

NOTES ON THE DISTRIBUTION AND PHYLOGENETIC SIGNIFICANCE OF POST-CLOACAL SACS AND BONES AS OCCURRING IN THE GEKKOTA (REPTILIA)

by

J. BASTINCK

c/o Institute of Taxonomic Zoology, P.O. Box 20125, 1000 HC Amsterdam, The Netherlands

ABSTRACT

On the basis of Kluge's (1982) paper on post-cloacal sacs and bones in the Gekkota the following matters are presented: (1) the situation in the gekkonid genera *Microscalabotes* and *Paragehyra* is recorded, (2) the situation in the gekkonid genus *Lygodactylus* is extensively reviewed and commented upon, (3) the post-cloacal sac variability in the gekkonid genus *Thecadactylus*, first noted by Hoogmoed (1973) and evidently overlooked by Kluge, is confirmed and commented upon, (4) Kluge's interpretation of the phylogenetic significance of post-cloacal sacs is discussed.

ZUSAMMENFASSUNG

Anhand Kluges (1982) Veröffentlichung über Postkloakalspalten und -knochen bei den Gekkota, wird Folgendes behandelt: (1) die Situation innerhalb der Gekkoniden-Gattungen *Microscalabotes* und *Paragehyra* wird dokumentiert, (2) die Situation innerhalb der Gekkoniden-Gattung *Lygodactylus* wird kritisch zusammengefasst, (3) die Variabilität der Postkloakalspalten bei der Gekkoniden-Gattung *Thecadactylus*, erstmalig wahrgenommen von Hoogmoed (1973) und offenbar übersehen von Kluge, wird bestätigt und besprochen, (4) Kluges Interpretation der phylogenetischen Bedeutung von Postkloakalspalten wird diskutiert.

INTRODUCTION

Kluge (1982) published an extensive review of the occurrence of post-cloacal sacs and bones in the Gekkota. In that paper Kluge noted that he had not been able to study the gekkonid genera *Microscalabotes* and *Paragehyra*, and that the situation in the gekkonid genus *Lygodactylus* required further study. I was able to study these three genera to some extent and I put my observations on record here.

A remarkable omission in Kluge's otherwise very comprehensive work is formed by the peculiar situation regarding post-cloacal sacs in the gekkonid genus *Thecadactylus*. The post-

cloacal sac variability in this genus, which was first noted by Hoogmoed (1973), is here confirmed and commented upon.

Kluge's use of the names Gekkota and Gekkonoidea, and his interpretation of the phylogenetic significance of post-cloacal sacs, are here commented upon as well.

RESULTS AND DISCUSSION

USE OF THE NAMES GEKKOTA AND GEKKONOIDEA

Kluge (1967: 10) used the name Gekkota sensu Underwood (1957). According to Underwood the infra-order Gekkota consists of the families Eublepharidae, Gekkonidae, Sphaerodactylidae (these three families collectively regarded as one family Gekkonidae by Kluge) and Pygopodidae. We may take it then, that whenever Kluge is using the name Gekkota he is referring to the Gekkonidae and Pygopodidae collectively.

Kluge also used the name Gekkonoidea. Perusal of his paper shows that Kluge is not referring here to the Gekkonoidea sensu Underwood, as could have been expected in view of his use of the name Gekkota, but to the Gekkonoidea sensu Hoffstetter (1964) (see Kluge, 1967: 12). Hoffstetter considers the superfamily Gekkonoidea to contain the families Ardeosauridae (†) and Gekkonidae (and, tentatively, Bavarisauridae (†) and Palaeolacertidae (†)). This would mean that Kluge, by using the name Gekkonoidea, is simply referring to the Gekkonidae as far as recent families are concerned. One gets the strong impression, however, that Kluge considers the Gekkonoidea to consist of the Gekkonidae and Pygopodidae. This notion is fully supported by Kluge's use of

the name Gekkonoidea in later works (Kluge, 1976; 1982). Reference to Underwood shows that this author considers the Gekkonoidea to contain the Eublepharidae, Gekkonidae and Sphaerodactylidae, which means that Kluge's use of the name Gekkonoidea is evidently not based on Underwood's definition either. For this apparently novel use of the name Gekkonoidea Kluge fails to give any line of reasoning or to cite any authority. Kluge's use of the names Gekkota and Gekkonoidea means that in effect he is treating them as synonyms.

In the remainder of this paper the name Gekkota will be used *sensu* Underwood; the name Gekkonoidea will not be used.

