Bijdragen tot de Dierkunde, 58 (1): 7-11 — 1988

THE SKULL OF *CHAMAELEO NASUTUS* ADDS MORE INFORMATION TO THE RELATIONSHIP OF *CHAMAELEO* WITH *RHAMPHOLEON* AND *BROOKESIA* (CHAMAELEONIDAE, REPTILIA)

by

D. HILLENIUS †

Institute of Taxonomic Zoology (Zoölogisch Museum), University of Amsterdam, P.O. Box 4766, 1009 AT Amsterdam, The Netherlands

ABSTRACT

The form of the skull of *Chamaeleo nasutus*, especially the broad, trigonal parietal, is strikingly similar to the skull of *Rhampholeon*. This supports the hypothesis (Hillenius, 1986) that of all chameleons the group of species around *Ch. nasutus* is the most closely related to *Rhampholeon*.

RÉSUMÉ

Le crâne de *Chamaeleo nasutus* est absolument similaire à celui de *Rhampholeon*, ce qui est surtout valable pour le pariétal qui est large et triangulaire. Ceci vient à l'appui de l'hypothèse (Hillenius, 1986) que les Caméléons les plus étroitement apparentés à *Rhampholeon* sont ceux du groupe d'espèces gravitant autour de *Ch. nasutus*.

INTRODUCTION

On several occasions it has been pointed out that *Brookesia* Gray, 1864 and *Rhampholeon* Günther, 1874 share a number of characters with the group of species around *Chamaeleo nasutus* Duméril & Bibron, 1836. Klaver (1979) argued that the agreements were parallellisms but in fact he did not provide the arguments for this assumption. In a later paper Klaver (1981) concluded that *Chamaeleo* was derived from *Brookesia*.

In a foregoing paper on the relationships of *Brookesia* and *Rhampholeon* with *Chamaeleo* (Hillenius, 1986) I concluded that both former genera are derived from *Chamaeleo* and that the probably nearest relatives can be found in the group of species around *Ch. nasutus*.

Microcomplement fixation has confirmed the first part of this conclusion: *Brookesia* and *Rhampholeon* — probably originally in one taxon — have split off from *Chamaeleo* long after other branches of *Chamaeleo* originated (Hofman et al., in press).

The skulls of *Rhampholeon* and *Brookesia*, however, differ considerably from all *Chamaeleo* skulls that were examined until recently. So I considered it of importance to obtain a skull of a member of the group of species around *Ch. nasutus* to see if any indication of relationship to the deviating form of skulls of *Rhampholeon* and/or *Brookesia* might be found.

MATERIAL AND METHOD

Thanks to the courtesy of Dr. E. R. Brygoo, curator of the herpetological department of the Muséum National d'Histoire Naturelle in Paris, I received in exchange a specimen of *Chamaeleo nasutus*. The skull was carefully macerated in the Zoological Museum of Amsterdam and inscribed under number 16170. It has been compared to skulls of representatives of all the species groups belonging to *Chamaeleo* (as described by Klaver, 1981), and to representatives of the group *Brookesia* + *Rhampholeon*. Skulls of the following specimens, all with the collection number of the Zoological Museum of Amsterdam, have been examined in detail:
Chamaeleo basiliscus no. 15223, *Ch. chamaeleon* no. 10267, *Ch. fischeri* no. 14409, *Ch. jacksonii* no. 16172, *Ch. johnstoni* no. 15216, *Ch. lateralis* no. 10168, *Ch. montium* no. 16174, *Ch. nasutus* no. 16170, *Ch. oustaleti* no. 15215 and no. 10165, *Ch. oweni* no. 15221, *Ch. pardalis* no. 14332, *Ch.*

† Note added by A. Zuiderwijk. — Dr. D. Hillenius unexpectedly died on May 4th, 1987. This posthumous publication contributes to the discussion on the taxonomy of chameleons, as did the main part of his scientific work.

The text of this paper is, in essential, an unchanged manuscript that was found in his papers. Drs. W. Bergmans was helpful to select the skulls for the illustrations. Mr. L. van der Laan made the photographs and Mr. J. Zaagman composed the figures. We thank Drs. Ch. Klaver for making some nomenclatural corrections in the manuscript.

