

## A new species of the *Chamaeleo dilepis* group (Sauria Chamaeleonidae) from West Africa

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We describe a new species of *Chamaeleo* Laurenti 1768 (subgenus *Chamaeleo* Laurenti 1768) related to *C. dilepis* Leach 1819, *C. quilensis* Bocage 1866 and *C. gracilis* Hallowell 1842, from two samples originating from Togo and Benin. The new species is apparently restricted to relict rain forests west of Nigeria. Besides its species level genetic divergence it is morphologically diagnosable through the following character combination: small but distinct occipital lobes, a feeble temporal crest, a markedly raised dorsal crest (supported by extended neural apophyses of the dorsal vertebrae), and — in males — the presence of four pairs of sulcal rotulae on the hemipenis.

KEY WORDS: Reptilia, Sauria, Chamaeleonidae, *Chamaeleo necasi* n. sp., taxonomy, West Africa, Togo, Benin.

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### INTRODUCTION

In tropical West Africa, meant here as the area west of the volcanic ridge separating western and eastern Cameroon, three species of the subgenus *Chamaeleo* Laurenti 1768 (sensu KLAVER & BÖHME 1986, 1997) are known with certainty, viz. *C. gracilis*

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Hallowell 1842, *C. quilensis* Bocage 1866, and *C. senegalensis* Daudin 1802 (KLAVER & BÖHME 1997, NEČAS 1999). A fourth species, the widespread tropical African flap-necked chameleon (*C. dilepis* Leach 1819), is sometimes cited from Cameroon and even Nigeria (see NEČAS 1999), but following the compilation of documented, published country records of the nominotypic form (see KLAVER & BÖHME 1997: 33), the northwestern-most places for this species are in Gabon and Equatorial Guinea. *C. dilepis* must therefore be regarded as lacking not only in Cameroon but all over West Africa.

A similar situation seems to concern *C. quilensis*, a small-lobed chameleon recorded also for Gabon and Equatorial Guinea (and southern Cameroon) but having its main distribution range in Angola, central, eastern and southern Africa (KLAVER & BÖHME 1997: 36). However, the syntypes of *C. parvilobus* Boulenger 1887, currently considered to be synonymous with *C. quilensis* (see KLAVER & BÖHME 1997), have locality data ranging from “Natal” to “Cameroon”: BOULENGER 1887, therefore we re-examined Boulenger’s syntype series.

The last species to be mentioned here is *C. laevigatus* Gray 1863, a lobeless species like *C. senegalensis*. It is known only from central and eastern Africa, and its close relative *C. anchietae* Bocage 1872 is restricted to central and southwestern Africa (KLAVER & BÖHME 1997), thus also lacking in West Africa.

Therefore, west African records of *C. dilepis* and *C. quilensis* (see DE WITTE 1965, DUNGER 1967) had to be viewed with scepticism. However, in 1982 a female small-lobed chameleon was found in a relict forest near Kpalimé, Togo, by Rolf Leptien and deposited in the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn. It had occipital lobes markedly more distinct than the tiny occipital skin folds typical of *C. gracilis*, but smaller than those in typical *C. dilepis* from the nearest geographical area, i.e. Gabon. The occipital flaps corresponded best with those of *C. quilensis*, but a relatively high dorsal crest made it unique with respect to the three species mentioned, so that a new taxon was suspected even then. NEČAS (1995: fig. 88, 1999: fig. 119) was the first to publish Rolf Leptien’s colour photo of the living female and termed it “*Chamaeleo* n. sp.”. However, due to the difficulty in assessing the subtle variation in external characters in a single female, a formal description was postponed pending the availability of more specimens, in particular males. Indeed, male would offer the possibility to study the hemipenial characteristics, which in this group are usually more reliable than external morphology for detecting systematic relationships (KLAVER & BÖHME 1986, ZIEGLER & BÖHME 1997: fig. 114).

In the following years additional specimens of this chameleon were imported from Togo through the international pet trade, therefore they lacked precise locality data. Two more females reached ZFMK in 1984, but Petr NEČAS was also able to secure, another two females, as well as the first two known males of this chameleon, which enabled us to study the hemipenial characters. Moreover, the senior author, during a herpetological survey of southern Benin (ULLENBRUCH 2003), discovered one male and two females of the same chameleon taxon in a relict forest area, so that we now consider our material sufficient for a formal description.

## METHODS USED

### *Morphology*

For the morphological analysis, the following abbreviations have been used: FS — flank scales; SVL — Snout-vent length, TL — Tail length; HL — Head length; LOF — Length of occipital flap, WOF — Width of occipital flap.

Institutional acronyms are:

BMNH — The Natural History Museum, London; CAS — California Academy of Sciences, Los Angeles; MNHN — Muséum National d'Histoire Naturelle, Paris; MRAC — Musée Royal de l'Afrique Centrale, Tervuren; ZMB — Museum für Naturkunde, Humboldt Universität, Berlin, Germany; ZFMK — Zoologisches Forschungsinstitut und Museum A. Koenig, Bonn, Germany.

The alcohol-fixed material was measured with a dial calliper to the nearest mm. Hemipenes were everted in two freshly dead males and described according to the terminology of KLAVER & BÖHME (1986). For skeletal comparisons showing the different heights of the neural spines of the dorsal vertebrae, specimens were x-rayed at ZFMK with a 43805N X-Ray System, Faxitron Series, Hewlett Packard.

### *Molecular genetics*

#### *Taxon sampling and laboratory methods*

For DNA analysis tissue samples (muscle or liver, fresh or preserved in 98% ethanol) were available from the species listed in the appendix. DNA was extracted using a modified Chelex-protocol (WALSH et al. 1991). Fragments of two mitochondrial genes (16S and 12S rRNA genes) were chosen for phylogenetic analysis. To amplify a section of the 12S gene, primers 12SA-L (light chain 5' — AAA CTG GGA TTA GAT ACC CCA CTA T — 3') and 12SB-H (heavy chain 5' — GAG GGT GAC GGG CGG TGT GT — 3') of KOCHER et al. (1989) were used. For amplification of a section of the 16S gene, the following primers were used: 16SCham1L (light chain 5' — TAA CGC CTG CCC TGT GGA A — 3') and 16SCham1H (heavy chain 5' — ATC ATA AGA TAG AAA CCG ACC TGG A — 3'). These primers were designed during this study using the computer-program Laser-Gene (DNASStar). The cycling protocols for the two primer pairs are as follows:

- 16S: Initial denaturation step: 90 sec at 94 °C; 36 cycles: denaturation 45 sec at 94 °C, primer annealing for 45 sec at 55 °C, extension for 45 sec at 72 °C.
- 12S: Initial denaturation step: 90 sec at 94 °C; 35 cycles: denaturation 45 sec at 94 °C, primer annealing for 45 sec at 50 °C, extension for 60 sec at 74 °C.