DISTRIBUTION OF POST-CLOACAL SACS AND BONES IN THE GEKKONIDAE

Introduction

According to Kluge (1982), who examined almost all genera constituting the family Gekkonidae, post-cloacal sacs and bones are distributed as follows:

- (1) present in all genera of the Diplodactylinae and Eublepharinae;
- (2) absent in all genera of the Sphaerodactylinae;
- (3) variably present in the Gekkoninae.

Kluge listed the following taxa belonging to the Gekkoninae as being characterized by the absence of both post-cloacal sacs and bones: the genera *Aristelliger*, *Asaccus*, *Millotisaurus*, *Narudasia*, *Pristurus*, *Quedenfeldtia* and *Saurodactylus*, and two species of the genus *Phyllodactylus*, viz., *P. riebeckii* (Peters, 1882), and *P. trachyrhinus* Boulenger, 1899.

Kluge noted that the situation in *Lygodactylus* required further study and declared not to have examined the genera *Microscalabotes* and *Paragehyra*.

The situation in Thecadactylus

One of the genera listed by Kluge (1982) as possessing post-cloacal sacs ($\sigma\sigma + \text{♀}\text{♀}$) and bones ($\sigma\sigma$) is *Thecadactylus* Oken, 1817. This genus is composed of a single species: *T. rapicauda* (Houttuyn, 1782).

In order to investigate the presence/absence of post-cloacal sacs and bones in this species, Hoogmoed (1973) examined 39 specimens. He found 21 specimens ($\sigma\sigma + \text{♀}\text{♀}$) in which sacs were present and 17 specimens ($\sigma\sigma + \text{♀}\text{♀}$) in which these structures were absent (in one juvenile specimen he could not decide whether sacs were present or not). He found all males to be in possession of post-cloacal bones.

I examined 17 specimens of *T. rapicauda* myself, among them 5 of the specimens already examined by Hoogmoed. Apart from 1 specimen in which I could not unequivocally determine whether sacs were present or not, I found 8 specimens (4 $\sigma\sigma$, 4 $\text{♀}\text{♀}$) in which sacs were present and 8 specimens (5 $\sigma\sigma$, 3 $\text{♀}\text{♀}$) in which they were absent. All males were in possession of post-cloacal bones. I can thus confirm Hoogmoed's observations.

The above-mentioned observations show that among the Gekkoninae there is at least one genus in which post-cloacal sacs are not invariably present or absent; in fact, this situation appears to be unique among the Gekkonidae in general. Apparently, Kluge overlooked this variability in *Thecadactylus* and/or was not aware of Hoogmoed's observations.

The situation in Microscalabotes and Paragehyra

As noted above, Kluge (1982) stated that he did not examine the genera *Microscalabotes* and *Paragehyra* in the course of his survey of the Gekkoninae.

The sole species of the genus *Microscalabotes* Boulenger, 1883 is *M. bivittis* (Peters, 1883), which is known from a very few specimens (Pasteur, 1967). According to Pasteur (1964b) the genus is characterized by the absence of post-cloacal sacs; Pasteur does not provide information concerning post-cloacal bones. I was able to study the single specimen of *M. bivittis* that is present in the collection of the Paris museum (MNHN A.61). Although the specimen is in a rather bad state, it is clear that no post-cloacal sacs are present; I can thus con-

firm Pasteur's (1964b) statement. I could not detect the presence of post-cloacal bones. The absence of bones is corroborated by the presence of a well-developed series of preanal pores, which makes it extremely likely that the specimen is a male, in which case post-cloacal bones, if present, should have been easily detectable (in the bone-bearing genera these structures are invariably present in males). Apparently, *Microscalabotes* is another member of the series of gekkonid genera characterized by the absence of post-cloacal sacs and bones.

The genus *Paragehyra* Angel, 1929 likewise is monotypic; its only member, *P. petiti* Angel, 1929, is known only from the holotype. This specimen was studied by Brongersma (1934), who observed that post-cloacal sacs were present, while post-cloacal bones were not. I was in the position to study the holotype of *P. petiti* (MNHNP 29-75) myself. Post-cloacal sacs are present in this specimen indeed, albeit rather weakly developed. I could not detect the presence of post-cloacal bones. Thus, Brongersma's observations apparently were correct. The evident absence of bones, the weak development of the sacs (in males sacs are almost always strongly developed), and the lack of a noticeably swollen tail-base make it very likely that the specimen is a female. It is to be expected that males, when found, will prove to be in possession of both post-cloacal sacs and bones. It therefore appears that as far as post-cloacal sacs and bones are concerned the genus *Paragehyra* does not differ from the majority of gekkonid genera.

