melanocephalus* *gutturalis*
t		*melanocephalus* *p. pumilus*		*taeniobronchus* *gutturalis*
v		*melanocephalus* *p. pumilus*	*taeniobronchus* *gutturalis*	*ventralis karr.*
w	*v. ventralis*		*pumilus transv.* *ventralis occident.* *damaranus*	*p. pumilus*

significant, but as long as we know nothing about the constancy or variation of these characters in, for instance, the species around *Ch. bitaeniatus* or the group around *Ch. chamaeleon*, I think there is no sense in establishing a separation between two species chosen at random.

As we have mentioned, GRAY (1864) made two genera out of the group around *Ch. pumilus*, viz. *Lophosaura* and *Microsaura*. I cannot understand why GRAY, being such a splitter, took *Ch. tigris* KUHL, 1820, in the same genus *Lophosaura* as *Ch. pumilus* (the latter in the old sense). Apart from a single scaled lobe on the chin (not resembling the gular lobes of *Ch. pumilus* by the way), I cannot find that *Ch. tigris* has much in common with *Ch. pumilus*. It is not even known yet if *Ch. tigris* is oviparous or ovoviviparous.

I examined two specimens (Paris Ch. 62^{2}):

FIGURE 27. Groups of dorsal cones of *Ch. tigris.*

FIGURE 28. Dorsal cones of *Ch. tigris.*

One specimen is labelled "Madagascar", which is probably not to be taken seriously. This specimen, perhaps a female, shows on the anterior part of the back a dorsal crest, comparable with this crest in *Ch. bitaeniatus* c.s. (see fig. 27), viz. groups of tubercles, each group above the spine of a dorsal vertebra. The second half of the dorsal keel has a double row of scales. The low cones of the gular crest give the impression of being grooved or even scaled. Differences from the description in WERNER (1911) are: distance between the commissure of the mouth and the extremity of the casque is equal to the length of the mouthcleft. The second specimen, a male, has a different type of dorsal crest (see fig. 28), the separate cones are not clearly connected with the dorsal spines; between the dorsal cones we do not find a single or a double row of scales, but the squamation is irregular; the gular cones are more clearly grooved than in the other specimen; there is an indication of a ventral crest.

If *Ch. tigris* might prove to be ovoviviparous, it may be regarded as a form intermediate between *Ch. pumilus* and *Ch. bitaeniatus* c.s. The scaled chin-lobe, though different, and the grooved or perhaps even scaled other gular cones are characters it has in common with *Ch. pumilus,* whilst its forked parietal crest and in some specimens the dorsal crest are characters which *Ch. bitaeniatus* possesses also. Its homogeneous squamation is different from either of them.

§ 17. THE OVOVIVIPAROUS CHAMELEONS II: GROUP OF *Chamaeleo bitaeniatus*

comprising: *Chamaeleo bitaeniatus* FISCHER, 1884; *Chamaeleo jacksoni* (BOULENGER, 1896); *Chamaeleo tempeli* (TORNIER, 1899); *Chamaeleo werneri* (TORNIER, 1899); *Chamaeleo fuelleborni* (TORNIER, 1900).

Though these species have much in common with *Ch. pumilus* (ovoviviparity, roughly heterogeneous squamation, moderate to small size) they are distinguished as a group by:

1) parietal crest forked anteriorly
2) gular crest absent, or formed by ordinary cones
3) dorsal crest with unequal cones, in most cases with groups of larger cones above the spines of the dorsal vertebrae (see fig. 29 and 30).

A subdivision can be made in:

a) species completely lacking occipital lobes (*Ch. bitaeniatus* and *Ch. jacksoni)*

FIGURE 29. Groups of dorsal cones of *Ch. bitaeniatus*

FIGURE 30. Groups of dorsal cones of *Ch. bitaeniatus*

b) species with large occipital lobes (*Ch. tempeli, Ch. werneri* and *Ch fuelleborni*).

a) *Ch. bitaeniatus* and *Ch. jacksoni.*

Ch. bitaeniatus and *Ch. jacksoni* are closely related. Besides the horns of *Ch. jacksoni,* Werner (1911) mentions as differences that *Ch. bitaeniatus* possesses a gular and ventral crest in contrast with *Ch. jacksoni,* which lacks either. Only embryos of the subspecies *Ch. jacksoni vauerescecae* possess, according to Werner, a short crest, of 6 cones only, on the chin and a distinctly developed ventral crest of 8 cones (separated from the crest on the chin). In adults these characters, according to him, degenerate and become indistinct.

Because these species are so much alike in other details, I paid special attention to the presence or absence of the ventral and gular crest.

Out of 25 specimens of *Ch. jacksoni* (Coll. Paris, 3 from Amboni, Kenya, 21 from Nairobi and 1 of unknown provenance), only 1 specimen completely lacks the ventral and gular crest, though even in this specimen I could distinguish 3 scales on the median line of the throat that differed from the surrounding scales. All the remaining specimens possess poorly developed gular and ventral crests (most of the latter were only indicated between the forelegs and just in front of the anus).

The first 4 specimens of *Ch. bitaeniatus* that came to hand all show but poorly developed ventral and gular crests:

Paris 04.257, provenance unknown, only a trace of a ventral and gular crest
„ 04.79 , Abessynia, poorly developed gular and ventral crest
„ 05.253, Lac Rodolphe, poorly developed gular and ventral crest
„ 33.175, Kitembo, Belgian Congo, poorly developed gular and ventral crest.

So the absence or presence of a ventral and a gular crest cannot be regarded as an important difference between *Ch. bitaeniatus* and *Ch. jacksoni.*

In my opinion there are not sufficient reasons for maintaining *Ch. jacksoni vauerescecae* as a valid subspecies. The cranial horns of *Ch. jacksoni vauerescecae* are equal in both sexes, whereas the females of *Ch. jacksoni jacksoni* are distinguished from the males by the absence of the praeorbital horns, of which only pointed cones are left. The rostral horn is equal in both sexes.

In the Paris collections I found 10 female specimens from Nairobi (the range of *Ch. jacksoni vauerescecae)* of which 6 specimens possess normal praeorbital horns, while in 4 specimens these horns were less developed to nearly absent, even less developed than in the type of *Ch. unicornis* (see p. 53). In the following list the measurements (in mm) taken on these ten specimens are given:

Praeorbital horn	*Rostral horn*	*Head & body*	*Tail*
7	11	93	80
12	15	125	95
6	12	110	88
3.5	10	98	85
2.5	12	104	109
12	12	117	114
1 & 4	6.5	112	106
5	17	132	115
± 0.75	5	100	87
18	20	113	104

For comparison I give some measurements of male specimens from the same provenance:

Praeorbital horn	*Rostral horn*	*Head & Body*	*Tail*
17	17	100	100
24	21	113	102
25	23	123	137

So, at least in the relative length of this praeorbital horns, all intermediates exist in the females between what has been regarded as typical female and typical male character. Another conclusion is, that there must be some mistake in the measurements given by WERNER (1911): "L. ♂ 122 mm, Hörner 7 mm, Schwanz 60 mm; ♀ 117 mm, Schwanz 88 mm". The first figure in both male and female is the length of head + body + tail. The measurements of the ♂ specimen are probably right, though they are obviously taken from a small specimen. The measurements of the female, however, cannot be right, for it seems improbable that in a specimen with a tail of 88 mm, the length of head + body would be 117 — 88 = 29 mm only.

b) *Ch. tempeli, Ch. werneri* and *Ch. fuelleborni.*

In this group the dorsal crest is practically always formed by about 16 groups of larger cones, each group placed above the spine of a dorsal vertebra. The squamation is more roughly heterogeneous, with larger scales. All species of this group possess large occipital lobes. Though different in detail, they all possess a V-shaped pattern of gular squamation, more or less corresponding with that of *Ch. affinis* and *Ch. goetzei* (see p. 69).