PCR products were purified using Qiaquick purification kits (Qiagen) and a single strand of the respective gene-fragment was sequenced with an automated sequencer. Only unambiguous parts of the sequence were retained for phylogenetic analyses, while difficult to read (starting and ending) parts of the sequences were discarded. The obtained sequences (lengths referring to the aligned sequences including gaps) comprised 475 bp (16S) and 370 bp (12S). Sequences were submitted to GenBank (Accession numbers AY927239-AY927276, Table 2).

#### *Phylogenetic analyses*

Before carrying out the phylogenetic analyses, we edited the sequences manually and aligned them with the computer program ClustalX (THOMPSON et al. 1997) using the default parameters. The alignment was subsequently checked for misalignments using BioEdit (HALL 1999): we omitted 2 short sections (together 9 bp) from the original 16S+12S data set which were too variable to be reliably aligned. Prior to phylogenetic analyses, a partition homogeneity test was run as implemented in PAUP\*4.0b10 (SWOFFORD 2002). Since the test indicated no conflicting phylogenetic signals between the 16S and 12S data sets, the combined data set was analysed. A dwarf chameleon (*Rhampholeon kerstenii*) was chosen as outgroup-species. Maximum parsimony and Bayesian reconstructions (HUELSENBECK et al. 2001) were also performed.

### *Maximum parsimony*

An unweighted maximum parsimony (MP) analysis using an heuristic search was performed on the combined DNA sequence data set using PAUP\*4.0b10 (SWOFFORD 2002). All alignment gaps were treated as a fifth character, characters were unordered and TBR branch swapping with random addition of taxa (100 replicates) was in effect. When more than a single most parsimonious tree was found, a strict consensus tree was generated. Confidence in the nodes was assessed by 2000 bootstrap pseudoreplicates (FELSENSTEIN 1985) with random addition of taxa. Only bootstrap supports of 70% and higher were considered reliable, as such values were found to indicate 95% probability of correct topology (HILLIS & BULL 1993). A dwarf chameleon of the genus *Rhampholeon* Günther 1874 (*R. kerstenii* Peters 1868) was used as outgroup.

### *Bayesian inference*

All Bayesian analyses were performed with MRBAYES, version 3.0b3 (HUELSENBECK et al. 2001), which approximates the posterior probabilities of trees. To select the best-fit model of nucleotide substitution for our data set, the hierarchical likelihood-ratio test was carried out using MRMODELTEST 1.1b (NYLANDER 2002). Besides the specific parameters calculated by MRMODELTEST (a GTR model of evolution was used for this analysis), the default settings of MRBAYES were used. We ran two MCMC analyses for  $10^6$  generations each. The topologies of the sampled trees were used to generate a strict-consensus tree, with the percentage of samples recovering any particular clade representing that clade's posterior probability (HUELSENBECK et al. 2001). Unlike the conventional bootstrap methodology the posterior probabilities of a Bayesian analysis can sometimes overestimate the true support for a given clade (HUELSENBECK et al. 2001, SUZUKI et al. 2002). Consequently, we consider probabilities of 95% or greater to be significantly supported.

## RESULTS

The new chameleon described below is compared with the species of the subgenus *Chamaeleo* that have a flat casque and bear occipital flaps or traces of such flaps, i.e. with the *C. dilepis* species group. This group comprises *C. dilepis*, *C. gracilis*, and *C. quilensis*. The latter species is lacking in the genetic analysis, as no suitable tissue sample was available. *C. dilepis* is currently subdivided into seven subspecies (*dilepis*, *idjwiensis*, *isabellinus*, *martensi*, *petersii*, *roperi* and *ruspolii*). Their geographical ranges are described in KLAVER & BÖHME (1997) who stress the urgent need of a revision of this entire complex and who suspect that some of the nominal subspecies may be invalid whereas others may even represent distinct species (e.g. *roperi*). Therefore we compare the new species with the three full species mentioned above and — within the *C. dilepis* species complex — with the wide-ranging nominotypic form and the presumed full species *roperi*.

### *Molecular genetics*

#### *Sequence variation*

Of the 836 sites examined, 91 were parsimony informative. For the combined 16S+12S data set, the inter-clade sequence differentiation was 2.5-4.7% between *C. dil-*

Table 1.

Summary of the uncorrected p-distances between taxa based on sequence differentiation of a 836 bp fragment of the combined mitochondrial 12S and 16S rRNA genes (gaps treated as fifth base).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
1 <i>Chamaeleo roperi</i> Mt. Kwaraha 3	—											
2 <i>Chamaeleo roperi</i> Mt. Kwaraha 4	0.00120	—										
3 <i>Chamaeleo roperi</i> Mt. Kwaraha 1	0.00120	0.00240	—									
4 <i>Chamaeleo roperi</i> Mt. Kwaraha 2	0.00120	0.00240	0.00000	—								
5 <i>Chamaeleo roperi</i> Mt. Hanang 4	0.00240	0.00360	0.00360	0.00360	—							
6 <i>Chamaeleo roperi</i> Mt. Hanang 5	0.00240	0.00360	0.00360	0.00360	0.00000	—						
7 <i>Chamaeleo roperi</i> Mt. Hanang 3	0.00120	0.00240	0.00240	0.00240	0.00120	0.00120	—					
8 <i>Chamaeleo roperi</i> Mt. Hanang 1	0.00120	0.00240	0.00240	0.00240	0.00120	0.00120	0.00000	—				
9 <i>Chamaeleo roperi</i> Mt. Hanang 2	0.00120	0.00240	0.00240	0.00240	0.00120	0.00120	0.00000	0.00000	—			
10 <i>Chamaeleo dilepis</i> Tanga/TZ	0.04582	0.04701	0.04704	0.04704	0.04581	0.04581	0.04462	0.04462	0.04462	—		
11 <i>Chamaeleo dilepis</i> Mt. Kenya	0.03371	0.03491	0.03252	0.03252	0.03371	0.03371	0.03251	0.03251	0.03251	0.03470	—	
12 <i>Chamaeleo dilepis</i> Lindi	0.03034	0.03153	0.02915	0.02915	0.03032	0.03032	0.02912	0.02912	0.02912	0.03988	0.02885	—
13 <i>Chamaeleo dilepis</i> Gabun	0.03400	0.03520	0.03524	0.03524	0.03644	0.03644	0.03524	0.03524	0.03524	0.04351	0.03011	0.02649
14 <i>Chamaeleo dilepis</i> Mbeya	0.02881	0.03001	0.02763	0.02763	0.02882	0.02882	0.02762	0.02762	0.02762	0.03740	0.02763	0.01332
15 <i>Chamaeleo dilepis</i> Matema	0.02641	0.02761	0.02522	0.02522	0.02643	0.02643	0.02523	0.02523	0.02523	0.03738	0.02523	0.01453
16 <i>Chamaeleo gracilis</i> Nandi Forest	0.06504	0.06624	0.06387	0.06387	0.06511	0.06511	0.06390	0.06390	0.06390	0.07704	0.06979	0.06539
17 <i>Chamaeleo gracilis</i> Benin	0.06217	0.06336	0.06221	0.06221	0.06217	0.06217	0.06096	0.06096	0.06096	0.07768	0.06420	0.06188
18 <i>Chamaeleo necasi</i> Togo	0.07241	0.07363	0.07245	0.07245	0.07246	0.07246	0.07124	0.07124	0.07124	0.08700	0.08550	0.08065
19 <i>Rhampholeon kerstenii</i> Tanzania	0.12721	0.12842	0.12735	0.12735	0.12973	0.12973	0.12851	0.12851	0.12851	0.13867	0.12977	0.12541
Species	13	14	15	16	17	18	19					
13 <i>Chamaeleo dilepis</i> Gabun	—											
14 <i>Chamaeleo dilepis</i> Mbeya	0.02308	—										
15 <i>Chamaeleo dilepis</i> Matema	0.02426	0.00959	—									
16 <i>Chamaeleo gracilis</i> Nandi Forest	0.07038	0.06154	0.05792	—								
17 <i>Chamaeleo gracilis</i> Benin	0.06436	0.05975	0.05729	0.03168	—							
18 <i>Chamaeleo necasi</i> Togo	0.08329	0.07983	0.07612	0.06854	0.06970	—						
19 <i>Rhampholeon kerstenii</i> Tanzania	0.13306	0.12854	0.12714	0.12352	0.12427	0.14536	—					