Genera not mentioned by Kluge

Two genera belonging to the Gekkoninae were not mentioned by Kluge (1982) either as studied or not studied; these are *Rhinogekko* and *Carinatogekko*.

The genus *Rhinogekko* was erected by De Witte in 1973 and contains one species: *R. misonnei* De Witte, 1973. Up to now the genus has only been mentioned in literature by De Witte himself (1973, 1980), apart from a non-informative reference in Welch (1983). As this

genus is apparently very close to *Agamura* (De Witte, 1980), I suspect that Kluge treats it as a junior synonym of the latter. It should be noted that up to now the genus *Rhinogekko* has not been formally suppressed.

Golubev & Szczerbak (1981) erected the genus *Carinatogekko* to accommodate the species originally known as *Bunopus aspratilis* Anderson, 1973 and *Tropicolotes heteropholis* Minton, Anderson & Anderson, 1970. It seems possible that Kluge was unaware of the description of this genus at the time he was writing his 1982 paper. However, since both *Bunopus* and *Tropicolotes* were found by Kluge to be in possession of both post-cloacal sacs and bones, and since *C. aspratilis* and *C. heteropholis* do not seem to differ from their former respective congeners in this respect (Anderson, 1973; Minton et al., 1970), it seems certain that *Carinatogekko* too is characterized by the presence of these structures.

The situation in *Lygodactylus* will be discussed at the end of this paper.

DISTRIBUTION OF POST-CLOACAL SACS AND BONES IN THE PYGOPODIDAE

Kluge (1982) examined all genera of the Pygopodidae and found post-cloacal bones to be present in all genera constituting this family. Post-cloacal sacs were found to be variably present in the Pygopodidae. This variability is summarized in table I.

TABLE I

Distribution of post-cloacal sacs among the genera of the Pygopodidae according to Kluge (1982).

	♂♂	♀♀
<i>Aclys</i>	?	?
<i>Aprasia</i>	present	variable
<i>Delma</i>	absent	absent
<i>Lialis</i>	absent	absent
<i>Ophidiocephalus</i>	variable	variable
<i>Paradelma</i>	present	present
<i>Pletholax</i>	present	absent (?)
<i>Pygopus</i>	present	present

♀♀ *Aprasia* display inter- and intraspecific variation;
♂♂ + ♀♀ *Ophidiocephalus* display intraspecific variation.

PHYLOGENETIC SIGNIFICANCE OF POST-CLOACAL BONES

From his observations on post-cloacal bones in the Gekkonidae, Pygopodidae, Xantusiidae and the extinct protorosaurians *Tanystropheus* and *Tanytrachelos*, Kluge (1982) draws the following conclusions, with which I completely agree:

- (1) post-cloacal bones in the Gekkonidae and Pygopodidae are homologous structures;
- (2) post-cloacal bones in the Gekkota are not homologous with either those in the Xantusiidae or those in *Tanystropheus* and *Tanytrachelos*;
- (3) post-cloacal bones in the Gekkota are a unique synapomorphy.

PHYLOGENETIC SIGNIFICANCE OF POST-CLOACAL SACS

In the suborder Sauria post-cloacal sacs are a unique feature of the Gekkota: they occur only in the Gekkonidae and Pygopodidae (Kluge, 1967). On the basis of his observations Kluge (1982) draws the following conclusions, with which I fully agree:

- (1) post-cloacal sacs in the Gekkonidae and Pygopodidae are homologous structures;
- (2) post-cloacal sacs in the Gekkota are a unique synapomorphy.

In view of the post-cloacal sac variability in the Pygopodidae (see table I) Kluge stated that "the fact that cloacal bones and sacs do not always co-occur in pygopodids is sufficient justification for treating them as separate characters in the Gekkonidea" (Kluge, 1982: 349). In other words, Kluge here suggests that post-cloacal sacs and bones (as occurring in the Gekkota) are phylogenetically non-correlated characters. This hypothesis gains strength when the (intraspecific) post-cloacal sac variability in the gekkonid genus *Thecadactylus* (which Kluge overlooked) is also taken into account.

The consequences of the above-mentioned hypothesis, however, are difficult to accept. Under Kluge's hypothesis the combined loss of both post-cloacal sacs and bones in 15 gekkonid genera must be regarded as purely coincidental.