1) *Ch. tempeli.* Hornless. Occipital lobes fused a little, just behind the occiput. A V-shaped gular crest of large triangular cones. As in *Ch. affinis* the scales on the middle of the throat, surrounded by the V-shaped crest, are smaller than the other gular scales.

2) *Ch. fuelleborni.* On the whole resembling *Ch. tempeli.* Different are the 3 horns (in both sexes; plumper than in *Ch. jacksoni*) and the gular squamation. The latter shows a V-shaped pattern, with smaller scales on the middle of the throat and larger scales on the outer sides just as in *Ch. tempeli,* but the large cones are absent. So the gular squamation quite resembles that of *Ch. affinis* and *Ch. goetzei* (see page 69).

3) *Ch. werneri.* Most features the same as in the preceding two species. Different are: the pattern of the gular squamation (larger scales on the middle field of the throat, smaller ones on the outer fields) which is exactly the reverse of that of *Ch. fuelleborni*; besides the absence of praeorbital horns in females (only a rostral horn present).

The other difference mentioned by WERNER (1911), viz. the complete fusion of the occipital lobes, was not evident in the only specimen I had the opportunity of examining (Paris 31.55 1♀, Kigogo Utschangwe Mts, collected by LOVERIDGE 13.I.1930), as the fusion of the occipital lobes is not longer than 2 mm.

If we compare the diagnostic characters provided by the horns in different groups, it is possible to draw up comparable series, viz.

bitaeniatus: werneri: fuelleborni =
bitaeniatus: jacksoni vaueresceae: jacksoni jacksoni =
hornless: 3 horns in male and 1 in female: 3 horns in both sexes.

Such parallel series can be made in many cases: they point to parallel developments in the different groups.

Perhaps *Chamaeleo incornutus* (LOVERIDGE, 1931) also belongs to this group. The description by LOVERIDGE corresponds with the descriptions of the preceding species, especially in the following sentence: "Well-developed occipital flaps fused in a short median suture behind the casque; a decidedly indistinct parietal crest forked anteriorly; a low dorsal crest comprised of sharply spinose scales (well separated or in groups of two or three followed by an interspace) from the nape to the base of the tail".

§ 18. MISCELLANEOUS

In this section a few short notes are given on species which cannot be grouped with certainty. In some cases this is caused by lack of material, in other cases, really isolated species are concerned.

1) *Chamaeleo wiedersheimi* (NIEDEN, 1910). We mentioned *Ch. wiedersheimi* in connection with *Ch. namaquensis* (p. 52).

We found that the peculiar dorsal knobs of *Ch. namaquensis* resemble very much those of *Ch. wiedersheimi* (see fig. 25 and 26). This might suggest a connection with the *Ch. chamaeleon* group, but apart from a white midventral line (not continued on the throat) there are few resemblances. The most striking differences from *Ch. chamaeleon* c.s. are:

a) a clearly distinct temporal crest
b) a lateral row of larger shields on the flank
c) a little groove on the upper lip from nostril to nostril.

Chamaeleo serratus (MERTENS, 1922) is a synonym of *Ch. wiedersheimi*, as the author (in litteris 1955) concluded.

2) *Chamaeleo affinis* RÜPPELL, 1845 has many characters in common with *Ch. wiedersheimi* as appeared to me after examination of 13 specimens of the Paris collection Ch. 1 etc.), viz.:

a) a clearly distinct temporal crest;
b) one specimen (32.104) possesses a homogeneous squamation, all other specimens possess a clearly distinct lateral row of larger shields on the flank;

FIGURE 31. Paired scales alternating with unpaired scales on the dorsal keel of *Ch. affinis.*

c) a little groove on the upper lip from nostril to nostril;
d) 8 specimens show a flat casque, just as *Ch. wiedersheimi* (i.e. the parietal crest on the same level as the lateral crests), the other 5 specimens possess a casque more or less corresponding with that of *Ch. laevigatus*, with the parietal crest somewhat higher than the lateral crests;
e) in all specimens a white, more or less distinct, midventral line occurs, not continuing on the throat.

It differs from *Ch. wiedersheimi* in the following characters:
a) a single row of scales on the dorsal keel (though sometimes alternating with paired scales. See fig. 31);
b) no gular crest, but a gular squamation pattern more or less corresponding with that of *Ch. tempeli, Ch. werneri* and *Ch. fuelleborni* (see p. 67), viz. a central zone of smaller scales, surrounded by larger ones;
c) in 3 specimens (Paris Ch. 1-05.151, Ch. 1^2-02.305 and one specimen of Ch. 1^1-05.148) I found a slight indication of occipital lobes (hardly a slit). Though rudimentary, these little slits point to a connection with the following species, which suggests a certain affinity among *Ch. wiedersheimi, Ch. affinis* and *Ch. goetzei*. Contrary to WERNER (1911), I found 5 specimens only of which the casque is "fast unmittelbar in den Nacken übergehend", whereas in 8 other specimens the casque is distinctly higher than the dorsal keel.

3) *Chamaeleo goetzei* (TORNIER, 1899). I had the opportunity of examining 1 specimen only (Paris Ch. 33-31.35). It showed the following characters either in common with *Ch. affinis* or with *Ch. wiedersheimi:*
a) a clearly distinct temporal crest;
b) WERNER, 1911, records a lateral row of larger shields on the flank; in this specimen it is hardly discernable;
c) the gular squamation pattern resembles that of *Ch. affinis*;
d) very small occipital lobes (something like those of *Ch. gracilis*, compare also *Ch. affinis*);
e) the shape of the casque is more or less corresponding with that of the 5 specimens of *Ch. affinis* mentioned above.

The last two points can hardly be called similarities. An important difference with *Ch. wiedersheimi* and *Ch. affinis* is the absence of the little groove on the upper lip.

The dorsal scales are sometimes alternating with paired scales just as in *Ch. affinis* (see fig. 31).

4) *Chamaeleo montium* BUCHHOLZ, 1874. The male specimens are at first sight recognizable by the large finshaped dorsal keel, but the females in general appearance rather resemble *Ch. wiedersheimi*. In two female specimens (Paris 39.94 and 39.95, Buea, Cameroon, 100 m) I found the following resemblances to *Ch. wiedersheimi*:

a) a somewhat elevated, flattened shoulder;
b) a poorly developed gular crest;
c) a lateral row of larger shields on the flank;
d) one specimen (39.94) possesses a poorly developed temporal crest;
e) a double row of scales on the dorsal keel (also in the males) one specimen (Paris 39.94) with 3 unpaired cones in the neck region.

5) *Chamaeleo deremensis* (MATSCHIE, 1892). I have seen one specimen only (Paris Ch. 21-31.56, Amani, Tanganyika, Utschungwe Mts, LOVERIDGE 24237), which differs from the description of WERNER (1911) in the following points: instead of a parietal crest a little groove; distance from the commissure of the mouth to the extremity of the casque equal to distance to the tip of the snout; the fusion of the occipital lobes only short (± 2mm); dorsal "fin" not wavy above the back, but wavy above the tail; dorsal keel with 4—5 unpaired cones in the neckregion, followed by a double row of (more or less alternating) scales; no temporal crest.

6) *Chamaeleo cristatus* STUTCHBURY, 1837. I have examined 4 specimens (Paris Ch. 19⁷ and Brussels, Tervueren 2104). The general appearance is not unlike *Ch. deremensis*, apart from the absence of the occipital lobes, the absence of gular and ventral crests and the casques being more elevated posteriorly. Contrary to WERNER (1911) I found: dorsal keel with a double row of scales; sometimes a few unpaired cones in the neck region; no parietal crest but a little groove; all 4 specimens lack a white midventral line; temporal crest present, though sometimes almost fused with the lateral crest.

