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Notes on Chameleons IV. A New Chameleon, from the Miocene of Fort Ternan, Kenya (Chamaeleonidae, Reptilia)

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ABSTRACT

A new, fossil chameleon is described, † *Chamaeleo intermedius*, found on the surface at Fort Ternan, Kenya. Most probably it eroded from a layer of fossilized lahar, close to 14 million years old. † *Chamaeleo intermedius* possesses characters which still occur in recent chameleons, in fact it combines characters of two groups of recent species which are considered to be widely apart from each other (the oviparous group around *Ch. chamaelon* - particularly *Ch. namaquensis* - and the ovoviviparous group around *Ch. bitaeniatus).*

INTRODUCTION

Fossil remains of several reptiles have been ascribed to the family Chamaeleonidae, e.g. *Palaeochamaeleo* Stefano, 1903 (Eocene, Italy), *Tinosaurus* Marsh, 1872 (Eocene North America, East Asia) and *Mimeosaurus* Gilmore, 1942 (Under Cretaceous, East Asia), but in all these cases many doubts existed about the validity of the designation.

So Gilmore (1928) wrote of a certain character in the fossil *Tinosaurus pristinus* and *T. stenodon* that it was at first considered to be peculiar to chameleons, but examination of *Calotes* Cuvier, 1815 (Agamidae) showed a similar character. In 1942 Gilmore found that his new species (and new genus) *Mimeosaurus crassus* had characters in common with *Sphenodon* and *Chamaeleo.* Considering the facts that all specimens consist of small pieces of jaw only and that the localities are so far away from the recent distribution (mainly African), we may well agree with Romer's (1956) remark on chameleons: "Fossil representatives are few, fragmentary, and doubtful in nature; most may be as well or better referred to the equally acrodont agamids."

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Therefore I felt very happy the moment Mr. R. E. F. Leakey, director of the National Museums of Kenya, showed me a fossil that undoubtedly belongs to the family Chamaeleonidae and even to the genus *Chamaeleo* Laurenti, 1768. It was found on the site that became famous by L. S. B. Leakey's discovery in 1971 of *Ramapithecus wickeri,* until now the earliest known hominid species.

In general the age of fossils found at this site is considered to be close to 14.0 million years "because they are found just above the micaceous horizon in what is, for all intents and purposes, a continuous sedimentary sequence". (Walker, 1974).

Description

The total length of the specimen is 43 mm. It consists of the complete head and foremost part of the back. The body is broken off on an almost straight line starting at the end of the throat and continuing to a point probably half way on the dorsal keel. The specimen consists probably of calcite. Mr. Walker wrote me in a letter: "The Fort Ternan environment is highly calcic, and all the fossil wood in the lahar is in the form of natural geodes and it is my impression that the chameleon was the same." The form of the body - much higher than broad - the sharply keeled back, the form of the head with the rooflike heightened helmet, the pronounced parietal crest, temporal crests, the large eyesockets, are all pointing unmistakably towards the genus *Chamaeleo.*

More arguments may be found in the slightly swollen throat, suggesting the presence of a typical chameleon tongue. Because the upperlip is partly curled up some of the teeth are shown, the frontal ones are small and tricuspid, some other ones have the form of a single cone surrounded by a little cup. This too can be found in *Chamaeleo.* At the right side a small part of the upper arm is preserved, enough to see the narrowness of it which in recent lizards only is equalled in the family Chamaeleonidae. Also all the other details - see description of the type - are typical for the genus *Chamaeleo.*

For several reasons: the state of preservation, the material of which it consists, the part of the body and the size, this fossil chameleon reminds one of the fossil *Gerrhosaurus* Wiegmann, 1828, found at Mfwanganu Island, Lake Victoria, and described by Estes (1962).

Though this *Gerrhosaurus* is older than the chameleon from Fort Ternan (in a letter Mr. Walker let me know that the age is estimated at 19.6×10^6 years), according to Estes the deviations from the recent species *G. major* are so small that it may be regarded as belonging to that species. The chameleon can, however, not be included in one of the recent species, though it clearly belongs to the genus *Chamaeleo.* All the characters that can be discerned do also occur in recent species, but in different combinations.