*epis* and *C. roperi* and 5.7-7.7% between the taxa of the *C. dilepis* species group (containing both *C. dilepis* and *C. roperi*) and the specimens of *C. gracilis*. The sequence differentiation was 7.1-8.5% between *C. necasi* n. sp. and the *C. dilepis* species group and 6.8% between *C. necasi* n. sp. and *C. gracilis*. Intraspecific differentiation was 0.1-0.24% within the *C. roperi* clade and 3.4-4.3% within the *C. dilepis* clade (Table 1).

### *Phylogenetic analyses*

In the MP analysis, nine equally most-parsimonious trees with a length of 194 steps were found. A relatively low amount of homoplasy (CI = 0.644, RI = 0.7356, rescaled CI = 4740) could be observed in the data set (FARRIS 1996). Both the MP and Bayesian approaches produced similar topologies. Alternative topologies only represent branch swapping among nodes not supported by bootstrap or Bayesian posterior probabilities. Fig. 1 shows the Bayesian tree with the posterior probabilities (PP) above the nodes and the MP bootstrap values (BS) below the nodes.

Three major clades are evident. All members of the *C. dilepis* species group cluster together in a well supported clade in both the MP and Bayesian trees (BS:90; PP:100). This clade is divided into a monophyletic subclade with all sampled specimens of *C. roperi* and into a second also monophyletic group including all specimens of *C. dilepis*. The sister group relationship of the *C. dilepis* group and *C. roperi* receives very high statistical support. A third, only weakly supported clade (BS:58; PP:53) includes the two specimens of *C. gracilis* and *C. necasi* n. sp.

### *Morphological diagnosis and discussion of the new species*

The new species is described as:

#### ***Chamaeleo necasi* n. sp.**

*Diagnosis.* A stoutly built, flap-necked chameleon belonging to the *C. dilepis* group within the subgenus *Chamaeleo* which is distinguished from *C. dilepis* by (1)

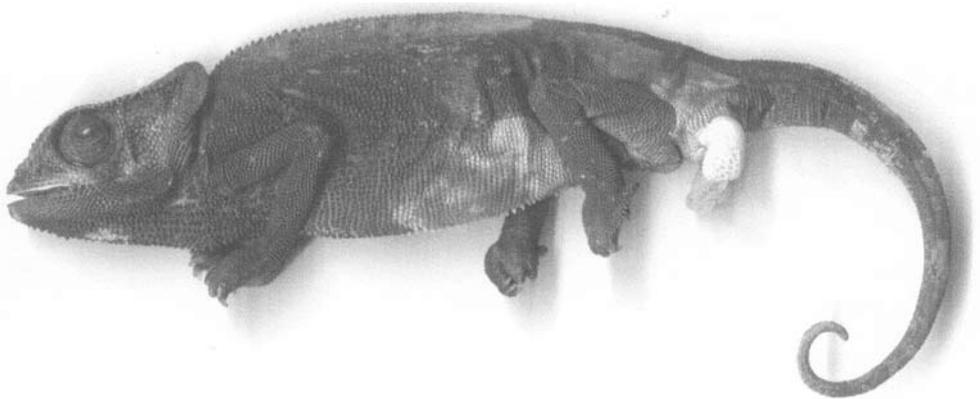


Fig. 1. — Lateral view of the holotype of *Chamaeleo necasi* n. sp., ZFMK 76922 (photo by P. Nečas).

the much smaller occipital flaps, (2) a weakly raised parietal crest forming a distinct (though flat) helmet, (3) the highly elevated dorsal crest which is supported by elongated neural spines of the dorsal vertebrae, (4) a weakly expressed, merely indicated temporal ridge, (5) the possession of four (instead of three) fully differentiated sulcal rotulae on the hemipenis, and (6) much smaller calyces on the trunk of this organ. In contrast, *C. gracilis* has only rudimentary skin folds in the occiput, a much flatter head and a much lower dorsal ridge. *C. quilensis* is comparable in lobe size, but has a less raised parietal crest, a much lower dorsal ridge, a different shape of hemipenis, and marked sexual dimorphism in size, the females growing considerably larger than males. This is true — and even more pronounced — for *C. roperi*, whose occipital flaps are separated by a gap in the nape, (they are in contact in *C. dilepis* and in *necasi* n. sp.). Moreover, *C. roperi* has only two differentiated hemipenial sulcal rotulae, versus three in *C. dilepis* and four in *necasi* n. sp.

*Holotype.* ZFMK 76922, adult male, Togo, West Africa, no specific locality data, native collector, without known collecting date (Figs 1-2).

