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Notes on Chameleons I

Comparative cytology: aid and new complications in Chameleon-taxonomy¹⁾

by

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INTRODUCTION

In my paper "The Differentiation within the Genus *Chamaeleo* Laurenti, 1768" (1959) I proposed a preliminary subdivision of the genus *Chamaeleo* in groups of species. This division was entirely based on taxonomic considerations. At the time I did not know the work of ROBERT MATTHEY (Lausanne, Switzerland) and JANNY M. VAN BRINK (Utrecht, Holland) dealing with comparative cytology of reptiles and mammals.

MATTHEY and VAN BRINK (1956):

"(MATTHEY) avait rencontré chez de nombreuses espèces appartenant à des familles différentes, souvent très éloignées, un type de formule chromosomique identique, soit 12 grands chromosomes métacentriques (*M*-chromosomes ou *M*) et 24 très petits éléments (*m*-chromosomes ou *m*). Une telle formule caractérise des *Iguanidae* (*Anolis*), des *Agamidae* (*Agama*, *Uromastix*), des *Gerrhosauridae* (*Gerrhosaurus*), des *Amphisbaenidae* (*Trogonophis*). De cette formule dérivent aisément par mécanismes robertsoniens de nombreux autres génomes qui, tout en conservant un nombre de *m* égal ou voisin de 24, offrent à l'observateur toutes les combinaisons que permettent les 24 bras de 12 *M* métacentriques: 10 V + 4 I (*Heloderma*), 8 V + 8 I (*Varanus*), 6 V + 12 I (*Xanthusia*), 4 V + 16 I (*Pseudopus*). Notons

¹⁾ Received October 8, 1962.

que cette distribution en M et m n'est pas générale: dans une même famille, MATTHEY a rencontré des espèces où elle existe, d'autres où l'on observe un déclin graduel de la taille en passant d'une paire à la suivante: chez les *Tejidae*, *Tupinambis* est du premier type, *Cnemidophorus* et *Ameiva* du second: chez les *Amphibaenidae*, *Trogonophis* et *Blanus* possèdent M et m , mais non *Rhineura*."

In 1943, MATTHEY found that chameleons offered greater facilities for cytological research. Since then he has studied the chromosome-patterns of 25 species of chameleons (MATTHEY 1961). This is 36% of the number of species (69) I recognized in my paper.

The great surprise was that in chameleons, a rather homogeneous group, the chromosome-patterns show a great variety. This is the more surprising when we consider the almost identical chromosome-patterns in non-related genera as *Anolis*, *Agama*, *Gerrhosaurus*, *Trogonophis*. On the other hand, the identical chromosome-patterns in these groups ($12 M + 24 m$) — which are not to be considered as primitive, because they are absent in the archaic types (*Geckonidae* and *Rhynchocephalidae*) — correspond to a particular stable balance, realized by convergent evolution in a whole series of families (MATTHEY & VAN BRINK, 1956).

Independently of my taxonomic work, MATTHEY & VAN BRINK also proposed a subdivision of the genus *Chamaeleo*, based on the differences in chromosome-patterns.

Taxonomic conclusions in general have to be more or less hypothetic. The work of MATTHEY & VAN BRINK gives a factual base, sometimes contradicting my hypotheses, sometimes confirming them, and sometimes adding new complications. In an appendix to one of their papers (1960), MATTHEY & VAN BRINK already gave a generous account of my paper (1959) and compared our results. Making some additions to my list of groups, I here compare their subdivision with mine.

Groups of species according to MATTHEY & VAN BRINK

(mainly after their paper of 1960)

- I) Clear separation between 12 meta- or submetacentric M and a series of 12—24 m .
 - A) $12 M + 24 m$ (*Ch. fischeri*, *Ch. cristatus*, *Ch. oweni*, *Ch. johnstoni*, *Ch. quadricornis*, *Ch. wiedersheimi*, *Ch. parsonii* and the related *Brookesia stumpffi*)
 - B) $12 M + 22 m$ (*Ch. pumilus*, *Ch. gallus*)
 - C) $12 M + 12 m$ (*Ch. chamaeleon*, *Ch. dilepis*, *Ch. senegalensis*, *Ch. calcaratus* = *Ch. chamaeleon zeylanicus*, see Hillenius, 1959)
 - D) $12 M + 14 m$ (*Ch. campani*)
- II) Less clear separation between more than 12 meta- or submetacentric M and more than 12 m .
 - E) $14 M + 14 m$ (*Ch. willsi*)
 - F) $16 M + 18 m$ (*Ch. nasutus*)
 - G) $18 M + 14 m$ (*Ch. brevicornis*)

III) No clear separation between *M* and *m*, the latter may be absent or present in a number of 2 or 4.

H) *a.* 20 chromosomes, of which 2 *m* (*Rhampholeon spectrum*, of a related genus), *b.* 22 chromosomes, no *m* (*Ch. lateralis*), *c.* 22 chromosomes of which 4 *m* (*Ch. monoceras*, see discussion furtheron), *e.* 22 chromosomes of which 4 *m* (*Ch. oustaleti*), *f.* 24 chromosomes, of which 2 *m* (*Ch. voeltzkowi*, see discussion furtheron), *g.* 28 chromosomes, of which 4 *m* (*Ch. cephalolepis*)

IV) No clear separation between *M*, showing an acrocentric tendency, and *m* (4).

I) 24 chromosomes, of which 4 *m* (*Ch. bitaeniatus* and *Ch. jacksoni*)

An important feature of the division according to chromosome-patterns is that, apart from *Ch. gallus* and *Ch. parsonii* (and *Brookesia stumpffii*), the groups A, B, C and I are completely continental African, whereas the groups D, E, F, G and H are all from Madagascar (apart from *Rhampholeon spectrum*). The groups A, B, C and D (clear separation between 12 meta- or submetacentric *M* and a series of 12—24 *m*) are considered continental by MATTHEY, 11 continental species belonging to it as well as three from Madagascar (in the following we only give our attention to the genus *Chamaeleo*). The other groups, E-I, in which the separation between *M* and *m* is less clear, are called insular by MATTHEY, 9 Madagascar species and 2 continental ones belong to it.