7) *Chamaeleo adolfi-friederici* (STERNFELD 1913). In the Congo Museum, Tervueren, I had the opportunity of examining 2 specimens (11879 ♂ Kongbwalu and 8991 ♀ Mombassa, près de Lubero). Contrary to SCHMIDT (1919) I found the squamation in both specimens to be moderately heterogeneous. By the absence of all striking characters, even of dorsal, ventral and gular crests (sometimes about 10 isolated cones are present on the foremost part of the back), this species resembles *Ch. polleni* (see § 2, p. 8). Most probably this resemblance is caused by convergent degeneration.

Conclusions

§ 19. SOME CONCLUSIONS ON THE DIAGNOSTIC VALUE OF THE CHARACTERS.

As stated in section 1 the value of WERNER's "key" characters is only relative, how much so has been demonstrated in several sections. Here may follow a summary of my remarks on the more important characters.

1. The occipital lobes. These can vary from slightly visible to well developed within the limits of one single species, without any indication of geographical correlations (*Ch. dilepis* for instance).
2. The dorsal keel. This may be constituted of:
   a. an unpaired row of scales or greater cones, from neck to tail,
   b. an unpaired row of scales on the foremost part of the back, followed by irregularly placed scales,
   c. irregularly placed scales from neck to tail,

d. a double row of scales from neck to tail, mixed in the neck region only with some unpaired cones,

e. a double row of scales or cones from neck to tail.

As will be shown in the following section, the first, viz. an unpaired row of scales or cones from neck to tail, is probably to be regarded as the most original condition, which means that conditions c (via b) and e (via d) are derived from condition a independently. As we have seen in *Ch. oweni, Ch. johnstoni, Ch. cristatus, Ch. montium* etc. the character "double row of scales on the dorsal keel' is much more common than suggested by WERNER (1911). It is shown also that in several species which are officially described as having a double row of scales, we meet with specimens with some unpaired cones in the neck region (d).

3. The gular and ventral crest have little value as diagnostic characters. In *Ch. chamaeleon* the subspecies *chamaeleon* and *calcarifer* are easily distinguished by respectively the absence and the presence of clearly developed ventral crests.

   In the area between the ranges of the subspecies *Ch. ch. chamaeleon* and *Ch. ch. calcarifer,* we find all kinds of intermediates between completely absent ventral crests and clearly developed ones.

   In *Ch. cucullatus* c.s. also, absence and presence of a ventral crest is correlated with the geographical distribution. In *Ch. basiliscus, Ch. johnstoni* and *Ch. oweni* the absence or presence of a (feebly developed) ventral crest shows no correlation with the geographical distribution of the specimens. In *Ch. polleni* and *Ch. lateralis* also we find all kinds of variations.
4. The scaled gular lobes. As recorded in section 16, many intermediates are known between smooth gular cones, scaled gular cones and scaled gular lobes. In the Amsterdam Zoological Museum two specimens are present which each even show a combination of these three characters. From these and other facts I concluded that all species around *Ch. pumilus* are to be regarded as subspecies of *Ch. pumilus,* with many intermediate forms present.
5. Several types of squamation may be distinguished, varying from finely, granularly homogeneous to coarsely heterogeneous. The squamation of the species around *Ch. chamaeleon* is generally called homogeneous, but in most species of this group we find rosette-shaped arrangements of scales, surrounded by little granules. Purely homogeneous are, for instance, *Ch. laevigatus, Ch. anchietae, Ch. gastrotaenia.* In *Ch. oweni, Ch. lateralis, Ch. polleni* and especially *Ch. rhinoceratus,* all kinds of intermediates occur between purely homogeneous and distinctly heterogeneous, as for instance *Ch. oustaleti* c.s. and all ovoviviparous species.
6. The axillary pits (and inguinal pits) — only present in Madagascar — have no diagnostic value, though eventually they may be of some help to define subspecies, for it is a remarkable fact that several different groups of species show this character in the northern populations, whilst it is absent or less distinct in southern populations of the same species or groups of species (see § 11).
7. The shape of the casque may vary greatly, especially its posterior elevation. Most variations within the limits of a single species occur

in east Africa (*Ch. bitaeniatus*) and in Madagascar (*Ch. lateralis, Ch. polleni* and *Ch. rhinoceratus*).

8. The tarsal spur is found in members of the *Ch. chamaeleon* group only. Within this group it is not a very reliable diagnostic character.
9. A white midventral line is a rather constant character in members of the *Ch. chamaeleon* group, in *Ch. lateralis* c.s., *Ch. affinis* a.o. In other species this character varies quite a lot. For instance in *Ch. polleni* it is present in all female specimens and in some of the males. In *Ch. rhinoceratus* and in *Ch. oustaleti* it is sometimes present.
10. The absence and presence of cranial horns may sometimes be regarded as a help to separate subspecies, for instance *Ch. ituriensis* probably is to be regarded as the hornless subspecies of *Ch. johnstoni*. In *Ch. oweni* we find all kinds of intermediates between completely absent praeorbital horns, traces of these horns and distinctly developed horns.

Also in many other characters we found a wide variety between several conditions, for instance in the cranial crests, but here I resumed only the most important.

With a few exceptions — for instance the rostral appendix of *Ch. melleri* — no character is typical for one species only. In several different groups of species we find not only the same characters, but parallel series of variation too. For instance we can draw up the following comparable series:

nasutus + *fallax* + *gallus* : *guibei* : *boettgeri* =
basiliscus : *chamaeleon* : *monachus* =
? : *brevicornis* : *malthe* + *cucullatus* =
bitaeniatus + *jacksoni* : *tempeli* : *werneri* =
occipital lobes absent : occipital lobes separated : occipital lobes fused

Such parallel series can be made in many cases (see also § 17). This means that many characters originated several times independently in different groups.

§ 20. SELECTIVE VALUE OF THE CHARACTERS.

Biologists generally believe that all characters that can be distinguished in organisms have adaptive i.e. selective value, or at least are linked with characters of selective value. According to this belief a character exists only because it gave more profit in the struggle for life than a preceding character, that therefore became lost.

Theoretically this belief is not an indispensible premiss. If we accept the view that all new characters originate as a result of gene-mutation (or inversion, duplication etc.) it is quite thinkable that some characters without any selective value become spread over a population by means of repeated mutation and hybridization only.

This phenomenon will be more common in groups which have reached already a high degree of specialized adaptation, for most changes in characters — at least if they leave the important adaptations intact — can be regarded as superficial changes of fringe, unimportant from the selective point of view.

In my opinion this is the case in the genus *Chamaeleo*. All members have in common: the body laterally compressed, hands and feet pincershaped, the specialized eyes, the specialized tongue, the specialized tail etc. (cf. a.o. BÖKER, 1935), all highly specialized adaptations to the typical life of the chameleon: magnificent insect-catchers, slowly balancing on narrow twigs.

On the whole I think that only a few characters of those listed in § 1 have selective value and even then selection cannot be the only agency responsible for the distribution of the characters (see § 21).

Perhaps some characters have the meaning of a mark for recognizing members of the same species, but this is at least improbable in such highly variable species as *Ch. polleni, Ch. rhinoceratus* and in *Ch. pumilus* with so many intergrades between the subspecies.

Selective value may probably be assigned to:

1. ovoviviparity. Obviously the protection of the maternal body is of great advantage in colder climates. Ovoviviparous chameleons can be found in mountains of east Africa up to 3000 m and more (*Ch. bitaeniatus*). Oviparous chameleons seldom reach 1700 m (*Ch. chamaeleon* in the Atlas mountains). On the other hand the ovoviviparous *Ch. bitaeniatus* lives in the same region as the oviparous *Ch. dilepis* (in South Africa), whereas in the Atlas mountains, were ovovoviviparity would be certainly of advantage, only the oviparous *Ch. chamaeleon* is found. These inconsistencies in the distribution will be dealt with in § 21.
2. cranial horns. In the film "Lords of the Forest", made in the Belgian Congo by the "Wetenschappelijke Internationale Stichting, 20th CENTURY FOX", a very fine scene is given of a fight between two male *Ch. johnstoni*. It is clearly shown that the horns are used as effective weapons especially dangerous for the protruding eyes. As the selective value of this character is present in the whole range of the genus, the question arises why horns are present only in species from central and east Africa (see § 21).
3. axillary pits. The adaptive value of this character can only be deduced from its singular distribution. It is present in the northern populations of several species, but absent in the southern populations of the same species (in Madagascar).