Body shape slender, laterally strongly compressed. Tail shorter than head and body. Tail base swollen with well developed hemipenial pockets. Hind feet with well developed tarsal spurs. Snout less blunt than in e.g. *C. quilensis*. Distance from

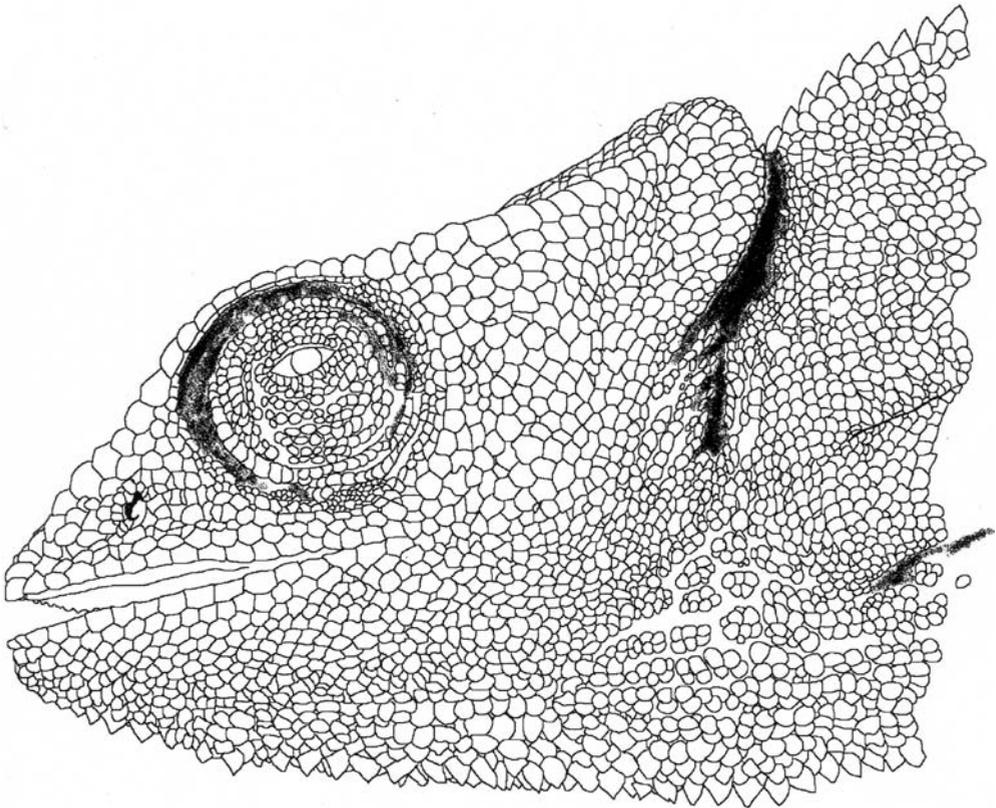


Fig. 2. — Lateral view of the head of the holotype of *C. necasi* n. sp. (drawing by P. Nečas).

mouth angle to tip of helmet ca 1/3 longer than the length of mouth. Canthus parietalis indistinct. Helmet flat, hardly exceeding the dorsal crest, with distinct occipital flaps separated at their basis on the helmet's tip which is, however, a bit pointed (Figs 2-3). Body scalation homogenous, on the lower flanks arranged in roundish or oval-shaped groups. Midline of dorsum, throat and belly with a series of enlarged scales forming low, slightly serrated crests. The dorsal crest is elevated because of elongated neurapophyses of the dorsal vertebrae (Fig. 3).

Colouration (in alcohol, after several years of preservation): light to dark blue-grey. Crests of the same colour, except the tips of the ventral crest which are whitish. SVL 120.5 mm, TL 112 mm, HL (from tip of snout to the end of the parietal crest) 28.5 mm, LOF 14.5 mm, WOF 9.3 mm. Distance mouth angle-tip of helmet 28.5 mm, length of mouth gap 20.9 mm, number of flank scales (between dorsal and ventral crests) 59.

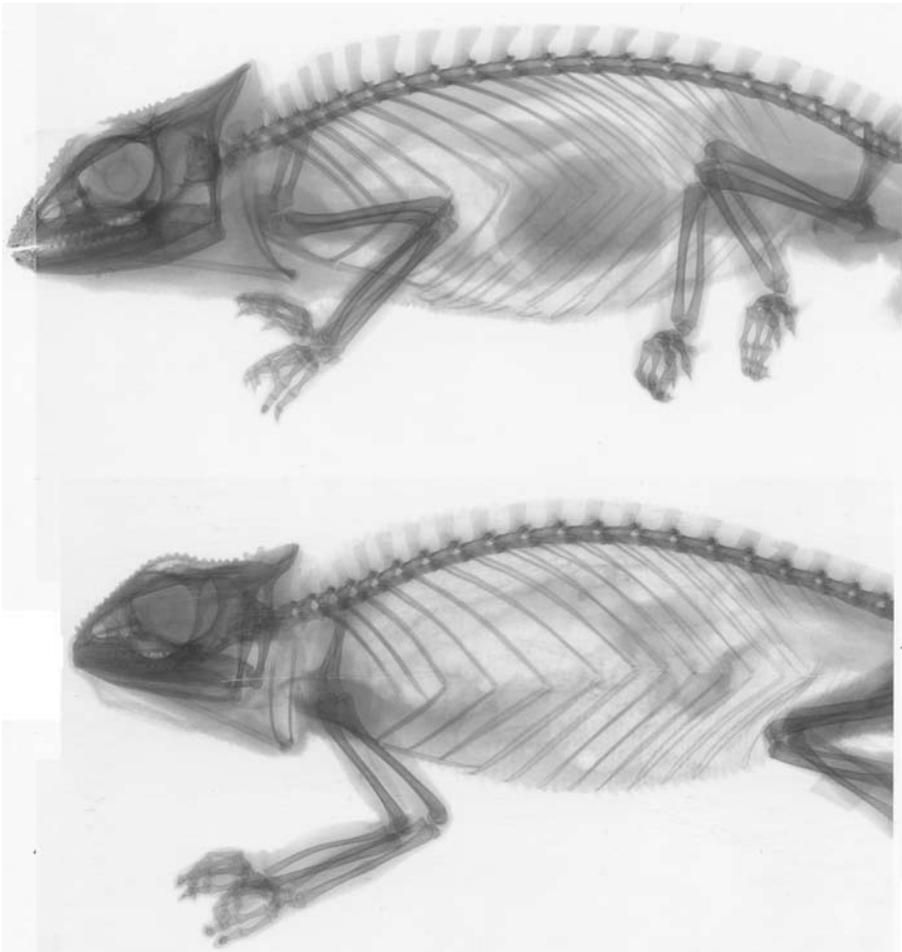


Fig. 3. — X-ray of the holotype of *C. necasi* n. sp. (above) and of *C. dilepis* from Lambaréné, Gabon (below; ZFMK 66613), to show the different height of the neurapophyses of the anterior dorsal vertebrae (photo by K. Busse).