It should be noted that even when species are listed in the same group, their chromosome-patterns are not in all details identical: the size of the chromosomes and the position of the centromere may vary (see a.o. figures in MATTHEY, 1957). I am not qualified to assay these variations, nor do I know what kind of variation may occur within the limit of a single species (see MEYLAN, 1960, and MATTHEY and MEYLAN, 1961, on the chromosomal polymorphism in *Sorex araneus*).

Groups of species according to HILLENIUS

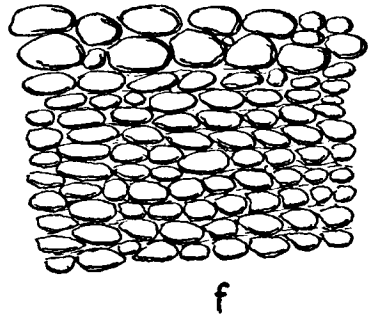
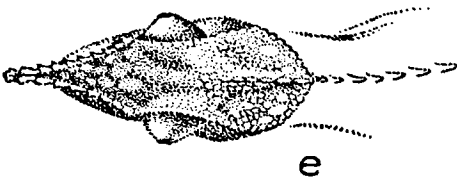
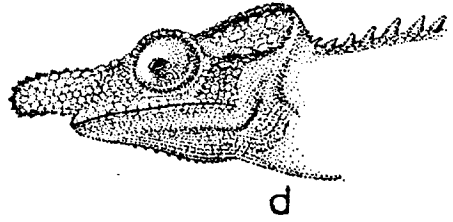
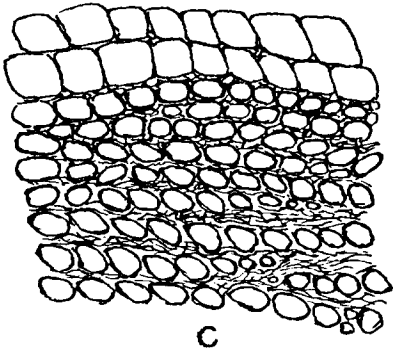
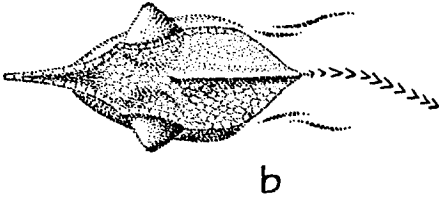
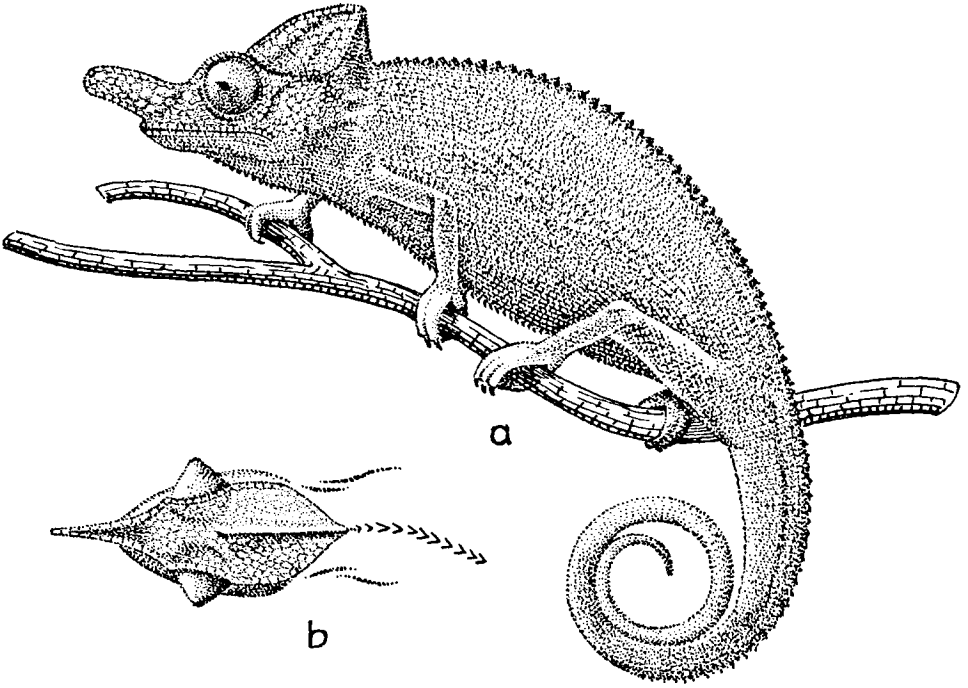
(the letters in parentheses indicate the groups according to MATTHEY & VAN BRINK)

1. Group of *Chamaeleo polleni*, comprising *Ch. polleni* and *Ch. cephalolepis* (Hg.).

More or less homogeneous squamation, occipital lobes absent, feebly developed crests, ventral crest almost always present, size not exceeding 22 cm, axillary pits occur.

Ch. cephalolepis possesses a somewhat prominent rostral edge in males, which may be an indication of relationship with the group of *Ch. oustaleti* (4), at least with *Ch. pardalis* and *Ch. guentheri*.

Comoro islands.



2. Group of *Chamaeleo rhinoceratus*, comprising *Ch. rhinoceratus* (Hf), *Ch. monoceras* (Hd), *Ch. xenorhinus*, *Ch. carpenteri*.

Characterized in males by a rigid paired or single rostral appendix, laterally compressed and, if paired (*Ch. xenorhinus*), generally only separated at the edges. The upper side of the appendix is formed by the canthi rostrales (see fig. 1), different in this respect from the bony protuberance on the snout of *Ch. melleri*.

Madagascar and East Africa.

3. Group of *Chamaeleo lateralis*, comprising *Ch. lateralis* (Hb) and *Ch. campani* (D).

Double row of scales on the dorsal keel, white midventral line, axillary pits generally present, usually one or more white lateral lines on the flank.

Madagascar.

4. Group of *Chamaeleo oustaleti*, comprising *Ch. oustaleti* (He), *Ch. verrucosus*, *Ch. pardalis* (Hc), *Ch. guentheri*.