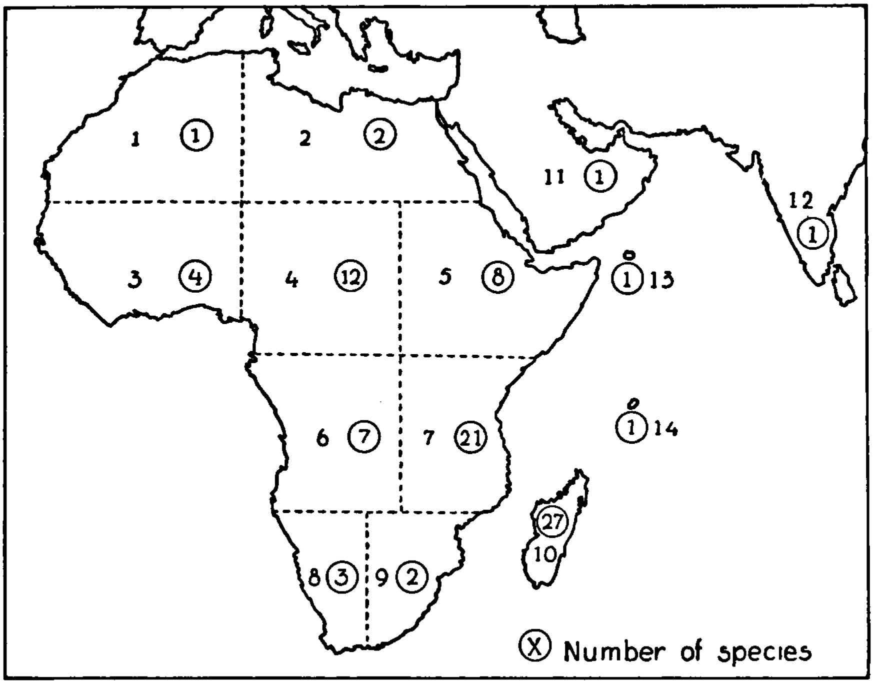
   In future it may be found perhaps that the rigid protuberances on the snout of *Ch. rhinoceratus, Ch. fischeri, Ch. melleri* etc. are also used as weapons, but as far as I know, this has never been observed.

   All the other characters that can be distinguished in chameleons are indeed to be considered as "fringe" without selective value: ventral, dorsal, cranial crests, tarsal spurs, body squamation etc. (see fig. 1—19). This view is supported by the fact that several of these characters can be found in the same area.

§ 21. THE ELIMINATION THEORY AND THE RECONSTRUCTION OF THE ANCESTRAL FORM OF THE CHAMELEON.

As the exact geographical ranges of the species of *Chamaeleo* remain doubtful, it is only possible to use a rather rough method for trying to find out the pattern of their distribution.

For this purpose the total range of the genus is divided into a number of more or less equal areas (map 18). The limits of these areas are not meant to be exact, they are rough indications only, partly suggested by

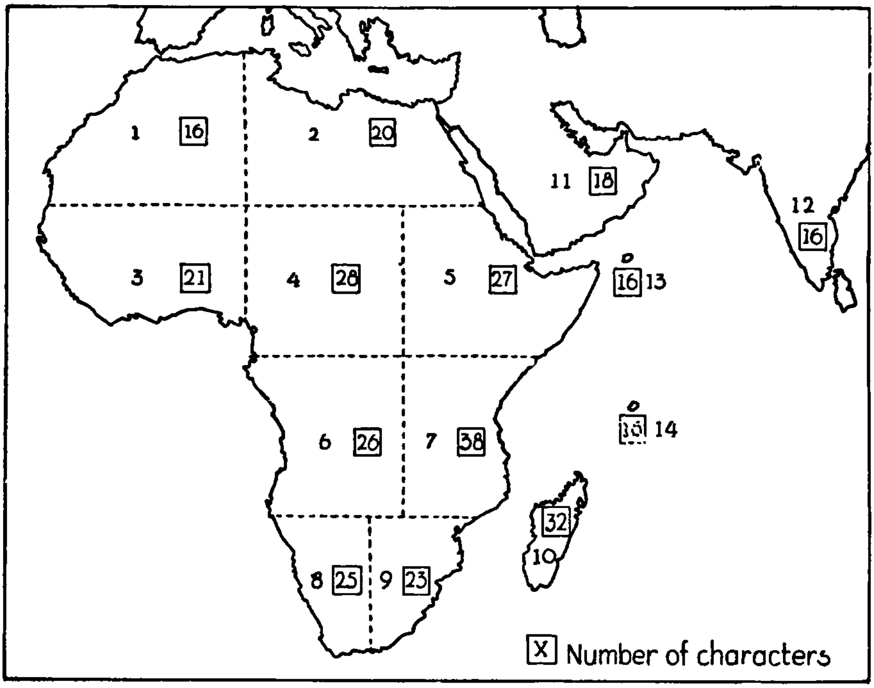


MAP 18. Africa and adjacent countries. The geographical range of the genus *Chamaelo*. Numbers of species per district. (see table U).

the limits of the ranges of some species. For instance, area 4 is supposed to include all Cameroon species (*Ch. camerunensis, Ch. quadricornis, Ch. feae,* etc.). Area 6 is characterized by *Ch. anchietae,* area 5 by *Ch. affinis,* the line between area 7 and 9 is approximately the southern limit of *Ch. bitaeniatus,* in area 8 and 9 *Ch. pumilus* s.l. is at home, in area 8 *Ch. namaquensis,* etc. (Cf. list U). The number of species is largest in area 10 (Madagascar and adjacent islands), more or less gradually decreasing from area 7 to the other areas. This might suggest Madagascar to be the centre of distribution, perhaps the centre of origin too.

Since, however, the species of this genus are rather doubtful units and since, moreover, the number of species in a certain area is sometimes rather an information on the geographical particularities of the area than on the variability of the species, I have tried to map out the geographical distribution of the most important characters instead of that of the species.

In map 19 the numbers of characters (the "key" characters of WERNER, 1911 and BOULENGER, 1887) are given that are found in each area. For the present purpose the gradual variability in these characters is neglected. For instance the presence or absence of occipital lobes is taken as a distinct character, not the relative size of these lobes, however. By this method, and comparing table V (summing up the characters that are present in each area), a first rough picture of the distribution of the characters is obtained.



Map 19. Africa and adjacent countries. The geographical range of the genus *Chamaeleo*. Numbers of characters per district. (see table V).

An important difference as compared with the distribution of the species (map 18) is, that the largest number of characters is found not in Madagascar (area 10), but in east Africa (area 7). The number of characters gradually decreases from area 7 to the periphery of the total range of the genus.

Area 7 is still more important, as practically all the characters occur in it (cf. table V). This means that the chameleons in the other areas practically never possess characters that are not found in area 7. The characters "scaled gular lobes" and „axillary pits" are the only exceptions. Scaled gular lobes, however, occur in South Africa and in the Seychelles ; it seems not improbable that they once occurred in the area in between (i.e. east Africa) too. For the axillary pits a similar reasoning may be possible (cf. § 11).

What may be the reason of this curious pattern of distribution ?

Dobzhanski (1951, p. 134) remarks on this instance :

"Polymorphism is higher where the species is more abundant and wide spread than its competitors, and less where the competitors exceed in abundance the species in question.