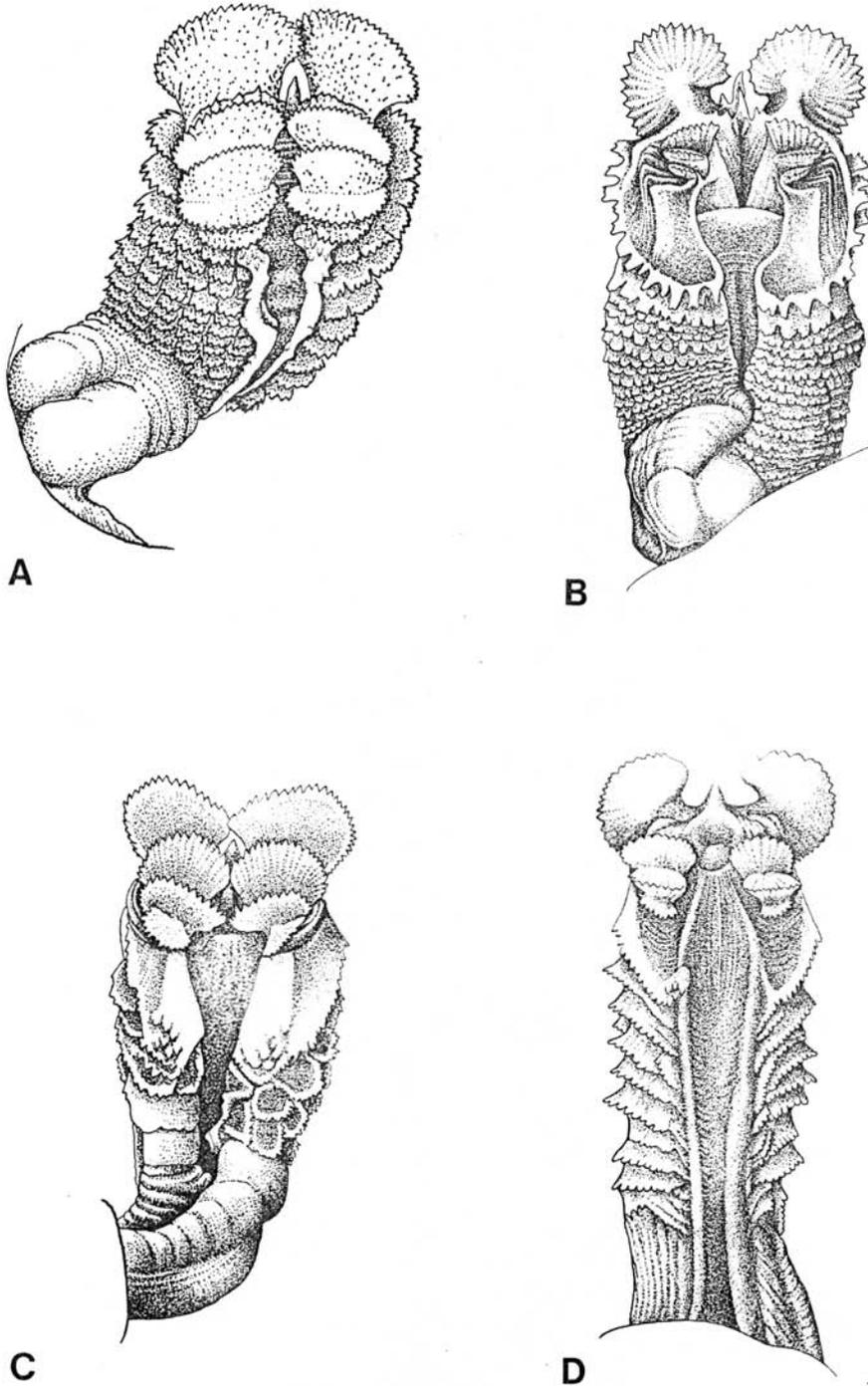


Fig. 4. — Hemipenes in sulcal view of A: *C. necasi* (ZFMK 76922, holotype); B: *C. quilensis* (UM 25287); C: *C. dilepis* (ZFMK 18895, see KLAVER & BÖHME 1986); D: *C. gracilis* (ZFMK 8841) (drawings by W. Hartwig).

Hemipenis (Fig. 4A): Stoutly built, with dense calyculate ornamentation on the distal two thirds of the organ. The calyces have extended, serrated margins hiding the original calyculate “honeycomb” pattern (see KLAVER & BÖHME 1986), and they decrease in size towards the organ’s pedicel. There are two asulcal rotulae, and two groups of four well differentiated sulcal rotulae which also become smaller towards the pedicel. Sulcal lips distinct, apically equipped with several small papillae.

*Paratypes.* Togo: ZFMK 41092, female from Kpalimé, coll. R. Leptien, 1982; ZFMK 41709, female, ZFMK 73608, male, and ZFMK 73609-610, females from “Togo”, without specific locality data, native collector, no date; MRAC 27085, “Yoh, entre Palamé et Messaboué”, coll. Y. Duc, May 1963; Benin: ZFMK 77058, male, Za-Kpota, coll. K. Ullenbruch, May/June 2002, ZFMK 77059-77060, 2 females, Houé-gbo, coll. K. Ullenbruch, May/June 2002.

The paratypes generally resemble the holotype, except for the lack of tarsal spurs in the females. For measurements, see Table 2. The females seem to grow larger than the males, but sample size is still much too small to corroborate this tendency.

Table 2.

Morphometrics of the type series of *C. necasi* n. sp.

Species	Locality	Collection number	Accession number	
<i>Chamaeleo roperi</i>	Mt. Kwaraha 3	ZFMK 82304	AY927258	AY927239
<i>Chamaeleo roperi</i>	Mt. Kwaraha 4	voucher not collected	AY927259	AY927240
<i>Chamaeleo roperi</i>	Mt. Kwaraha 1	ZFMK 82305	AY927260	AY927241
<i>Chamaeleo roperi</i>	Mt. Kwaraha 2	voucher not collected	AY927261	AY927242
<i>Chamaeleo roperi</i>	Mt. Hanang 4	voucher not collected	AY927262	AY927243
<i>Chamaeleo roperi</i>	Mt. Hanang 5	ZFMK 82361	AY927263	AY927244
<i>Chamaeleo roperi</i>	Mt. Hanang 3	voucher not collected	AY927264	AY927245
<i>Chamaeleo roperi</i>	Mt. Hanang 1	ZFMK 82362	AY927265	AY927246
<i>Chamaeleo roperi</i>	Mt. Hanang 2	ZFMK 82363	AY927266	AY927247
<i>Chamaeleo dilepis</i>	Tanga/TZ	CAS 168922	AY927267	AY927248
<i>Chamaeleo dilepis</i>	Mt. Kenya	ZFMK 68459	AY927268	AY927249
<i>Chamaeleo dilepis</i>	Lindi	ZFMK 44875	AY927269	AY927250
<i>Chamaeleo dilepis</i>	Gabun	ZFMK 73110	AY927270	AY927251
<i>Chamaeleo dilepis</i>	Mbeya	ZFMK 77319	AY927271	AY927252
<i>Chamaeleo dilepis</i>	Matema	ZFMK 77355	AY927272	AY927253
<i>Chamaeleo gracilis</i>	Nandi Forest	ZFMK 82055	AY927273	AY927254
<i>Chamaeleo gracilis</i>	Benin	ZFMK 77056	AY927274	AY927255
<i>Chamaeleo necasi</i>	Togo	ZFMK 41082	AY927275	AY927256
<i>Rhampholeon kerstenii</i>	Tanzania	ZFMK 82301	AY927276	AY927257