† **Chamaeleo intermedius** nov. spec.(Fig. 1)

Type specimen — KNM-FT 3833, Kenya National Museums, Nairobi.
Locality — Fort Ternan, found on the surface (1968).

Description — A species of *Chamaeleo* with the following characters: a fine, homogeneous squamation, casque roof-shaped, abruptly descending to the neck-region. Well developed crests on the head, formed by conic tubercles,

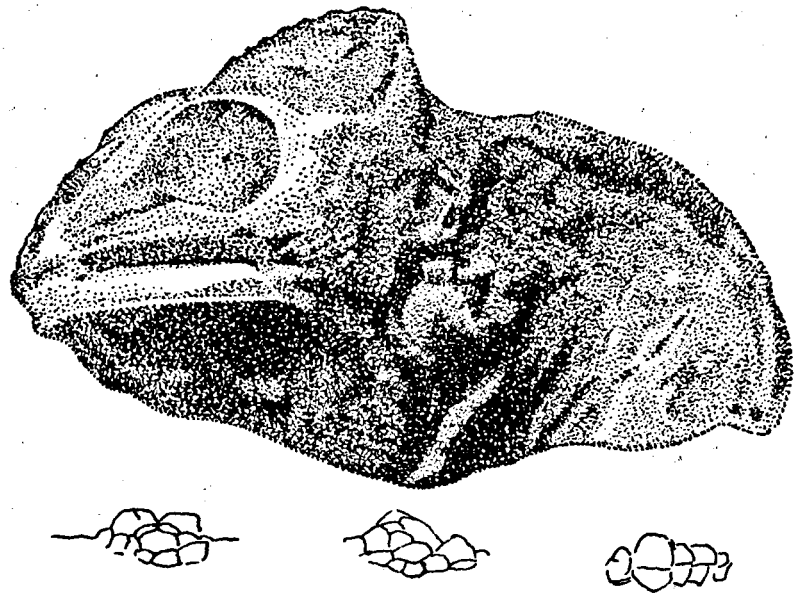

Fig. 1. The type specimen of † *Chamaeleo intermedius* nov. spec. (after a photograph, drawing by J. A. Mastro). Underneath, the enlarged (±x10) dorsal knobs, two from the side, the third from above.

an elevated parietal crest, temporal crests, canthi rostrales, the eye-socket is lined by the same conic tubercles. The parietal crest is forked. The dorsal keel is formed by a double row of scales. In the neck-region a group of larger scales can be seen, forming a structure that resembles the dorsal knobs in *Ch.namaquensis* Smith, 1831 (fig. 2) and still more - because of the paired arrangement of the scales - the dorsal knobs in some males of *Ch. wiedersheimi* Nieden, 1910 (see fig. 26 in Hillenius, 1959). Further on the back about 5 similar but smaller knobs are discernable, probably situated above the spines of the dorsal vertebrae. No gular crest, no lateral crests, no occipital lobes, no horns or other conspicuous ornaments. Length of the jaw (from the angle of the jaw to the tip of the snout) 22 mm, height of casque (from the corner of the mouth to the top of the casque) 15 mm, length of the beak (from the corner of the mouth to the tip of the snout, estimated because the corner of the mouth is slightly covered with sediment) 17—18 mm.

Comparison with recent Chameleons

As stated above all characters that can be discerned in *Chamaeleo intermedius* are known already from other species of *Chamaeleo,* however, in different combinations. This in itself is typical for members of this genus, of which almost no one is typified by a unique character, but always by different combinations of a limited number of basic characters. The combination of homogeneous squamation, elevated parietal crest, dorsal knobs and absence of gular crest also occurs in *Chamaeleo namaquensis.* But *Ch. namaquensis* differs from *Ch. intermedius* in the possession of lateral crests, absence of temporal crests, parietal crest not forked, the scales on the dorsal keel irregularly placed, not in a double row, the extraordinary broad skull and body. However, the collection of the Zoological Museum of Amsterdam contains a juvenile specimen (ZMA 15178, from Jakhalswater, Klein Namaqualand) in which the lateral crest has such a low attachment to the orbits that it resembles very much a temporal crest and moreover the dorsal keel clearly shows a double row of scales (see fig. 2d).