Vavilov (1926) advanced the generalization that the genetic variability in populations is greatest in the territory in which the species arose and from which it subsequently spread elsewhere. This "center of origin" hypothesis may at present be re-stated as follows. The evo-

TABLE U. The distribution of the species of the genus *Chamaeleo*. The numbers of the areas are indicated on the maps 18 and 19.

Areas:	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Ch. adolfi-friderici						+	+							
Ch. affinis					+									
Ch. anchietae						+								
Ch. basiliscus		+	+	+	+									
Ch. bifidus										+				
Ch. bitaeniatus					+		+							
Ch. boettgeri										+				
Ch. brevicornis										+				
Ch. calyptratus					+									
Ch. camerunensis				+										
Ch. campani										+				
Ch. carpenteri							+							
Ch. cephalolepis										+				
Ch. chamaeleon	+	+									+	+		
Ch. cristatus				+										
Ch. cucullatus										+				
Ch. deremensis							+							
Ch. dilepis			+	+	+	+	+	+	+					
Ch. fallax										+				
Ch. feae				+										
Ch. fischeri							+							
Ch. fuelleborni							+							
Ch. furcifer										+				
Ch. gallus										+				
Ch. gastrotaenia										+				
Ch. globifer										+				
Ch. goetzei							+							
Ch. gracilis			+	+	+	+								
Ch. guentheri										+				
Ch. guibei										+				
Ch. incornutus							+							
Ch. ituriensis						+								
Ch. jacksoni					+		+							
Ch. johnstoni							+							
Ch. laevigatus				+	+	+								
Ch. lateralis										+				
Ch. laterispinis							+							
Ch. linotus										+				
Ch. malthe										+				
Ch. melleri							+							
Ch. minor										+				
Ch. monachus													+	
Ch. monoceras										+				
Ch. montium				+										
Ch. namaquensis								+						
Ch. nasutus										+				
Ch. oshaughnessyi										+				

Areas:	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Ch. oustaleti										+				
Ch. oweni				+		+								
Ch. pardalis										+				
Ch. parsonii										+				
Ch. pfefferi				+										
Ch. polleni										+				
Ch. pumilus								+	+					
Ch. quadricornis				+										
Ch. rhinoceratus										+				
Ch. senegalensis			+											
Ch. spinosus							+							
Ch. tavetensis							+							
Ch. tempeli							+							
Ch. temporalis							+							
Ch. tenuis							+							
Ch. tigris														+
Ch. uthmölleri							+							
Ch. verrucosus										+				
Ch. werneri							+							
Ch. wiedersheimi				+										
Ch. willsi										+				
Ch. xenorhinus							+							
Number of species in each area	1	2	4	12	8	7	21	3	2	27	1	1	1	1

lutionary process which generates adaptive polymorphism, and thereby enables the species to conquer and control more and more habitats, requires time. Therefore, the longer a territory is occupied by a species the greater will tend to be the adaptive polymorphism and the variability in populations. Conversely, at the margins of its distribution area, unless the species is stopped by an insuperable geographic barrier, it is likely to have a toehold in only few ecological niches. A limited adaptive variability is likely to characterize marginal populations."

This explanation does not suffice in the case of the genus *Chamaeleo*. First of all chameleons are not more abundant in the area with the highest polymorphism than in the area with the lowest polymorphism. The only species of north Africa, *Ch. chamaeleon chamaeleon*, shows very little polymorphism, but is as abundant as all the east African species together. For instance MARINKELLE (1959) got 3000 specimens of *Ch. chamaeleon chamaeleon* from the neighbourhood of Kettena (southern Tunis). As far as I know this number is never equalled, not even on the expeditions of LOVERIDGE in east Africa.

Probably these differences between the situation sketched by DOBZHANSKI and that in the genus *Chamaeleo* are caused by the fact that DOBZHANSKI meant his reasoning for groups within the limits of one species only, whereas I am comparing different species.

TABLE V. The distribution of the "keycharacters" of the genus *Chamaeleo*. The numbers of the areas are indicated on the maps 18 and 19.

areas :	1	2	3	4	5	6	7	8	9	10	11	12	13	14	characters with almost general distribution
occipital lobes separated	+	+	+	+	+	+	+	+	+	+	+	+			+
occipital lobes grown together							+			+			+		
occipital lobes absent		+	+	+	+	+	+	+	+	+				+	
dorsal crest		+	+	+	+	+	+	+	+	+	+	+	+	+	+
dorsal crest absent	+	+	+	+		+	+			+	+				
gular crest +	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
gular crest absent				+	+	+	+	+		+					
ventral crest		+	+	+	+	+	+	+	+	+	+	+	+		+
ventral crest absent	+	+	+	+	+	+	+	+		+				+	
homogeneous squamation	+	+	+	+	+	+	+	+	+	+	+	+		+	+
heterogeneous squamation				+	+		+	+	+	+			+		
axillary pits										+					
axillary pits absent	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
finshaped dorsal keel				+			+								
finshaped dorsal keel absent	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
roof-shaped casque	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
flat casque			+	+	+	+	+	+	+	+					
casque elevated posteriorly	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
casque as in *Ch. laevigatus*					+	+	+			+					
ovoviviparous					+		+	+	+					?	
oviparous	+	+	+	+	+	+	+	+	+	+	+	+	+	?	+
white midventral line	+	+	+	+	+	+	+	+	+	+	+	+	+		+
white midventral line absent				+	+	+	+	+	+	+				+	
no distinct dorsal rows of scales				+		+	+			+					
double row of scales on dorsal keel				+		+	+		+						
single row of scales on dorsal keel	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
tarsal spur		+	+	+	+	+	+	+	+		+	+	+		
tarsal spur absent	+	+	+	+	+	+	+	+	+	+	+			+	
scaled gular lobes								+	+					+	
scaled gular lobes absent	+	+	+	+	+	+	+	+	+	+	+	+	+		+
horns				+	+		+								
horns absent	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
nasutus-nose							+			+					
rhinoceratus-nose							+			+					
bifidus-nose							+			+					
melleri-nose							+								
bitaeniatus-nose					+		+			?					
xenorrhinus-nose							+								
canthus rostralis varieties*)							+			+					
absence of protuberances on the snout	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
total number of characters per area	16	20	21	28	27	26	38	25	23	32	18	16	16	16	

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*) cf. page 8 and fig. 18 & 19.

Secondly DOBZHANSKY's reasoning holds good only for those characters that possess survival value with regard to the habitat. For instance, the absence of ovoviviparity in chameleons living in the Atlas Mountains (1700 m), where ovoviviparity certainly would be of importance, may be explained by DOBZHANSKI's reasoning that their staying in these regions is of too recent a date. But his reasoning does not hold when a character is to be considered as caused by sexual or interindividual selection. For instance, the character horns is of some advantage for a quarrelling male (see § 20). The selective agency of quarrel among males is present everywhere in the range of the genus, at least if there are enough specimens to compete with.