Figs 5-8. — Fig. 5: Living female paratype of *C. necasi* n. sp. (ZFMK 41092) from Kpalimé, Togo, stress colouration (photo by R. Leptien); Fig. 6: Living male paratype of *C. necasi* n. sp. (ZFMK 77058) from Za-Kpota, Benin (photo by K. Ullenbruch); Fig. 7: Living female paratype of *C. necasi* n. sp. (ZFMK 77059) from Houégbo, Benin (photo by K. Ullenbruch); Fig. 8: Living female paratype of *C. necasi* n. sp. (ZFMK 77060) from Houégbo, Benin (photo by K. Ullenbruch).

The colouration in life of this species was shown by NEČAS (1995: fig. 88; 1999: fig. 119; 2004: fig. 153) using a photograph of the Kpalimé specimen taken by R. Leptien. Fig. 5 shows this female (paratype 41092) in stress colouration: yellowish-greenish with numerous small black dots. The interstitial skin in the throat area was described as yellowish orange (R. LEPTIEN in litt., 27 September 1982). All three specimens from Benin were uniformly light to dark green (Figs 6-8). Female 77059 from Houégbo, Benin, showed a larger white fleck above shoulder and a broad white ventrolateral band in a greenish groundcolour (Fig. 7), whereas female 77060 (also from Houégbo) exhibited a large reddish-brown patch in the neck region (Fig. 8). The interstitial throat skin was yellow to orange in all three Benin specimens.

*Distribution and habitat.* *Chamaeleo necasi* n. sp. is currently known only from Togo and Benin in West Africa. The two respective parts of its range (Kpalimé and Yoh in Togo as well as Houégbo and Za-Kpota in Benin) are both relict forest areas within the arid Dahomey gap. The Kpalimé area in Togo is close to the easternmost margin of the West African rain forest that stretches from Ghana westwards to Sierra Leone. The locality of the MRAC paratype (“entre Palamé et Messaboué”: DE WITTE 1965) is also transcribed as Palimé and Missaboué, which refers to Kpalimé and the former German name Misahoehe (see Fig. 9). Za-Kpota, Benin, is situated in an agriculturally shaped landscape, but the neighbouring river Zou has degraded

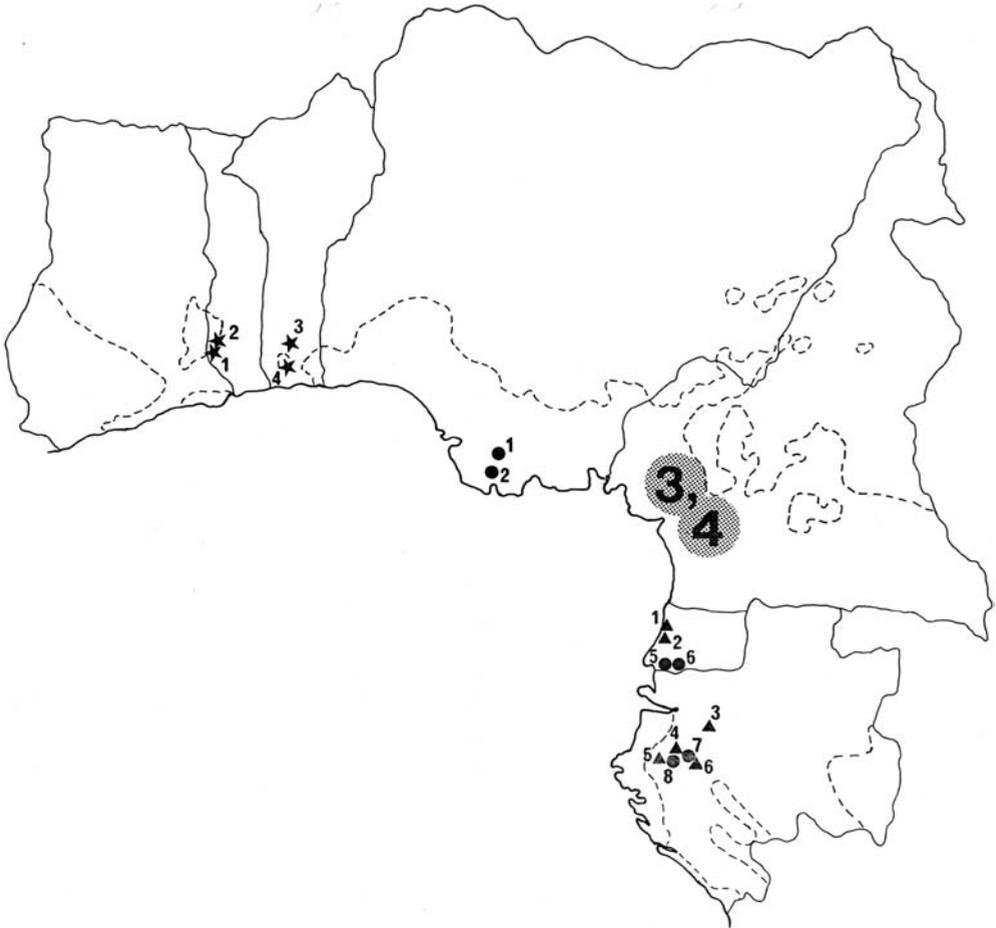


Fig. 9. — Distribution map of *C. necasi* n. sp. (stars), also showing neighbouring localities of *C. quilensis* (dots and shadowed circles) and of *C. dilepis* (triangles). References or vouchers are in parentheses. Dashed line shows limit of rain forest.

*C. necasi* n. sp.: 1 — NW Kpalimé, Togo (ZFMK 41092), 2 — Yoh, between Palimé and Missaboué, Togo (MRAC 27085); 3 — Za-Kpota, Benin (ZFMK 77058); 4 — Houégbo, Benin (ZFMK 77059-060).