Coarse heterogeneous squamation, prominent parietal crest, highly elevated casque, occipital lobes absent, large size (*Ch. oustaleti* is the biggest chamaeleon, maximum length 63 cm).

Madagascar.

5. Group of *Chamaeleo nasutus*, comprising *Ch. nasutus* (F), *Ch. fallax*, *Ch. gallus* (B), *Ch. boettgeri*, *Ch. linotus*, *Ch. guibei*, *Ch. tenuis*, *Ch. spinosus*.

Flexible rostral appendix (absent only in some females), weak and elongated structure of the cones on the dorsal crest (if present), absence of ventral and gular crest, the smallest species of the genus.

Madagascar, East Africa.

6. Group of *Chamaeleo cucullatus*, comprising *Ch. cucullatus*, *Ch. malthe*, *Ch. brevicornis* (G).

Large occipital lobes, in male specimens small, more or less paired protuberances on the snout, on the junction of the canthi rostrales.

Madagascar.

7. Group of *Chamaeleo parsonii*, comprising *Ch. parsonii* (A), *Ch. globifer*, *Ch. oshaugnessyi*.

Broad flat casque, feebly developed occipital lobes, parietal crest absent

FIG. 1. *a, b, c*, "*Chamaeleo voeltzkowi*" ♂ Geneva No. 912/92. Madagascar 2.56. leg. R. Matthey.

a animal seen from the left side, *b* head from above, *c* the squamation approximately in the middle of the flank (the large scales on top form the lateral line along the flank).

d, e, f "*Chamaeleo monoceras*" ♂ Geneva No. 926/69. Madagascar 9.1957. leg. R. Matthey.

d head from the left, *e* head from above, *f* the squamation approximately in the middle of the flank (same as *c*).

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, male specimens possess a pair of laterally compressed, rigid rostral protuberances, comparable with those in *Ch. bifidus* c.s. but much shorter. Perhaps related to group 8.

Madagascar.

8. Group of *Chamaeleo bifidus*, comprising *Ch. bifidus*, *Ch. minor*, *Ch. willsi* (E), *Ch. fischeri* (A), *Ch. tavetensis*.

Parietal crest absent, or if present only slightly higher than lateral crests, occipital lobes absent, in many cases an indication of gular and ventral crests, 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, lacking in the female or only slightly indicated. This last feature connects this group 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.

Madagascar, East Africa.

9. Group of *Chamaeleo furcifer*, comprising *Ch. furcifer* and *Ch. gastrotaenia*.

Fine, homogeneous squamation, gular and ventral crests absent, very poorly developed occipital lobes, only indicated by a small slit, just behind the casque.

Madagascar.

10. Group of *Chamaeleo chamaeleon*, comprising *Ch. chamaeleon* (the nominal form as also the subspecies *chamaeleon zeylanicus* belong to group C of MATTHEY & VAN BRINK), *Ch. dilepis* (C), *Ch. senegalensis* (C), *Ch. gracilis*, *Ch. laevigatus*, *Ch. calypttratus*, *Ch. basiliscus*.

Homogeneous squamation, white midventral line, in most cases a dorsal crest, at least on the anterior part of the back a single row of scales, in most cases a gular and a ventral crest. Though not occurring in all species, a tarsal spur is typical for this group. No temporal crests, no axillary pits. Absence of horns and other cranial protuberances, fin-shaped dorsal keels and other conspicuous features may superficially suggest a relationship with *Ch. polleni* (group 1, but the species around *Ch. chamaeleon* never possess axillary pits) and with *Ch. adolfi-friederici* (group 15).

Continental Africa, Spain, Asia minor, Persia, India, Ceylon.

10a. Group of species more or less related to *Chamaeleo chamaeleon* c.s., comprising:

Ch. anchietae, only different from the former group by the double row of scales on the dorsal keel.

Angola.

Ch. monachus, different from the former group by the heterogeneous squamation and the fused occipital lobes.

Socotra.

Ch. melleri, resembling in several respects *Ch. monachus*, differing from this species by the rostral process and the more or less fin-shaped dorsal keel. Thus this species can only indirectly be linked with the group around *Ch. chamaeleon*.

East Africa.

Ch. namaquensis, only differing from the former group by the peculiar dorsal crest (16—17 knob-like groups of scales, each group situated above a spine of a dorsal vertebra).

S.W. Africa.

11. Group of *Chamaeleo oweni*, comprising *Ch. oweni* (A), *Ch. johnstoni* (A), *Ch. ituriensis* (the latter may be regarded as a subspecies of *Ch. johnstoni*, hornless in both sexes, see LOVERIDGE, 1942).

Generally one or three horns in male specimens, double row of scales on the dorsal keel, ventral and gular crests absent, occipital lobes very small or absent. Perhaps related to the following group.

Cameroon to East Africa.

12. Group of *Chamaeleo cristatus*, comprising *Ch. cristatus* (A), *Ch. doremensis*, *Ch. feae*, *Ch. pfefferi*, *Ch. montium*, *Ch. camerunensis*, *Ch. quadricornis* (A), *Ch. wiedersheimi* (A).

If present (in males) the horns are paired (2 or 4), double row of scales on the dorsal keel, wavy in outline (above the dorsal spines), heterogeneous squamation, often larger shields in one or more horizontal lines, no parietal crest. I hope to discuss this group later on.

Perhaps related with the former group: double row of scales on dorsal keel, tendency towards wavy outline of this keel, horns, geographical distribution.

Cameroon.

13. Group of *Chamaeleo pumilus*, comprising in my opinion (HILLENUS, 1959) only one species: *Ch. pumilus* (B), with (perhaps) 10 subspecies (*pumilus*, *transvaalensis*, *melanocephalus*, *gutturalis*, *ventralis*, *occidentalis*, *karrooicus*, *damaranus*, *caffer*, *taeniobronchus*).

Ovoviviparous, coarse, heterogeneous squamation, small size, ventral crest absent, in most cases gular lobes or scaled tubercles on the gular crest.

South Africa.

14. Group of *Chamaeleo bitaeniatus*, comprising *Ch. bitaeniatus* (I), *Ch. jacksoni* (I), *Ch. tempeli*, *Ch. wernerii*, *Ch. fuelleborni*, *Ch. incornutus*, *Ch. laterispinis*.