So we have to consider the following points :

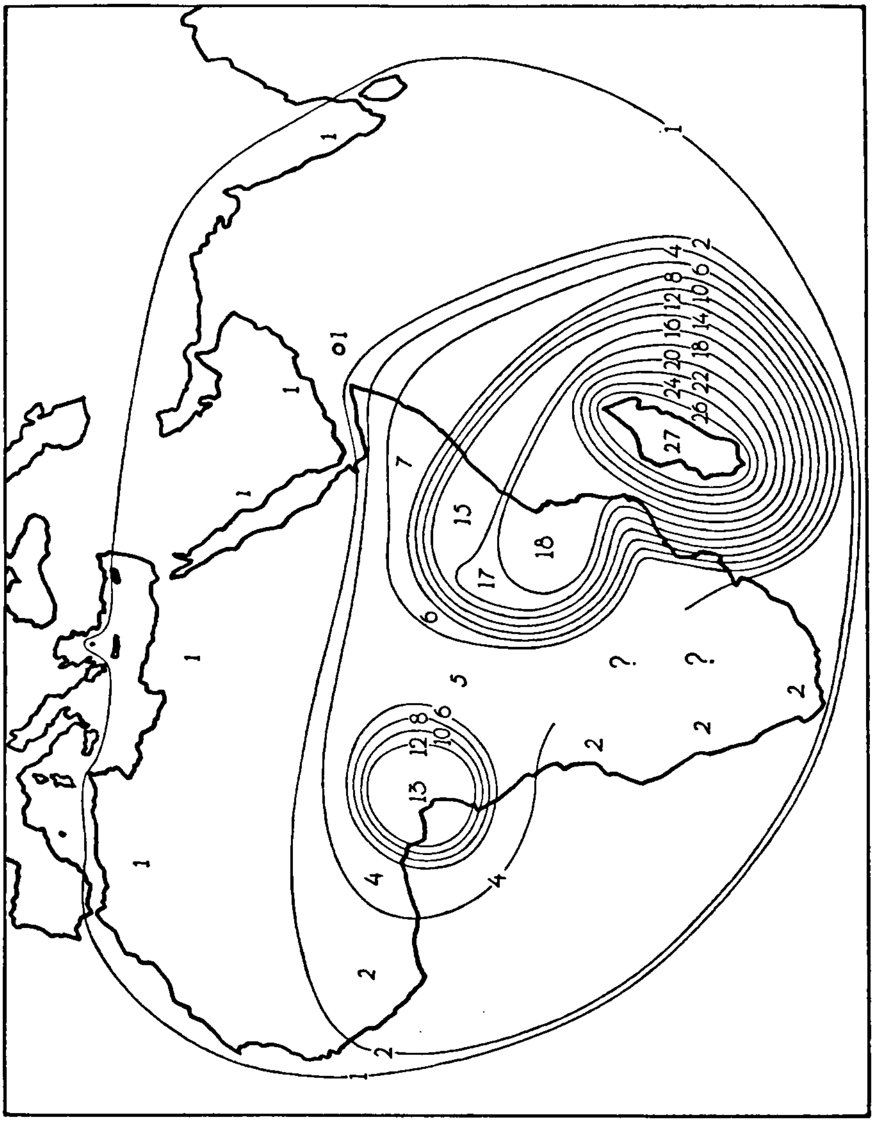
1. the selection of the character horns, being not caused by the new environments, but by the constant presence of other (male) specimens, could work during as much time in the emigrating (afterwards marginal) populations as in the central populations,
2. horns probably originated several times independently in different groups of chameleons (see § 17 and § 19),
3. this advantageous character is present in a few areas only.

In my opinion the only possible explanation is that this character never reached the other areas, i.e. that the gene(s) causing this character, never reached these areas with the emigrating specimens, nor originated there by means of mutation : the gene(s) which by mutation would change into the gene(s) causing the character horns, did not arrive in the hornless area too.

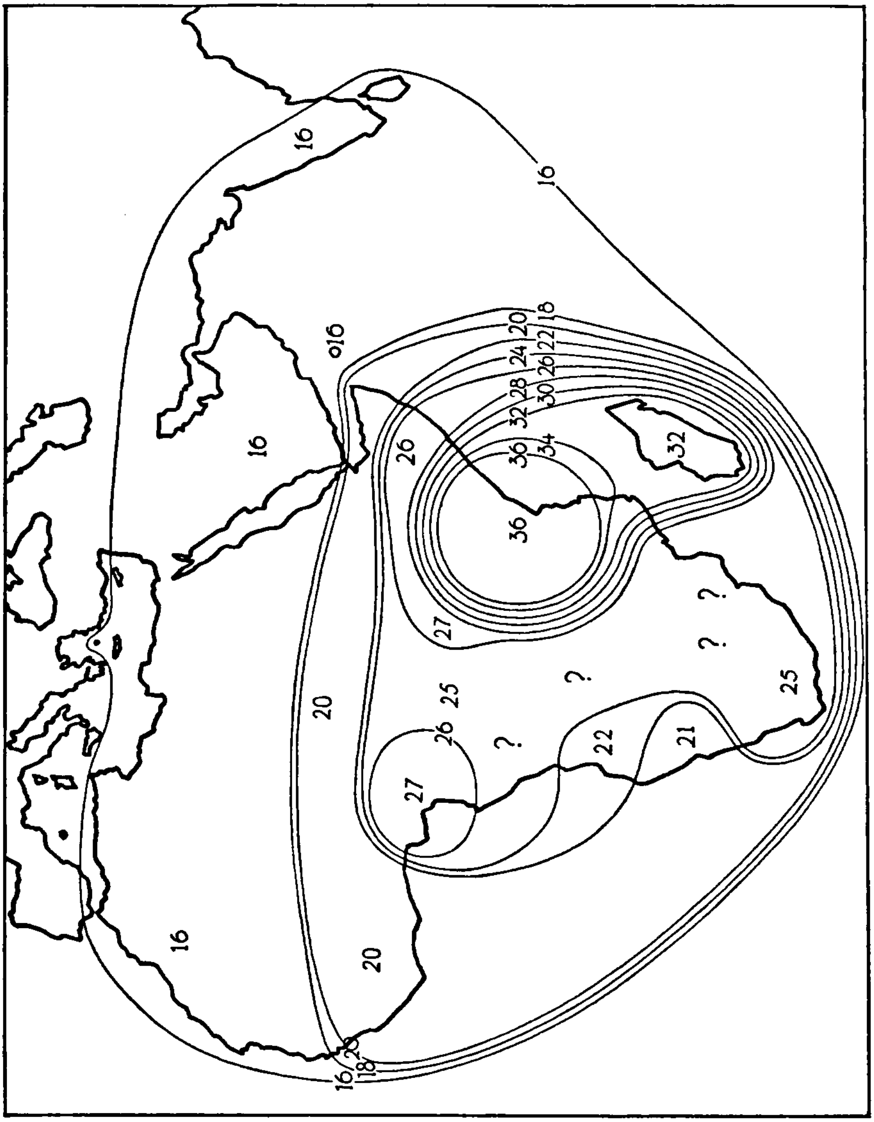
Though we may never be sure about it, it is not unlikely that the major part of the characters has no selective value at all (see previous section). The same reasoning holds here as in the case of the character horns : in areas where these characters cannot be found, they probably never arrived, neither the genes causing the characters, nor the genes predisposed to change into these.

This reasoning fits in with REINIG's elimination theory (1938) :

„Die genetische Mannigfaltigkeit innerhalb der Populationen findet ihr Gegenstück in der morphologischen Mannigfaltigkeit, die ja zu einem sehr beträchtlichen Grade durch die genetische verursacht wird. Entnehmen wir einer Population einige Individuen, so werden wir nur einen Teil der überhaupt vorhandenen Mannigfaltigkeit bei ihnen nachweisen können. Diese jedem Phänanalytiker bekannte Tatsache dürfen wir auf Grund der vorausgeschickten Betrachtungen auch für die genetischen Grundlagen dieser Mannigfaltigkeit annehmen. Daraus geht aber hervor, dasz bei Einzelwanderungen nur ein Teil des gesamten Allelbestandes einer Art mitgeführt wird... Nehmen wir weiterhin an, dasz sich von einer auf diese Weise entstandenen Population durch Einzelwanderung eine neue Population abzweigt, so wird auch diese wiederum nur einen Teil der Allele der Ausgangspopulation erhalten. Denken wir uns diese Reihe bis zur absoluten Arealgrenze fortgesetzt, so erhalten wir vom Ausbreitungszentrum bis zur absoluten Arealgrenze eine Kette von Populationen, die durch eine stetig fortschreitende Abnahme des Allelbestandes und dementsprechend auch durch eine Abnahme der heterozygotie bzw. durch eine Zunahme der Homozygotie gekennzeichnet ist".