*C. quilensis*: 1 — about 150 miles up to the Niger river, Nigeria (BMNH 22, 3.V.1895); 2 — Mouth of the Niger river, Nigeria (BMNH 1, 30.VII.1894); 3 and 4 — “Cameroon”: no specific locality (BMNH 3,8.III.1876 and MCZ 6284); 5 — river N of Rio Muni, San Benito, Equat. Guinea (MNHN 85-458, 85-459); 6 — Rio Muni, Benito, Equat. Guinea (AMNH 16.928-16.929, 1920); 7 — 50 km SE of Lambaréné, Gaboon (MNHN 01-518, 01-519, 1901); 8 — Valley of the river Ogoué, Lambaréné, Gaboon (MNHN 96-487).

*C. dilepis dilepis*: 1 — Bata, Equat. Guinea (MNHN 92-3); 2 — Benito river, Equat. Guinea (BMNH 10, 17.II.1900); 3 — N’Djola, Gaboon (MNHN 92-4); 4 — Lambaréné, Gaboon (ZFMK 73110); 5 — 50 km SW of Lambaréné, Gaboon (MNHN 01-517, 01-519); 6 — km 50, road from Lambaréné to Fougamou, Gaboon (ZFMK 74519) (drawing by U. Bott).

through dense gallery forests which serve as the main hunting grounds for the local human population. Houégbo in southern Benin lies in the immediate vicinity of the Forêt de Lama which is one of the last remnants of the forest-savanna mosaic

between the West African (Upper Guinean) and Central African (Lower Guinean or Congolian) rain forest. According to ADJANOHOON (1989), Forêt de Lama consists of semi-deciduous humid forest (AKOEGNINOU 1984).

It may be interesting to note that the local hunters in Benin (including those collecting chameleons) consider this species to be identical with *C. gracilis*, for which they also use the same local name.

It is possible that specimens of "*Chamaeleo gracilis*" with small occipital flaps mentioned by DUNGER (1967) from forests around Lagos might refer to *C. necasi* n. sp. as well, and also his presumed record of "*C. dilepis*" from Ghana may be viewed in this respect, the more so as the Togolese locality Kpalimé is situated near the Ghanaian border. However, the former could also be representatives of *C. quilenensis* because this taxon is listed for the Niger delta area by DE WITTE (1965). On the other hand, MRAC 27085 from Yoh near Kpalimé in Togo was also listed as "*C. quilenensis*" in DE WITTE (1965) although it is clearly a representative of *C. necasi*. Hence, much further study is needed to work out the distribution of these two related chameleons in West Africa. It may be noted here that DE WITTE (1965) listed MNHN 01-519 (from Lambaréné, Gabon) twice: once as *C. dilepis*, and once as *C. quilenensis* (Fig. 9).

#### *Systematic relationships*

The observed sequence differences (6.9-8.7%) of *C. necasi* n. sp. with respect to the *dilepis* species group (*C. roperi* and *C. dilepis*) and *C. gracilis* were clearly above the values found at intraspecific levels, thus clearly separating *C. necasi* n. sp. from all other included species (Table 1). The sister relationship of *C. necasi* n. sp. to *C. gracilis* does not receive sufficiently high bootstrap support and the topology of the tree does not allow any statements about the position of *C. necasi* n. sp. with respect to the members of the *dilepis* species group. The exact phylogenetic position of *C. necasi* n. sp. still needs to be analysed based on broader regional sampling with a wider range of taxa and additional mitochondrial and nuclear gene-regions. Sequence variation between populations of *C. gracilis* from east and west Africa (3.2%) indicates differentiation at least at the subspecies level. Within the *C. dilepis* species group, only *C. roperi* can be regarded as a valid and homogenous species with very low internal genetic variation. In contrast, *C. dilepis* as currently recognized is a highly variable species complex including two distinguishable groups: specimens from inland southern Tanzania and the coast (Lindi, Mbeya, Matema) with relatively small genetic distances (1.3-1.4%) cluster together, while a more variable group including specimens from Mt. Kenya, NE Tanzania and Gabon forms the rest of the clade (3.0-4.3%). Since we only included a limited number of specimens and a relatively small genetic database (836 bp) was available for phylogenetic analyses, it is not surprising that we did not get better resolution in the difficult and closely related *C. dilepis* species group. Clear by many more specimens and further genetic data are required to clarify the taxonomic situation of the members of this group. This will be the subject of further studies.

Moreover because *C. quilenensis* could not be included in the genetic analysis, the results must be regarded as preliminary. However, the much blunter head, flatter helmet and much more expressed sexual dimorphism in size of the latter clearly exclude taxonomic identity with *C. necasi* n. sp. In addition, we were able to include *C. quilenensis* in the comparison of hemipenial characters (Fig. 4B). Its hemipenis

resembles that of *C. necasi* n. sp., but has more semicircular-shaped and relatively smaller asulcal rotulae, much smaller sulcal rotulae grouped in two series of only