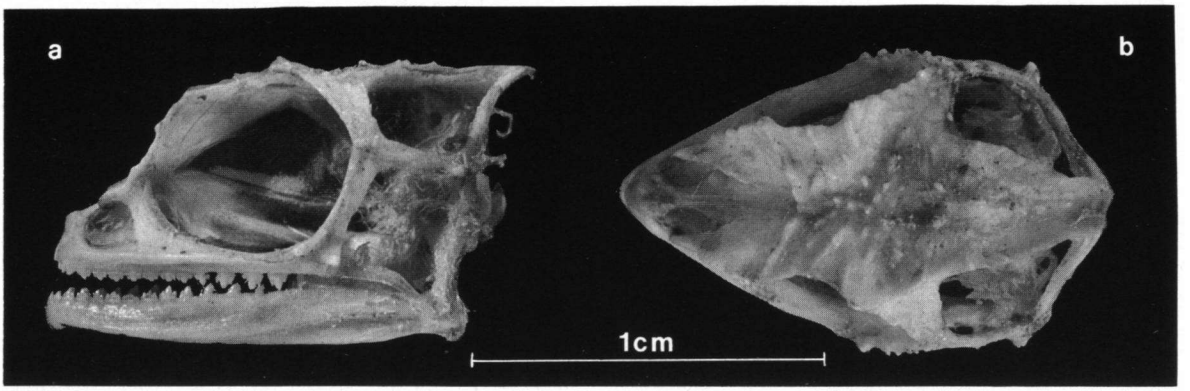

Fig. 1. *Rhampholeon spectrum*, lateral view (a) and dorsal view (b) of the same skull.

pumilus no. 15217, *Ch. senegalensis* no. 15224, *Ch. tigris* no 16173, *Ch. zeylanicus* no. 15222, *Rhampholeon kerstenii* no 15565, and *Rh. spectrum* no. 10264.

DESCRIPTION AND DISCUSSION

The skull of *Chamaeleo nasutus* proves to be quite different from skulls of other chameleons of the genus *Chamaeleo* (see figs. 2 and 3), and less different from skulls of members of Klaver's group A, consisting of *Brookesia* and *Rhampholeon*. The likeness of the *nasutus* skull with that of *Rhampholeon* in particular is striking (see figs. 1 and 2).

In most chameleons the parietal is a narrow crestlike bone, horizontally straight or curved in a vertical plane. We find this type of skull in (see fig. 3):

group B: *Ch. oustaleti* Mocquard, 1894, *Ch. lateralis* Gray, 1831, *Ch. pardalis* Cuvier, 1829, *Ch. fischeri* Reichenow, 1887 and *Ch. tigris* Kuhl, 1820;

group C: *Ch. chamaeleon* (Linnaeus, 1758), *Ch. chamaeleon zeylanicus* Laurenti, 1768, *Ch. basiliscus* Cope, 1868, and *Ch. senegalensis* Daudin, 1802;

group E: *Ch. oweni* Gray, 1831, *Ch. montium* Buchholz, 1874, and *Ch. johnstoni* Boulenger, 1901;

group F: *Ch. jacksonii* Boulenger, 1896, *Ch. bitaeniatus* Fischer, 1884, *Ch. hoehnelli* Steindachner, 1891, and *Ch. ellioti* Günther, 1895.

The only deviating skull known until now was *Ch. pumilus* c.s. (group B, see fig. 4), in which the parietal forms a broad bone with parallel lateral borders. This parietal was one of the main arguments of several herpetologists (among whom most South Africans, see Raw,