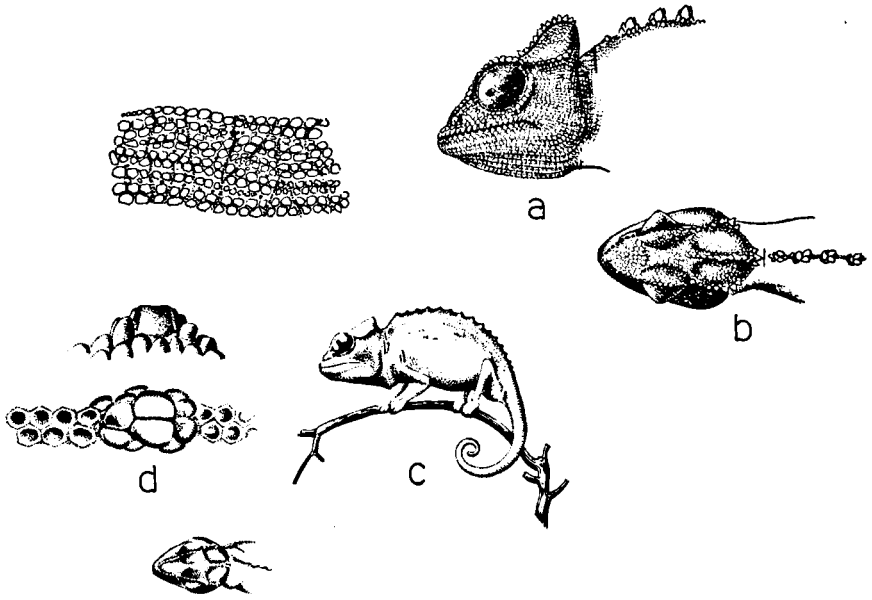

Fig. 2. *Chamaeleo namaquensis* Smith, a. adult head from the side, b. adult head from above, c juvenile specimen (ZMA 15178), d. dorsal knob from the side and from above of speci men c. (Drawing by J. A. Mastro)

Some male specimens of *Ch. wiedersheimi* also possess dorsal knobs comparable with those in *Ch. namaquensis* and *Ch. intermedius,* but there are more differences: heterogeneous squamation, flat casque, gular crest, lateral and temporal crest.

The combination of an elevated parietal crest, all crests on the head

formed by conic scales, absence of lateral crests, presence of temporal crests, the parietal crest being forked, also occurs in *Ch. bitaeniatus* Fischer, 1884 (see fig. 3). Similar headstructures also occur in other species from the group around *Ch. bitaeniatus* (*Ch. jacksoni* Boulenger, 1896, *Ch. fuelleborni* Tornier, 1899, *Ch. werneri* Tornier, 1899, etc.) as well as - but with still more pronounced cones - in *Ch. tigris* Kuhl, 1820.