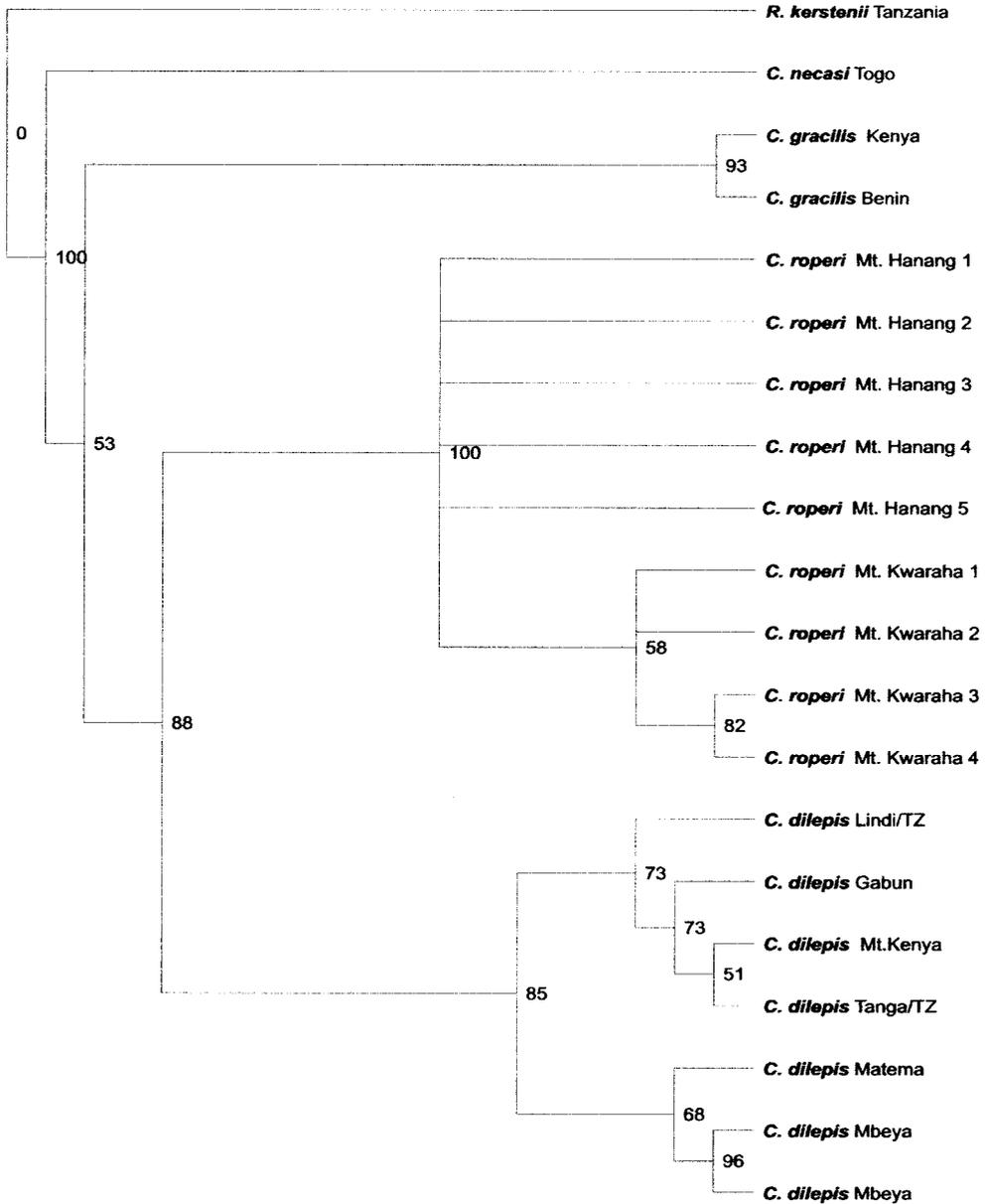


Fig. 10. — Phylogenetic tree of the taxa studied, produced by the Bayesian inference using MRBAYES 3.0b3 and based on a combined fragment of the mitochondrial 12S and 16S rRNA genes with 836 bp. Parsimony bootstrap values are given above the nodes and Bayesian posterior probabilities are given below each node. Nodes with less than 50% bootstrap support and less than 90% posterior probabilities are not labelled.

three elements each, and also smaller calyces forming much more numerous series between apex and pedicel. *C. dilepis*, in contrast, has rather large and shallow calyces which despite their serrated margins still form a “honeycomb” structure. The large asulcal rotulae form a common series with the slightly decreasing three sulcal rotulae on each side of the organ (Fig. 4C). *C. gracilis* has the most slender hemipenis with two large sickle-shaped asulcal rotulae, with two series of three small sulcal rotulae at the apical end of the sperm groove (Fig. 4D).

If smaller numbers of rotulae are considered plesiomorphic (KLAVER & BÖHME 1986), *C. necasi* n. sp. seems to be the most derived species among the group under consideration. In regard to the magnification of the calyces, however, *C. dilepis* seems most derived, whereas *C. necasi* shows an intermediate pattern between *dilepis* on the one side and *C. quilensis* and *C. gracilis* on the other.

A unique feature of *C. necasi* within the *C. dilepis* species group is certainly the raised dorsal crest, which is supported by elongated neural spines of the vertebral column (Fig. 3). Whether this character is due to some character displacement with a sympatric chameleon (*C. gracilis*) remains an open question.

The synonym of *C. quilensis*, viz. *C. parvilobus*, poses another problem. Its type locality is “Cameroon, Gaboon, Natal, and S. Africa” (BOULENGER 1887: 450) and refers to six syntypes. Of these, only four seem to be still in existence, having catalogue nos BMNH 53.10.59.23 (young, “South Africa”), 58.4.11.4 (female, “Natal”), 69.3.22.1 (female, “Gaboon”), and 76.3.8.3 (male, “Cameroon”) (see KLAVER & BÖHME 1997: 36; C. MCCARTHY pers. comm.). Since it is not certain whether all *C. quilensis* (not even all syntypes of *C. parvilobus*) really represent the same taxon over their vast distribution range, we restrict the type locality of the latter to Natal, South Africa (where four of the six original syntypes came from), and we designate BMNH 58.4.11.14 as the lectotype of *Chamaeleo parvilobus* Boulenger 1887, which fits also fig. 5 on pl. 39 accompanying the original description. It is an adult female, collected by Reverend H. Callaway on April 11, 1858, and has the following measurements: SVL 116.2 mm, TL 107.5 mm, WOF 6.2 mm, LOF 10.1 mm, distance mouth angle to tip of helmet 20.3 mm, length of mouth gap 17.5 mm, number of flank scales (between dorsal and ventral crest) 65. Colouration (after many years of alcohol preservation) dark blue-grey, including the dorsal crest. Ventral and gular crests white.

*Etymology.* The new species is named after Petr Nečas, Brno, Czech Republic, in recognition of his contributions to our knowledge of chameleons and the diffusion of this knowledge to a broad readership. Moreover, he provided a significant part of the type series of the new species, and he was the first who mentioned and figured it as an unknown taxon in the literature and also provided the head drawing reproduced here. As diacritic signs may not be used in scientific names, we decided in agreement with Petr Nečas to spell the species’ name in this way, without phonetically relevant additions. The pronunciation, however, should be as if it was spelled “necasi”.

## OUTLOOK

In the past, particularly since the Pleistocene, the African rain forest has undergone strong fluctuations. The Dahomey gap area is also primarily a result of the climatic oscillations, pluvials and interpluvials, since the Pleistocene (MARTIN

1989, MALEY 1995). However, human impact has caused a dramatic acceleration of the deforestation: a large part of the disjunct forest relicts in the Dahomey gap has been destroyed and replaced by agricultural landscapes, and the very few surviving forest patches are dramatically threatened for this reason. However not only habitat destruction and fragmentation, but also the flourishing ethnomedical and pet trade in chameleons put great pressure on the new species described here. It is not surprising therefore, that *Chamaeleo necasi* n. sp. was found in Benin in only a small number of individuals (ULLENBRUCH 2003). The situation in Togo should be similar. Further studies are necessary to demonstrate whether stricter conservation measures will be necessary to help the newly discovered silvicolous species to survive, and whether its assumed forthcoming listing in appendix B of CITES will be sufficient. We think that the activities of the BIOLAMA project in Benin are particularly important in this context, since it has already been demonstrated that a considerable number of silvicolous plant and animal species will disappear forever along with the vanishing residual forests of Benin.

Exactly the same is true for the last forest patches in Togo.

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