Ovoviviparous, coarse, heterogeneous squamation, small to moderate size, parietal crest forked anteriorly, dorsal crest with unequal cones, in most

cases with groups of larger cones above the spines of the dorsal vertebrae, 1 or 3 horns may occur.

A subdivision can be made in:

- a. species completely lacking occipital lobes (*Ch. bitaeniatus*, *Ch. jacksoni*),
- b. species with large occipital lobes (*Ch. tempeli*, *Ch. weneri*, *Ch. fuelleborni*, *Ch. incornutus*, *Ch. laterispinis*).

East Africa.

15. Miscellaneous.

- a. *Ch. affinis*, perhaps related to group 12 (via *Ch. widdersheimi*).
Abessynia.
- b. *Ch. goetzei*, perhaps related to *Ch. affinis*.
East Africa.
- c. *Ch. adolphi-friederici*, shows resemblances to *Ch. polleni* and also to the group of *Ch. chamaeleon*, but these resemblances are rather negative: absence of conspicuous characters, perhaps caused by convergent degeneration and thus resembling a more primitive type. In this case the results of cytological study might be conclusive.
Congo.
- d. *Chamaeleo uthmölleri*. According to the author (MÜLLER, 1938) the animal resembles somewhat *Ch. longicauda* (= *pardalis*) but gular and ventral crests are absent and a double row of scales are on the dorsal keel. MERTENS (1955), who described a second specimen, suggested a relationship with *Ch. tavetensis*, "mit dem es, bis auf die fehlenden Hörner, habituell viel Ähnlichkeit hat".
Tanganyika.
- e. *Ch. laevigularis*. Difficult to suggest any relationship with other species.
South Africa?

DISCUSSION

Group A. This group may contain closely related species as well as less related species, because it is generally understood that the particular chromosome-pattern of this group may have originated several times independently (see Introduction). So, belonging to this group neither gives much support to my opinion, that *Ch. oweni* and *Ch. johnsoni* are closely related (HILLENUS, 1959), nor contradicts it.

As I hope to demonstrate in some future paper, *Ch. quadricornis* and *Ch. widdersheimi* are closely related. In general we find in group 12 egg-laying chameleons with paired horns, or chameleons closely related to species with paired horns: *widdersheimi* is almost indistinguishable from a female *Ch. montium*, *Ch. montium* and *Ch. quadricornis* have much in common.

As stated in my list of groups, groups 11 and 12 may perhaps be joined in one group. Their cytology would not contradict this.

The fact that *Ch. fischeri* and *Ch. parsonii* possess the same chromosome-pattern might be an indication of relationship of groups 7 and 8, both characterized by a rather flat casque and pairs of rigid rostral protuberances,

the main difference — absence of occipital lobes in group 8, presence of occipital lobes in group 7 — being in general a minor difference, at least between groups.

I do not think it taxonomically plausible to connect the groups 11 and 12 with the groups 7 and 8. So in this case (as in the case of *Brookesia stumpffi*) we may assume a convergence at the level of the chromosome-pattern.

Incomprehensible at first sight is the fact that *Ch. willsi* belongs to group E and *Ch. fischeri* to group A, as even now, reconsidering my system with reference to the new cytological findings, I cannot find sufficient grounds to put *Ch. willsi* in a group separate from *Ch. fischeri* (and *Ch. bifidus* and *Ch. minor*). In the Conclusion I shall revert to this.

Group B. Another incomprehensible fact is *Ch. gallus*, possessing the same chromosome-pattern as *Ch. pumilus*. This is probably caused (according to MATTHEY, 1961) by convergent evolution (comparable with the development of the pattern in group A), as these species differ in several important characters; the first is oviparous, the latter ovoviviparous. Other important differences may be found in squamation, in dorsal and gular crest, in rostral appendix, in absence and presence of inguinal and axillary pits, and in size.

In all these characters we find great resemblance between *Ch. nasutus* and *Ch. gallus*. Apart from one specimen of *Ch. fallax* (of the same group 5), *Ch. nasutus* and *Ch. gallus* are the only species in which I found the character of inguinal pits. In fact, the only consistent difference between them is the length of the rostral appendix, which is much longer in *Ch. gallus* than in *Ch. nasutus*. Therefore, I considered them (1959) to be closely related. But *Ch. nasutus* possesses an insular chromosome-pattern (group F) and *Ch. gallus* a continental one (B). In the Conclusion we shall return to this.

Group C. Lastly, in this group the cytological evidence supports the taxonomical conclusions. The four species listed here by MATTHEY & VAN BRINK belong to my group 10. two of them are even considered to be subspecies of the same species (*Ch. chamaeleon* and *Ch. calcaratus* = *Ch. chamaeleon zeylanicus*). As MATTHEY & VAN BRINK (1960) remarked: "La fraction C semble homogène, soit cytologiquement (12 M 12 m), soit morphologiquement, soit géographiquement."

Group D. On account of the large difference in chromosome-pattern between *Ch. campani* and *Ch. lateralis*, I do doubt their relationship, as the grounds on which I put them in the same group taxonomically are not very important indeed. They have in common a double row of scales on the dorsal keel, a white midventral line, axillary pits, often two white lines under the tail or a trace of them under the base of the tail only. All these characters occur in other groups too, but this particular combination is typical for these two species only.

My conclusion is that group 3 must be divided in one for *Ch. lateralis* and one for *Ch. campani*, neither having any clear relation to other groups.

MATTHEY & VAN BRINK (1960) do not think it possible to connect the

following 3 groups, as "l'augmentation du nombre de *M*, en passant de l'une à l'autre, (14, 16, 18), ne s'accompagne pas d'une diminution de l'effectif des *m* (14, 18, 14) à quoi on se serait attendu."

Group E. See group A.

Group F. See group B.

Group G. The fact that *Ch. brevicornis* possesses a particular chromosome-pattern, confirms my view that it belongs to a separate group (6).

Group H. The species belonging to this group all possess different chromosome-patterns. Even if the numbers of chromosomes are equal, their form is clearly different. For instance *Ch. monoceras* (for discussion of this name see further on) has the same number of chromosomes as *Ch. oustaleti*, 22 of which 4 *m*, but in *Ch. oustaleti* we find 9 pairs of more or less symmetrical V plus 2 pairs of *m*, in *Ch. monoceras* 8 pairs of V, 1 little pair of acrocentric chromosomes and 2 pairs of *m*.