Map 20. (In addition to map 18) Isopories, lines bordering the regions with the same number of species. Perhaps the Cameroons may be regarded as a secondary centre of development.



Map 21. (In addition to map 19) Isopseferes, lines bordering the regions with the same number of characters. In the Cameroons a little top, which may be due to insufficient knowledge of the region between the Cameroons and East Afrika.

Though REINIG used his theory within the limits of one species only, I think it quite possible to apply it to larger groups too. The main points of REINIG's theory are:

1. the emigrating populations carry with them only a part of the original genetic composition,
2. this genetic impoverishment holds out for longer periods because of the insufficient exchange of genes between central and marginal populations.

These two factors are also working in larger groups. For instance in chameleons the first factor remains constant and the second will even be stronger in effect: the reproductive barriers between species will blockade the gene exchange almost absolutely. In this connection it is important to know that apart from *Ch. dilepis, Ch. johnstoni* and *Ch. laevigatus* all chameleons are confined either to east Africa, or to regions outside east Africa, which means that the limits of the distributions of the species are indeed barriers between the centre and the periphery.

REINIG's theory has not been generally accepted without hesitation. As RENSCH demonstrated (1938, 1939 and a résumé in 1954) REINIG's first examples (in his criticism of the rules of BERGMANN, GLOGER and ALLEN) were not too well chosen. He tried to apply it to the specimens of one area, which were larger than those of another area. This is not a convincing example for the elimination theory. The gradually increasing gene-loss is better demonstrated in cases where the total variability in one area is greater than in other areas, especially in cases where the variability lessens towards the periphery. Such examples are given in REINIG's study on bumblebees (1939) and by RENSCH (1954).

The "Founder" principle of MAYR (1944) is based on the same idea, viz. that small parts of a population cannot present a true picture of the variability of the whole population. "The differences in composition of these populations (.. in the outposts of the range..) is very likely due to the genetic composition of the original founders. The same explanation probably covers most of the cases in which isolated populations of polymorphic species have a much-reduced variability." (MAYR, 1944, p. 237).

Fine examples of the "elimination pattern" were collected by BROWN (1957) in his article significantly titled "Centrifugal Speciation". But apart from this useful metaphor in the title, he gives no sufficient explanation why the centre remains "the principal source of evolutionary change leading to "potent" new species and higher categories", whereas I think that REINIG (1938) gave already a clear mechanistic base for further reasoning.

In most cases it will be difficult to trace exactly the working of the elimination process. Many characters which have selective value will make the pattern of distribution much more complicated, occasionaly working out a pattern contradictory to that predicted by the elimination theory. As we discussed before (§ 20) it may be assumed that in the case of the genus *Chamaeleo* most characters, at least those used in the diagnosis of the species, have no selective value, or may be regarded as being selected by factors that remain the same in emigrating populations as in those in the centre (horns e.g.).

Resuming, we arrive at this hypothetical picture of the history of the genus *Chamaeleo*:

A population of ancestral chameleons lived in east Africa (Kenya, Tanganyika). We may assume that before the divergence began which gave rise to the many forms of today, an initial genotypical differentiation existed already. Parts of the original population emigrated, but could not carry with them the total amount of the original genetic composition. As chameleons are slowly moving animals, there is little gene-exchange with the original population and therefore the larger the distance between the emigrated animals and the centre of distribution, the smaller is the part that remains of the original genetic composition.

In my opinion the consequence of the elimination theory is that we may expect in the marginal zones not only a reduced variability, but also a reduced number of mutations. The genetic composition of the marginal population being reduced, the occurence of genes with a certain predisposition to mutation is reduced too. That is why we might expect that the marginal populations are but slightly different from the original form. It is in the nature of the supposed elimination process that we may expect it in its purest form in "dynamic" marginal populations (Carson, 1955), i.e. populations which are living in the "front" zone of the migration, not limited by geographical or other barriers.

In the genus *Chamaeleo*, the total range is limited on almost all sides by geographical barriers (Africa, the main territory of the chameleons, is practically an island). Therefore most marginal populations are to be regarded as "static" (Carson, 1955). Here we may expect a disturbed elimination pattern, as the marginal populations will be provided constantly with genes from the central parts of the distribution area.

Only in the north east, towards Arabia and India, "dynamic" marginal populations can exist. It is difficult to decide whether the northern populations of *Ch. chamaeleon* in Spain belong to the static or dynamic type: temperature might be just as effective a barrier as the sea.

The chameleons of Arabia and India and perhaps those of north Africa may be expected to show the results of the elimination process in the clearest way. As shown in § 12 only one species (*Ch. chamaeleon)* with a few subspecies live in this area. The large area where this little varying form is found (from Marocco to Ceylon) gives a fine, illustrative argument for the elimination theory. If our reasoning is true, of all modern chameleons this chameleon must be the one resembling most the original chameleon.

We may arrive at the same conclusion by another reasoning too.

Reading table U vertically it is shown that in area 7 the greatest number of characters is found. Reading the same table horizontally we see that only a few characters are found throughout the range of the genus. Those characters are:

the presence of

- separated occipital lobes (except in 13 and 14)
- dorsal crest (except in 1)
- gular crest
- ventral crest (except in 1 and 14)
- homogeneous squamation (except in 13)
- casque elevated posteriorly
- casque roof-shaped
- oviparity (? in 14)

— white midventral line (except in 14)
— a single row of scales or tubercles on the dorsal keel
the absence of
— horns
— protuberances on the snout
— axillary pits
— fin shaped dorsal keel
— scaled gular lobes (except in 14)

(I am not certain about the tarsal spur, as presence and absence of this character is almost equally divided over the whole range of the genus.)

It seems plausible to state that the characters with a large distribution will be older than characters with a small distribution, the more so as we argued that most of the characters do not have selective value. So the above listed characters probably may be considered the most original ones, in fact the characters of the hypothetical ancestral chameleon.

Most remarkably, the combination of these characters does not give a purely imaginary form, but an animal that can even be determined by means of Werner's key of 1911. It seems probable that our hypothetical ancestral chameleon was but slightly different from the recent *Ch. chamaeleon* (especially in the broader sense, including the subspecies *calcarifer* and *zeylanicus*, cf. § 12). The character „tarsal spurs" probably was already present in the ancestral chameleon, as it is found today in the group of *Ch. chamaeleon* only.

So two ways of reconstructing the hypothetical ancestral chameleon give the same result, viz. an animal resembling *Ch. chamaeleon* s.l. Thus the position of the group of species around *Ch. chamaeleon* (§ 12) becomes clearer, it probably is the most ancient group, which has not changed much from the ancestral chameleon.

Summary

The main purpose of this study is to search for an explanation of the curious differentiation within the genus *Chamaeleo*. Since the species of this genus are rather doubtful units, I have studied the geograpical distribution of characters, not of the species, a method first used in botany (Baur, Rothmaler a.o.). I found that the number of characters is largest in east Afrika, gradually decreasing from this area to the periphery of the total range of the genus. East Africa proved to be still more important, as practically all the characters occur in it. This means that the chameleons in the other areas practically never possess characters that are not found in east Africa.

This pattern of distribution fits in rather well with Reinig's elimination theory (1938): „. . bei Einzelwanderungen wird nur ein Teil des gesamten Allelbestandes einer Art mitgeführt... eine durch Einzelwanderung entstandene Population weist eine geringere Zahl von Allelen auf als die Ausgangspopulation."

The existence of many parallel series of variation (meaning that several characters originated several times independently in different groups) led me to the conclusion that the mechanism described in Reinig's theory as elimination, has consequences also for the genes predisposed to change into others.

This reasoning gave a key to the reconstruction of the ancestral chameleon. By two different ways I arrived at the same conclusion, viz. the ancestral chameleon was probably an animal resembling mostly *Chamaeleo chamaeleon* s.l. (§ 21).