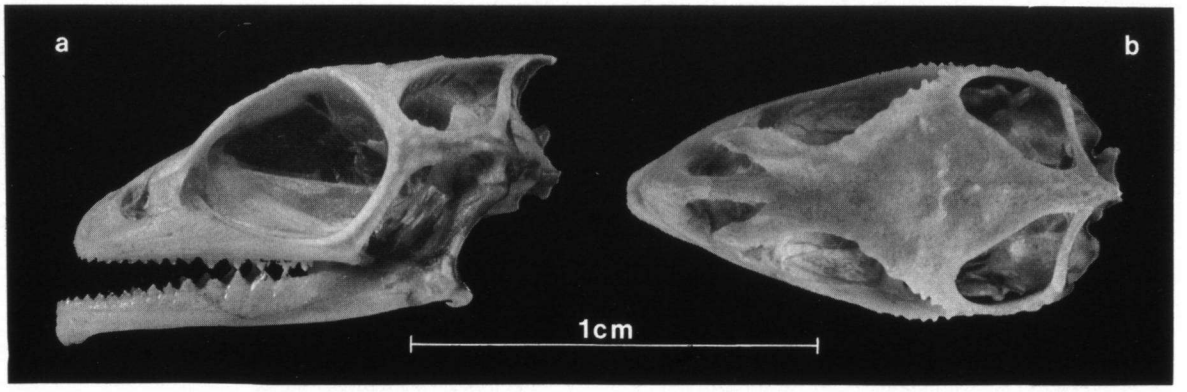

Fig. 2. *Chamaeleo nasutus*, lateral (a) and dorsal view (b) of the same skull.

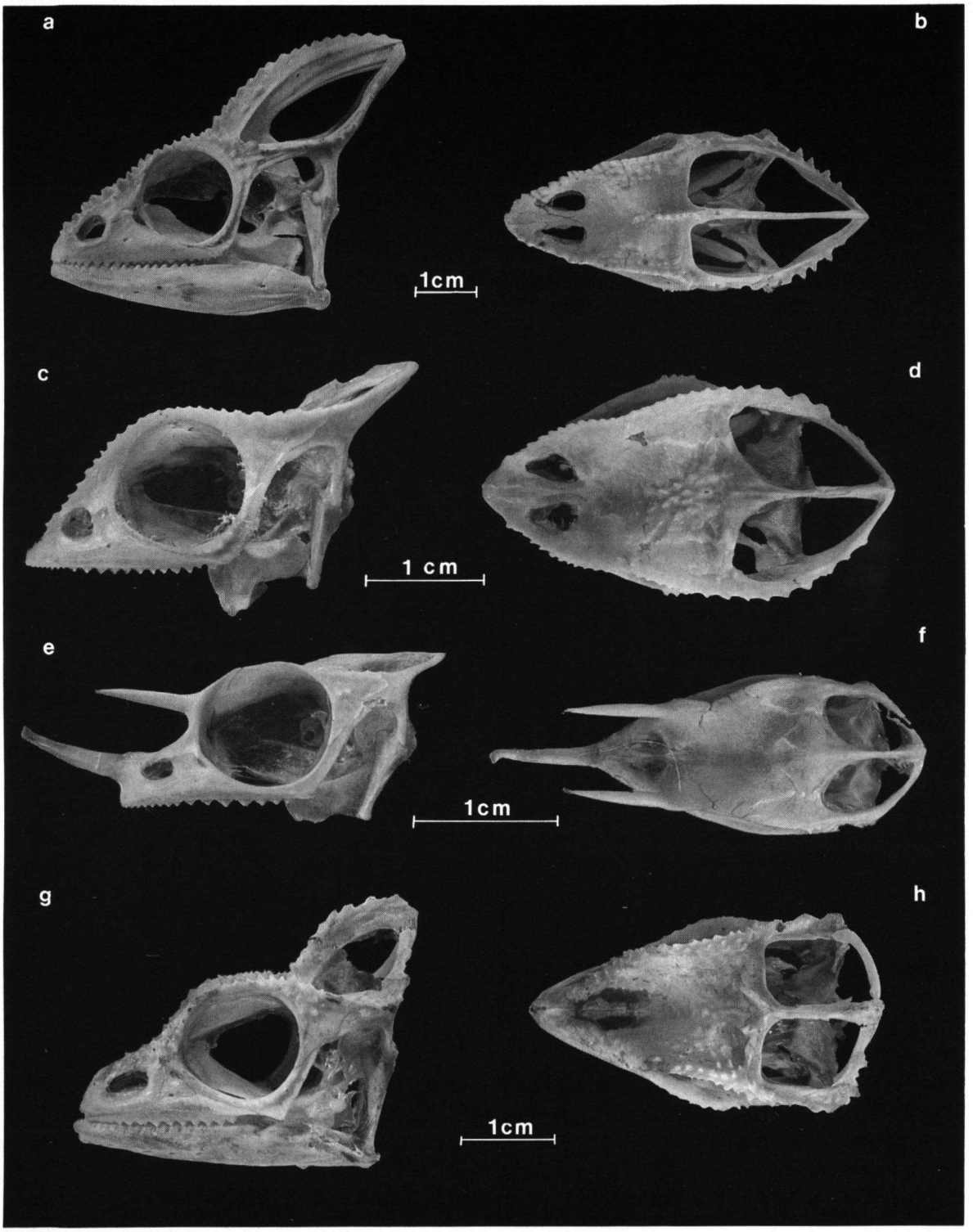

Fig. 3. Representatives of species group B, C, E and F, respectively. Left side: lateral view; right side: dorsal view of the same specimen; a & b: *Ch. oustaleti*, c & d: *Ch. senegalensis*, e & f: *Ch. oweni*, g & h: *Ch. jacksonii*.