So, cytologically the 6 species of this group show the same kind of vague relationship, but we do not find — as in the case of group C — a clear support for the division I proposed.

Hb. Ch. lateralis was considered in group D.

Hc. Ch. pardalis is cytologically clearly different from *Ch. oustaleti* (He), though in general appearance they are much alike, with many characters in common (large size, strong crests, roughly heterogeneous squamation etc.) I do not find sufficient reason for splitting up the group.

Hd and Hf. See the discussion of *Ch. monoceras* and *Ch. voeltzkowi*, further on.

Hg. The separate position of *Ch. cephalolepis* (in group I, with *Ch. poleni*) is confirmed by the deviating chromosome-pattern.

Group I. "Dans le cas précis de *C. bitaeniatus* et *C. jacksoni*, il est bien difficile d'admettre qu'une formule chromosomique si aberrante ait été acquise indépendamment par ces deux espèces que je considère donc comme étroitement alliées. [MATTHEY & VAN BRINK, 1960].

So, in this case also our taxonomical conclusions are confirmed by cytological evidence.

THE CASE OF *Ch. monoceras* AND *Ch. voeltzkowi*.

In § 3 of my paper (1959) I discussed the group of species around *Ch. rhinoceratus*, especially the Madagascar species: *Ch. rhinoceratus*, *Ch. labor-di*, *Ch. voeltzkowi* and *Ch. monoceras*. Comparing the descriptions of these species I found 12 characters, which in several combinations were characteristic for the species.

I had at my disposal 7 specimens of the Paris collection and 4 descriptions in literature detailed enough for comparing. Of my eleven specimens, only 4 answered to the description of one of the 4 species, not surprisingly so, as 2 of them were type-specimens (of *Ch. labor-di* and *Ch. monoceras*) and 2 others were the first females of *Ch. labor-di* described by ANGEL (1942). The other specimens possessed combinations of characters which put them in more or less intermediate positions among four known species (see table 1).

		<i>rhinoceratus</i>	<i>labordi</i>	<i>voeltzkowi</i>	<i>monoceras</i>
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
	12	10 (2 ?)	9	9	7 (1 ?)
	13	9 (2 ?)	4	4	10 (1 ?)

TABLE 1. Numbers of characters which each of the 13 specimens has in common with the types of *Ch. rhinoceratus*, *Ch. labordi*, *Ch. voeltzkowi* and *Ch. monoceras*. 10 (2 ?) means that a specimen has 10 characters (of which 2 uncertain) in common with the indicated type.

The specimens 1—7 belong to the Paris Museum of Natural History (for more details see Table B, HILLENUS, 1959), the data of the specimens 8—11 were abstracted from the original descriptions of *Ch. rhinoceratus lineatus* (8), *Ch. barboursi* (9, 10) and *Ch. monoceras* (11), the specimens 12 and 13 belong to the Geneva Museum of Natural History, recorded respectively as no. 912/92 and no. 926/69.

Considering that the comparison was based on 11 specimens and that the total number of specimens known in literature of the 4 species together amounted to 13 only, I felt (and still feel) quite justified to conclude that there is no sufficient reason to distinguish as separate species *Ch. rhinoceratus*, *Ch. labordi* and *Ch. voeltzkowi*, so I regard them all as synonyms of *Ch. rhinoceratus*.

In 1959 I had my doubts about the validity of the species *Ch. monoceras*. The only specimen of *Ch. monoceras* differs in two characters (much longer rostral appendix and presence of a gular crest only) from the then known specimens of *Ch. rhinoceratus*. MATTHEY & VAN BRINK (1956, 1960) give the chromosome-patterns of *Ch. voeltzkowi* (= *Ch. rhinoceratus*) and of *Ch. monoceras*.

The chromosome-pattern of *Ch. monoceras* consists of 8 pairs of V, 1 pair of little acrocentric chromosomes and 2 pairs of *m*, the chromosome-pattern of *voeltzkowi* (*rhinoceratus*) consists of 11 pairs of V and 1 pair of *m* (see fig. 2). So it seems quite impossible that these specimens can breed a fertile offspring. So far this case was not different from that of *pardalis-oustaleti* or *gallus-nasutus*: again the conclusions from cytological and classical taxonomical work differ.

Thanks to the kindness of Prof. V. AELLEN, Director of the Musée de l'Histoire Naturelle de Genève, I have been able to examine the specimens, both of which belong to the collection of his museum. Even now, however,

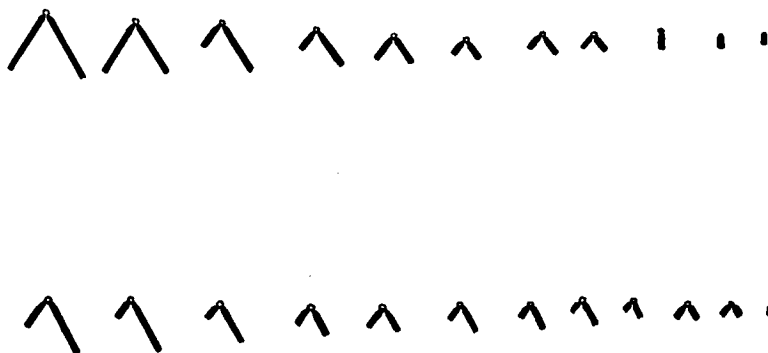


FIG. 2. Chromosome-patterns of "*Chamaeleo monoceras*" ♂ Geneva No. 926/69 (above) and of "*Chamaeleo voeltzkowi*" ♂ Geneva No. 912/92.

in possession of the cytological knowledge I cannot regard these specimens as belonging to separate species.