As for this theoretical part of my study a survey of the species was needed, I first made an attempt at a natural system. I have divided the genus into groups of related species. For practical reasons the chameleons of Madagascar are treated separately. Their connections with the species of the African continent are examined in a special section (§ 11).

As a result of my investigations I had to propose the following taxonomic changes:

Ch. rhinoceratus var. *lineatus* + *Ch. labordi* + *Ch. voeltzkowi* + *Ch. barbouri* = *Ch. rhinoceratus* (§ 3),
Ch. lambertoni = *Ch. lateralis* (§ 4),
Ch. semicristatus = ♀ *Ch. verrucosus* (§ 5),
Ch. guibei nov. spec. (§ 6),
Ch. calcarifer = *Ch. chamaeleon calcarifer*, *Ch. zeylanicus* = *Ch. chamaeleon zeylanicus*, *Ch. etiennei* = *Ch. gracilis etiennei* (§ 12),
Ch. anchietae vinkei + *Ch. anchietae mertensi* + *Ch. marunguensis* = *Ch. anchietae* (§ 13),
Ch. unicornis = *Ch. oweni unicornis* (§ 14),
Ch. pumilus = *Ch. pumilus pumilus*, *Ch. melanocephalus* = *Ch. pumilus melanocephalus*, *Ch. gutturalis* = *Ch. pumilus gutturalis*, *Ch. ventralis* = *Ch. pumilus ventralis*, *Ch. ventralis occidentalis* = *Ch. pumilus occidentalis*, *Ch. ventralis karrooicus* = *Ch. pumilus karrooicus*, *Ch. damaranus* = *Ch. pumilus damaranus*, *Ch. caffer* = *Ch. pumilus caffer*, *Ch. taeniobronchus* = *Ch. pumilus taeniobronchus*. (§ 16).

SAMENVATTING

Chamaeleons staan sinds lang bekend als een systematisch moeilijke groep. De algemeenste chamaeleons vertonen betrekkelijk weinig variatie (b.v. *Ch. chamaeleon* en *Ch. basiliscus*), zodat ze goed als aparte soorten te onderscheiden zijn met behulp van duidelijke, morphologische kenmerken. Omdat de algemeenste soorten uiteraard de eerste waren die beschreven werden, kregen hun verschilkenmerken een zekere practische waarde in de determinatietabellen van o.a. BOULENGER (1887) en WERNER (1902, 1911). Dit leidde tot de veronderstelling dat het voorkomen van deze „determinatiekenmerken" constant zou zijn bij alle soorten van het geslacht *Chamaeleo*, zodat het bezit of gemis er van min of meer automatisch als soortcriterium werd gehanteerd. Vooral van Oost Afrika en Madagascar, waar de grootste rijkdom aan vormen voorkomt, werden veel soorten beschreven op grond van slechts één of weinige exemplaren, die in enkele van de genoemde soortscriteria van de reeds bekende soorten afweken.

Het blijkt echter, vooral bij de bestudering van materiaal uit Oost Afrika en Madagascar, dat het voorkomen van de bovengenoemde kenmerken bij verscheidene soorten in het geheel niet constant is.

Het voornaamste doel van dit onderzoek is een verklaring te vinden voor de merkwaardige differentiatie binnen het geslacht *Chamaeleo*.

Omdat de soorten van dit geslacht vrij twijfelachtige eenheden zijn, heb ik de geografische verspreiding bestudeerd niet van de soorten, maar van bepaalde eigenschappen, een methode die het eerst werd gebruikt in de botanie door o.a. BAUR en ROTHMALER. Voor deze eigenschappen koos ik voornamelijk de door BOULENGER (1887) en WERNER (1911) gebruikte determinatiekenmerken, omdat deze in hun voorkomen en variatie het meest opvallen en dus ook het best bekend zijn.

Het bleek dat het aantal van deze eigenschappen het grootst is in Oost Afrika, geleidelijk afnemend daarvandaan naar de peripherie van het verspreidingsgebied van het geslacht. Bovendien bleek dat bijna alle eigenschappen naast elkaar voorkomen in Oost Afrika. Dit houdt in dat de chamaeleons in de andere gebieden bijna nooit eigenschappen bezitten die niet tevens gevonden worden in Oost Afrika.

Dit verspreidingspatroon laat zich goed verklaren met REINIG's eliminatie theorie (1938): „.. bei Einzelwanderungen wird nur ein Teil des gesamten Allelbestandes einer Art mitgeführt ... eine durch Einzelwanderung entstandene Population weist eine geringere Zahl von Allelen auf als die Ausgangspopulation." In dit geval zou dus het tegenwoordige areaal van *Chamaeleo* vanuit Oost Afrika bevolkt zijn.

Het bestaan bij *Chamaeleo* van vele parallele reeksen van variaties, waar uit af te leiden valt, dat een groot aantal eigenschappen en variaties meer dan eens zouden zijn ontstaan in verschillende groepen, bracht me tot de conclusie dat het eliminatie-mechanisme van REINIG niet alleen invloed uitoefende op eigenschappen die reeds bestonden vóórdat de tegenwoordige verspreiding een aanvang nam, maar ook op eigenschappen „in potentie", die eerst later, tijdens het verloop van deze verspreiding, door mutatie zijn ontstaan.

Deze redenering opende de mogelijkheid tot de reconstructie van de oer-chamaeleon. Langs twee verschillende wegen kwam ik tot dezelfde conclusie, n.l. dat de oer-chamaeleon waarschijnlijk de grootste overeenkomst heeft vertoond met de tegenwoordige *Chamaeleo chamaeleon* s.l. (§ 21).

Voor dit theoretische deel van mijn onderzoek was een overzicht van alle chamaeleons nodig. Me baserend op het werk van WERNER (1911) en ANGEL (1942), heb ik met behulp van critisch onderzoek van zoveel mogelijk materiaal een voorlopig natuurlijk systeem trachten op te bouwen. Ik heb het geslacht *Chamaeleo* daartoe ingedeeld in groepen van soorten die naar mijn mening een duidelijke verwantschap vertonen.

Om practische redenen heb ik de chamaeleons van Madagascar apart behandeld. De relaties met soorten van het Afrikaanse vasteland zijn in § 11 behandeld.

Als resultaat van mijn onderzoekingen heb ik de volgende taxonomische veranderingen voor te stellen :

Ch. rhinoceratus var. *lineatus* + *Ch. labordi* + *Ch. voeltzkowi* + *Ch. barbouri* = *Ch. rhinoceratus* (§ 3),

Ch. lambertoni = *Ch. lateralis* (§ 4),

Ch. semicristatus = ♀ *Ch. verrucosus* (§ 5),

Ch. guibei nov. spec. (§ 6),

Ch. calcarifer = *Ch. chamaeleon calcarifer*, *Ch. zeylanicus* = *Ch. chamaeleon zeylanicus*, *Ch. etiennei* = *Ch. gracilis etiennei* (§ 12),

Ch. anchietae vinckei + *Ch. anchietae mertensi* + *Ch. marunguensis* = *Ch. anchietae* (§ 13),

Ch. unicornis = *Ch. oweni unicornis* (§ 14),

Ch. pumilus = *Ch. pumilus pumilus*, *Ch. melanocephalus* = *Ch. pumilus melanocephalus*, *Ch. gutturalis* = *Ch. pumilus gutturalis*, *Ch. ventralis ventralis* = *Ch. pumilus ventralis*, *Ch. ventralis occidentalis* = *Ch. pumilus occidentalis*, *Ch. ventralis karrooicus* = *Ch. pumilus karrooicus*, *Ch. damaranus* = *Ch. pumilus damaranus*, *Ch. caffer* = *Ch. pumilus caffer*, *Ch. taeniobronchus* = *Ch. pumilus taeniobronchus* (§ 16).

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