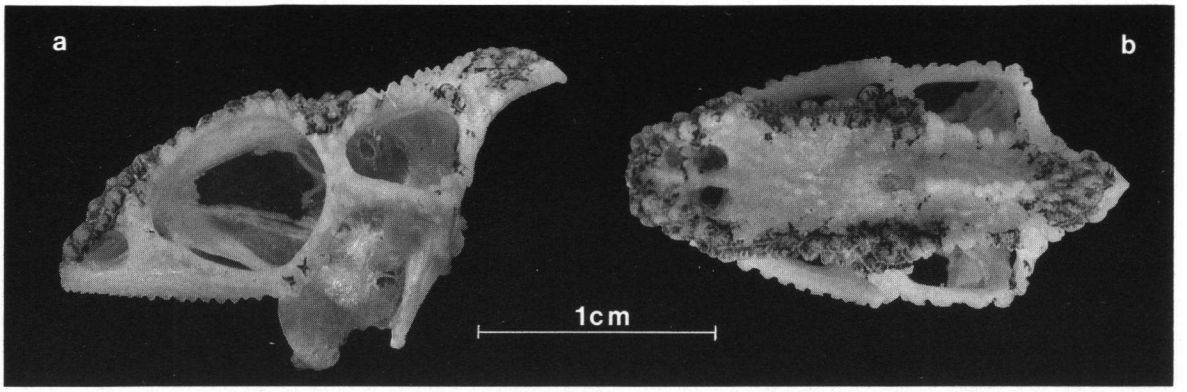

Fig. 4. *Chamaeleo pumilus*, lateral (a) and dorsal view (b) of the same skull.

1976) to regard *pumilus* c.s. as belonging to separate genera (*Microsaura*, *Bradypodion* etc.). Klaver (1981) argued that such a broad parietal would be a plesiomorphic character but I (1986) pointed out that broad and narrow parietals occur in the related families Iguanidae and Agamidae and that, moreover, *Sphenodon* Gray, 1872, the very conservative representative of the Rhynchocephalia (Romer, 1956), sister-group of the Squamata, also possesses a narrow parietal, which makes it more probable that a narrow parietal is plesiomorphic. Microcomplement fixation (Hofman et al., in press) also indicates that *Ch. pumilus* c.s. are a younger branch within *Chamaeleo* than the groups C, E and F.

The parietal of *Ch. nasutus* is trigonal, like that of *Rhampholeon*. The only difference is that the *nasutus* skull as a whole is narrower than the one of *Rhampholeon*. So all *Rhampholeon* and *Ch. nasutus* have the following characters in common:

- the trigonal form of the parietal (not occurring in other groups of *Chamaeleo*),
- the small size (*Ch. nasutus* and related species are the smallest chameleons, *Rhampholeon* is even smaller),
- the occurrence of flexible appendages on the snout in some of the species (not occurring in other groups of *Chamaeleo*),
- axillary pits in some of the species (also present in several other Madagascan species of *Chamaeleo*),
- inguinal pits in some species (not occurring in other groups of *Chamaeleo*).

The only important difference between *Rhampholeon* and *Ch. nasutus* c.s. is the deviating squamation which *Rhampholeon* has in common with *Brookesia*. *Brookesia* differs from *Ch. nasutus* in lacking the flexible appendages on the snout, although the snout of *Brookesia nasus* may be regarded as more or less similar. Axillary and inguinal pits do not occur in *Brookesia* and the form of the parietal is somewhat different from that of *Rhampholeon* and *Ch. nasutus* c.s., although it is closer to both these groups than to other species of *Chamaeleo*.

At the end of my 1986 paper I confirmed Klaver's (1979) suggestion that *Rhampholeon* is intermediate between *Chamaeleo* and *Brookesia*. The form of the skull of *Chamaeleo nasutus* adds more argument to this confirmation.

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Received: 10 April 1988