Let me first give the descriptions of the specimens:

"*Ch. voeltzkowi*" ♂ Genève No. 912/92. Madagascar. 2.56. leg. R. Matthey. Length of tail 110 mm., length of head and body 96 mm. Diameter of the eyesocket 7,5 mm, length of rostral appendix (measured from the upperlip) 7,5 mm. Squamation slightly heterogeneous, a horizontal row of large, flat, more or less quadrangular scales on the flank, probably of white colour in the living specimen. Parietal crest reaching the top of the casque, this is not clear for the lateral crests. Axillary pits present. Gular and ventral crest present, separated by somewhat less developed cones. Casque elevated posteriorly and laterally compressed. Dorsal crest distinct from neck to tail. A trace of paired white lines under the base of the tail. Upperside of the rostral appendix smooth.

"*Ch. monoceras*" ♂ Genève 926/69. Madagascar 9.1957. leg. R. Matthey. Length of tail 91 mm, length of head and body 97 mm. Diameter of the eyesocket 9,5 mm, length of rostral appendix 9,5 mm. Squamation slightly heterogeneous, horizontal row of larger scales on the flank, rounder than in the former specimen. Whitish lateral line on the flank. Parietal and lateral crests reaching the top of the casque. Deep axillary pits. Gular crest feebly developed. Ventral crest indicated (hardly discernable because the belly is cut open just on the median line). Casque only slightly elevated posteriorly. Dorsal crest only distinct on the foremost part of the back. No white lines discernable under the tail. Upperside of the rostral appendix slightly serrated.

Comparing these descriptions with those of the types of *Ch. rhinoceratus*, *Ch. labordi*, *Ch. voeltzkowi* and *Ch. monoceras* (as corrected by HILLENUS, 1959), I find that the first one has 10 characters (of which 2 uncertain) in common with the type of *Ch. rhinoceratus*, 9 characters in common with the type of *Ch. labordi*, 9 with the type of *Ch. voeltzkowi* and 7 (of which 1 uncertain) with the type of *Ch. monoceras*.

The second specimen has 9 characters (of which 2 uncertain) in common with the type of *Ch. rhinocerus*, 4 characters with the type of *Ch. labordi*, 4 characters with the type of *Ch. voeltzkowi* and 10 (of which 1 uncertain) with the type of *Ch. monoceras*.

In table 1 I combine these comparisons with those made on the 11 specimens already mentioned (the Genève specimens listed as numbers 12 and 13 respectively).

Of the specimens in this table, I could examine 9 specimens myself, 4 could be inferred from literature. The total number of specimens known will not reach far above 15, so that I feel justified in taking this table for a representative picture of the forms around *Ch. rhinocerus*.

Ch. monoceras is distinguished from all specimens known at present by the much larger rostral appendix and by absence of a ventral crest. Neither of these two characters is present in the specimens 12 and 13 of the Museum of Genève, so that I do not reckon them to belong to *Ch. monoceras*.

Considering the external characters only, I cannot find reasons to change my opinion that *Ch. labordi* and *Ch. voeltzkowi* are synonyms of *Ch. rhinocerus*, and that all specimens (apart from the type of *Ch. monoceras*, Nr. 11) including the 2 specimens of Geneva, do belong to *Ch. rhinocerus*. However, the difference in the chromosome-patterns of the specimens 12 and 13 is such, that most probably they cannot produce a fertile offspring, so that we have to consider them as belonging to different species. One of them is perhaps *Ch. rhinocerus*, but which one? And how then should the other specimen be named? The trouble is that this kind of cytological work can only be done on fresh specimens. We shall never know to what group of chromosome-pattern the types of *Ch. rhinocerus*, *Ch. labordi*, *Ch. voeltzkowi*, and *Ch. monoceras* belong, considering the fact that even in external characters none of the specimens are quite identical with any of the type-specimens (or with each other). According to the cytological findings we should choose new lectotypes, of which the chromosome-pattern is known. The consequence, however, would be that we shall never be able to identify a specimen, if we do not have it fresh enough to examine its chromosomes.

For the moment it seems better to leave things as they are, the more so as the localities of the two Geneva specimens — the only ones of which the chromosome-patterns have been studied — are not known.

CONCLUSIONS

What may be the reason that species which do not have much in common externally belong cytologically to the same group, whereas species no one would hesitate to call at least similar seem to belong to cytologically widely separated groups? There is as yet no definite answer, as it is unknown how the differences in chromosome-pattern originate, though in the robertsonian type of polymorphism (1 V corresponds with 2 I) the mechanism may be very simple. We have to accept the cytologists' information that some of the cytological resemblance may be caused by convergent evolution (group A

and perhaps B). If, however, the same more or less stable pattern might be reached along different lines of evolution, we might also accept a hypothetical ancestral type of chromosome-pattern, from which those different lines originally took their course. That would mean that there are two poles of chromosome-patterns, the ancestral and the more developed, stable one, between which the other patterns may be arranged.

The stable pattern of group A consists of 36 chromosomes, i.e. the greatest number known in chameleons. This would suggest an increasing number of chromosomes in the course of evolution, whereas generally a decrease of the number is probable (MATTHEY & VAN BRINK, 1960: "chez les Amphibiens, et à un moindre degré chez les reptiles, l'évolution chromosomique est caractérisée par une diminution du nombre des chromosomes en allant des familles les moins spécialisées aux plus spécialisées"). *)

On the other hand, MATTHEY (1958) demonstrates that in mammals of the infraclass *Eutheria* gains and losses occur almost with equal frequency.

MATTHEY & VAN BRINK distinguish two greater types of chromosome-patterns: the continental type (group I A, B, C, D), characterized by a clear division between *M* and *m* chromosomes, and the insular type (II E, F, G, III H and IV I), which shows a more or less gradual decrease in size from the 6 pairs of *M*-chromosomes to the smallest *m*-chromosomes. As we have seen, the continental type includes also some Madagascar species and the insular type some continental African species. The exceptions "pourraient être considérées comme provenant d'échanges anciens entre la grande île et le continent" (MATTHEY, 1957).

This is not very probable. It is impossible to imagine a chameleon resembling *Ch. nasutus* in most features, going to the continent and picking up there the *pumilus*-type of chromosome-pattern, the more so as the differences between *Ch. pumilus* and the group of *Ch. nasutus* are so great that fertile hybridization between them cannot possibly have taken place.