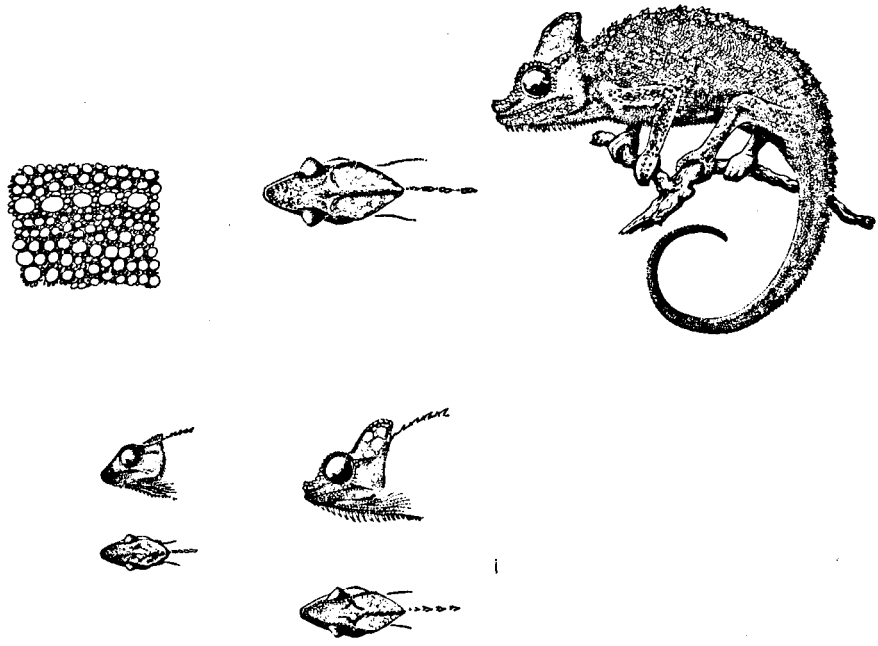

Fig. 3. *Chamaeleo bitaeniatus* Fischer (Drawing by J. A. Mastro)

Ch. bitaeniatus differs from *Ch. intermedius* in the heterogeneous squamation, the form of the dorsal crest (though some specimens also have groups of cones above the spines of the dorsal vertebrae), the gular crest.

As *Ch. namaquensis* (probably belonging to the group of species around *Ch. chamaeleon* (Linnaeus, 1758)) and *Ch. bitaeniatus* with its group of related species have to be considered widely separate from each other (Hillenius, 1959, 1963, Klaver, 1977), *Ch. intermedius* in a sense can be regarded as a missing link between the two, hence its proposed name.

In my paper of 1959 I speculated on the possibility of reconstructing the ancestral chameleon. Along two different ways I reached the conclusion that the ancestral chameleon probably resembled most the recent *Ch. chamaeleon* (Linnaeus). In 1963 further evidence was added to this suggestion (Hillenius, 1963: 214) that the group of species around *Ch. chamaeleon* is the most ancient group.

It is seldom that such hypotheses can be put to the test and although *Ch.*

intermedius certainly is not *the* ancestral chameleon it is worth while to compare it with the hypothetical ancestor proposed.

Of the characters that can be discerned on the fossil only 4 out of 11 resemble those in *Ch. chamaeleon*, but if we compare with the whole group of species around *Ch. chamaeleon* (including *Ch. namaquensis*) the only important differences are the presence of a forked parietal crest, the presence of temporal crests, the absence of lateral crests (and the latter difference seems to be less absolute if compared with the juvenile *Ch. namaquensis*). Then the only differences between *Ch. namaquensis* and *Ch. intermedius* are the deviant broad skull of the first and the forked parietal crest of the latter (see table I).

Table I Comparison of *Ch. intermedius* with some other species. + = the indicated character resembles that in *Ch. intermedius*.

	intermedius	*namaquensis*	*namaquensis juv.*	*wiedersheimi*	*bitaeniatus*	*chamaeleon*	*group around chamaeleon*
homogeneous squamation	+	+	+	—	—	+	+
double row of dorsal scales	+	—	+	+	—	—	+&—
dorsal knobs	+	+	+	±	±	—	+&—
occ. lobes absent	+	+	+	+	+	—	+&—
gular crest absent	+	+	+	—	—	±	+&—
parietal crest elevated	+	+	+	—	+	+	+&—
casque well separated from dorsal keel	+	+	+	+	+	+	+&—
lateral crest absent	+	—	+	—	+	—	—
temporal crest present	+	—	+	+	+	—	—
narrow skull	+	—	—	+	+	+	+&—
parietal crest forked	+	—	—	—	+	—	—

ACKNOWLEDGEMENTS

I am much obliged to Mr. Richard Leakey for the opportunity he gave me to describe this fossil, the first one that undoubtedly belongs to the genus *Chamaeleo*. I also take this opportunity to thank him for his great hospitality and the kindness with which he provided me with a lot of information. I am very grateful to Mr. Alan Walker for critically reading my manuscript and offering valuable suggestions.

Many thanks I owe to Dr. W. Böhme (Museum Alexander Koenig, Bonn, West-Deutschland) and Dr. M. S. Hoogmoed (Rijksmuseum voor Natuurlijke Historie, Leiden, Netherlands) for lending recent chameleons for comparison.

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