I do not think the assumption necessary. The exceptions (at least within the genus *Chamaeleo*) are the Madagascar species *Ch. parsonii*, *Ch. gallus*

*) As a layman in cytology I cannot refrain from playing with the following speculation:

When we take into consideration the robertsonian mechanism (by which 1 chromosome of the V-type is equivalent to 2 chromosomes of the I-type) the number of chromosomes of the group C (of *Ch. chamaeleon* c.s.) is the smallest, the number of chromosomes of the stable A-pattern is one of the highest. Especially if one agrees with the assumption of MATTHEY & VAN BRINK that the A-pattern (and probably the B-pattern too, which has still more chromosomes) originated convergently several times independently, the suggestion becomes very strong that the development goes from the smallest number of chromosomes towards greater numbers, along several lines. This would mean that the pattern with the smallest number of chromosomes, i.e. the pattern of group C is the most ancestral. In my paper of 1959 (§ 21) I came by two different ways to the conclusion that the ancestral chamaeleon was probably an animal resembling most *Chamaeleo chamaeleon* s.l. This confirms the cytological speculations, as the chromosomal group C is the same as my taxonomic group of *Ch. chamaeleon*.

Cytological groups of MATTHEY & VAN BRINK	Taxonomic groups of HILLENUS
A {	7
.	8
.	11
.	12
B	13
C	10
D	3 (<i>campani</i>)
E	5
F	6
G	6
Ha	Rhampholeon spectrum
b	3 (<i>lateralis</i>)
c	4
d	2
e	2
f	2
g	1
I	14

TABLE 2. Every cytological group of MATTHEY & VAN BRINK corresponds with one or more taxonomic groups of HILLENUS. The relatively few discordances are indicated by oblique lines.

and *Ch. campani* with a continental pattern and the continental species *Ch. bitaeniatus* and *Ch. jacksoni* with an insular type.

Considering the taxonomically concordant, but cytologically deviating cases (see table 2):

Ch. willsi (E) and *Ch. fischeri* (A),

Ch. gallus (B) and *Ch. nasutus* (F) (the Madagascar *Ch. gallus* in the same group as the obviously non-related *Ch. pumilus*)

and leaving apart the relatively smaller differences between *Ch. oustaleti* and *Ch. pardalis*, the two patterns of *Ch. rhinoceras* (all considered "chromosomiquement très proches" by MATTHEY & VAN BRINK, 1960), the following solution is suggested:

If the A-pattern (with which the B-pattern seems to be closely connected) can independently come about several times by convergence, it would be quite possible that the A-pattern of *Ch. fischeri* originated from the E-pattern of *Ch. willsi*. Perhaps we may regard the A-pattern of *Ch. parsonii* as an indication of this possibility, as the group of *Ch. parsonii* and the group of *Ch. bifidus* (to which *Ch. willsi* and *Ch. fischeri* belong) seem to be closely related.

The same reasoning may hold for the B-type of *Ch. gallus* as originated from the F-type of *Ch. nasutus*, whereas the B-type of *Ch. pumilus* most probably originated by convergence along other lines.

Also the bi-modal type of *Ch. campani* may be a step towards a more stable pattern.

Thus the discordances between our groupings of the species would become less incomprehensible.

In my opinion, the taxonomy and geographical distribution of the genus *Chamaeleo* suggest that the known forms developed only recently — palaeontologically speaking — from a single ancestral form. Firstly, because of the homogeneous structure of the genus. A more important argument seems to me the concentric distribution of the characters (see HILLENUS, 1959): all characters that can be distinguished are present in a relatively small area (Tanganyika and Kenya), the number of characters gradually decreasing when we go from this area to the periphery of the distribution of the genus.

The presence on Madagascar of an important population of chameleons does not necessarily contradict the assumption of a rather recent origin of the chameleons, because — as MILLOT (1952) convincingly demonstrated — it is most probable that the greater part of the fauna of Madagascar originated from specimens drifted ashore on disrooted trees from the continent. Especially chameleons, being such arboreal specialists, may relatively easily be transported that way *).

In my paper (1959) I demonstrated that the chameleons of Madagascar, though with less characters, showed the greatest number of species as compared with other areas. This is confirmed by the fact that on the continent we find 4 types of chromosome-patterns only (see fig. 3), at most 3 together (in East Africa), whereas we find 12 different chromosome-patterns in the relatively small area of Madagascar. Thus the diversity of chromosome-patterns has nothing to do with the diversity of external features.

All this suggests that chameleons started as a rather homogeneous, though variable group, for the greater part without fertility barriers and thus allowing almost any combination of characters. Then, relatively late, started the cytological evolution, creating fertility barriers and dividing the genus into groups of species, generally distinguished by combinations of characters, each of which, in other combinations, may also occur in other groups.

Later on other fertility barriers certainly will have originated, but the most important are those which are still dividing the groups of species along cytological lines.

*) It is sometimes held that chameleons, being such a successful group on Madagascar, should have reached this island very long ago; some authors even assume that chameleons came to Madagascar while it was still connected with the continent of Africa. According to MILLOT this connection must have been broken towards the end of the Cretaceous, not later than Campanien supérieur (\pm Senonian). Apart from the fact that it seems rather improbable to explain the concentric distribution of characters if started already in the Mesozoicum, it seems more improbable still that from that period on the Madagascar chameleons would have lived separate from the continental chameleons without diverging more widely from each other. For, as we have seen, there are no important characters on Madagascar which are not also present on the continent. The present variability of several species on Madagascar and in East Africa contradicts the possible assumption that evolution in chameleons had come to a standstill since the Cretaceous.

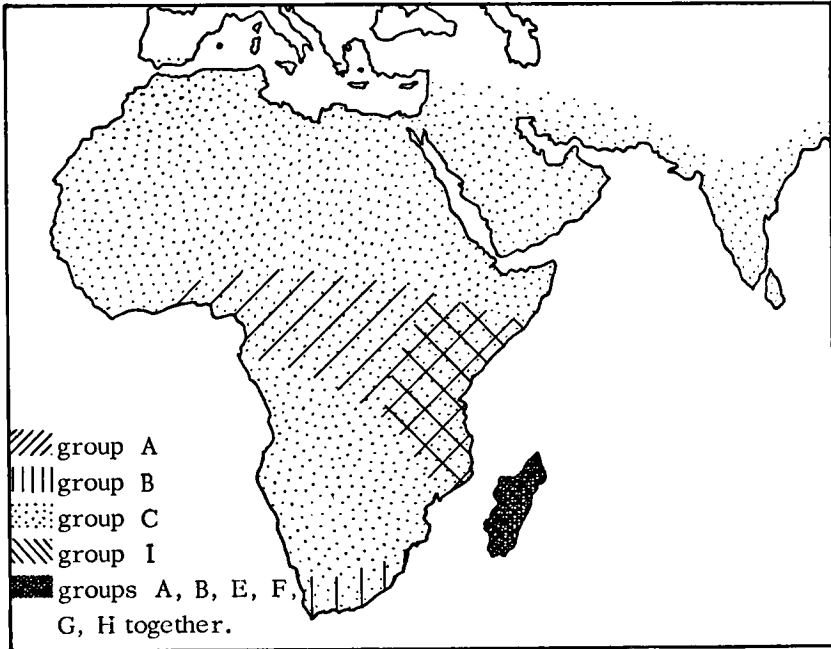


FIG. 3. Africa and adjacent countries. The geographical range of the genus *Chamaeleo*. Roughly indicated the distribution of the chromosome-patterns as defined by MATTHEY & VAN BRINK (mainly after their paper of 1960).

SUMMARY

1. Comparison is made between the subdivision of the genus *Chamaeleo* in groups of species based on *cytological* considerations (MATTHEY & VAN BRINK) and the subdivision of this genus in groups based on *taxonomical* considerations (HILLENUS). Both subdivisions were developed independently from each other and show relatively few discordances (see Table 2).
2. Detailed discussion is given of the case of two specimens (*Ch. voeltzkowi* and *Ch. monoceras*), taxonomically to be regarded as belonging to *Ch. rhinoceratus*. Their chromosome-patterns, however, differ so greatly as most probably not to be able to yield fertile offspring. They should then be regarded as belonging to different species. As the chromosome-patterns of the types of *Ch. rhinoceratus* c.s. are unknown (only accessible in fresh specimens), it is advised for the moment to let the taxonomic considerations prevail.
3. In the *Conclusion* an attempt is made to explain the discordances between the subdivision of MATTHEY & VAN BRINK and of HILLENUS.

LITERATURE

HILLENIUS, D.

- 1959 The differentiation within the Genus *Chamaeleo* Laurenti, 1768. *Beaufortia* Vol. 8, no. 89, 1—92.

LOVERIDGE, A.

- 1942 Scientific results of a fourth expedition to forested areas in East and Central Africa. 4 Reptiles. — *Bull. Mus. Comp. Zool. Harvard* 91 (4), 237—373.

MATTHEY, R.

- 1943 Le problème des hétérochromosomes chez les sauropsidés. *Reptiles. Arch. J. Klaus Stift.*, 18, 1—16.
1957 Cytologie comparée et Taxonomie des Chamaeleontidae (Reptilia-Lacertilia). — *Rev. Suisse de Zool.* 67, 19, 258—261.
1958 Les chromosomes des Mammifères euthériens. Liste critique et essai sur l'évolution chromosomique. — *Arch. J. Klaus Stift.*, 33, 253—297.
1961 La formule chromosomique et la position systématique de *Chamaeleo gallus* (Günther) (Lacertilia). — *Zool. Anz.* 166, 5/6, 153—159.

MATTHEY, R. et J. M. VAN BRINK

- 1956 Note préliminaire sur la cytologie chromosomique comparée des Caméléons. — *Rev. Suisse de Zool.* 63, 10, 241—246.
1960 Nouvelle contribution à la cytologie comparée des Chamaeleontidae (Reptilia-Lacertilia). — *Bull. Soc. Vaud. Sc. Nat.*, 67, 302, 333—348.

MATTHEY, R. et A. MEYLAN

- 1961 Le polymorphisme chromosomique de *Sorex araneus* L. (Mamm. Insectivora). Etude de deux portées de 5 et 9 petits. — *Rev. Suisse de Zool.* 68, 21, 223—227.

MERTENS, R.

- 1955 Amphibien und Reptilien aus Ostafrika. *Mitt. Staatl. Mus. f. Natk. Stuttgart*, no. 305, p. 55.

MEYLAN, A.

- 1960 Contribution à l'étude du polymorphisme chromosomique chez *Sorex araneus* L. (Mamm. Insectivora). (Note préliminaire). — *Rev. Suisse de Zool.* 67, 19, 258—261.

MILLOT, J.

- 1952 La Faune malgache et le mythe gondwanien. — *Mém. de l'Inst. Sc. de Madagascar. A. VII*, 1, 1—36.

MÜLLER, L.

- 1938 „Ueber die von den Herren W. Uthmöller und L. Bohmann im britischen Mandatsgebiet „Tanganyika Territory“ gesammelten Chamäleons“. *Zool. Anzeiger*, Bd. 122, p. 20.

NOTE

When my typescript was with the printers Prof. R. MATTHEY and Miss J. M. VAN BRINK kindly permitted me to mention two results of their cytological research which have not yet been published. I am very grateful as these fit in rather well with my conclusions.

1. The chromosome-pattern of *Chamaeleo basiliscus* is $12 M + 12 m$ and belongs clearly to the group I C (*Ch. chamaeleon*, *Ch. dilepis*, *Ch. senegalensis*, *Ch. calcaratus* = *Ch. chamaeleon zeylanicus*). So again these cytological findings confirm my taxonomic conclusions: as according to me *Ch. basiliscus* belongs to group 10, of *Ch. chamaeleon* c.s., comprising *Ch. chamaeleon*, *Ch. dilepis*, *Ch. senegalensis*, *Ch. gracilis*, *Ch. laevigatus*, *Ch. calyptratus* and *Ch. basiliscus*.
2. In *Chamaeleo melleri* the result is less certain till now; the general impression is that the chromosome-pattern is of the same type as of *Ch. basiliscus* ($12 M + 12 m$). This would confirm my assumption that *Ch. melleri* (group 10a) is to be regarded as a species more or less related to *Ch. chamaeleon* c.s.

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