Even if it were supposed that sacs and bones have been lost only once in the phylogeny of the Gekkonidae, it would be difficult to regard the combined loss of such closely associated structures as coincidental. It seems certain, however, that in the Gekkonidae sacs and bones have been lost several times: Russell (1977) convincingly suggests that loss of sacs and bones may have occurred at least three times, while Kluge (1982) maintains that loss may have occurred from three to six times independently! Under the afore-mentioned hypothesis we are asked to believe that these combined losses are due solely to coincidence. This is asking too much of anyone's credulity.

An alternative hypothesis suggests itself when considering the following facts:

1. If post-cloacal bones are present in a given species, post-cloacal sacs may be
 - (a) invariably present in this same species; e.g. *Hemidactylus* sp.;
 - (b) variably present in this same species; e.g. *Thecadactylus rapicauda*;
 - (c) invariably absent in this same species; e.g. *Pristurus* sp.
2. If post-cloacal bones are absent in a given species, post-cloacal sacs are absent too; e.g. *Pristurus* sp.

These observations lead to the conclusion that within a given species the presence of bones is a prerequisite for the presence of sacs. Once bones are present, the presence/absence of sacs may "fluctuate". Once bones are absent, sacs are of necessity absent too. This interpretation seems to fit the known facts better than Kluge's hypothesis.

Thus, the following picture of the phylogeny of gekkotan post-cloacal sacs and bones emerges. The ancestral gekkotan was in possession of both sacs and bones. Within the Pygopodidae bones were consistently retained, while the presence of sacs became variable (and even nonexistent) in a number of genera. Within the Gekkonidae post-cloacal sac variability evolved only once (in *Thecadactylus*), while loss of both bones and the closely associated sacs occurred at least once, but probably from three to six times.

THE SITUATION IN *LYGODACTYLUS*

Pasteur (1964a) divided the genus *Lygodactylus* Gray, 1864 into two subgenera: *Lygodactylus*, characterized by the absence of post-cloacal sacs, and *Domerguella*, characterized by the presence of post-cloacal sacs. Up to now, Pasteur has not supplied any information concerning the presence/absence of post-cloacal bones in the genus *Lygodactylus*. The subgenus *Lygodactylus* contains some forty species; the subgenus *Domerguella* consists of five, viz., *L. expectatus* Pasteur & Blanc, 1967, *L. guibei* Pasteur, 1964, *L. madagascariensis* (Boettger, 1881), *L. miops* Günther, 1891, and *L. rarus* Pasteur & Blanc, 1973. The subgenus *Domerguella* is strictly Madagascan in distribution.

Kluge (1982) stated that the genus *Lygodactylus* is characterized in its entirety by the absence of post-cloacal sacs and bones. However, he also stated that the situation in the genus *Lygodactylus* required further study. Unfortunately, Kluge supplied no list of the species he examined; in earlier work (Kluge, 1967) he mentioned *L. capensis* (Smith, 1849), *L. conraui* Tornier, 1902, and *L. picturatus* (Peters, 1870) as studied.

In order to clarify some of the confusion concerning the situation in the genus *Lygodactylus*, I examined representatives of the following species belonging to the subgenus *Lygodactylus*: *L. capensis*, *L. conraui*, *L. fischeri* Boulenger, 1890, *L. luteopicturatus* Pasteur, 1964, *L. ocellatus* Roux, 1907 (including the lectotype, ZMA 11347), *L. picturatus*, *L. robustus* Boettger, 1913, *L. tuberifer* Boettger, 1913, and *L. verticillatus* Mocquard, 1895. Neither post-cloacal sacs nor bones could be detected in any of the specimens examined.

I also examined representatives of the five species of the subgenus *Domerguella*: 2 ♂♂ + 2 ♀♀ of *L. expectatus* (including the holotype, BP 640), 1 ♂ + 2 ♀♀ of *L. guibei*, 1 ♂ + 2 ♀♀ of *L. madagascariensis*, 2 ♂♂ of *L. miops* and 1 ♀ (the holotype, BP 1.72) of *L. rarus*. All specimens were in possession of clearly discernible post-

cloacal sacs. All males were in possession of easily detectable post-cloacal bones.

Thus, it should now be clear that the genus *Lygodactylus* exhibits intrageneric (but not intraspecific) variation regarding the presence/absence of post-cloacal sacs and bones. This means that this type of intrageneric variation is now known from two gekkonid genera (*Lygodactylus* and *Phyllodactylus* (see above)).

The variation within the genus *Lygodactylus* might be indicative of generic status of the subgenera *Domerguella* and *Lygodactylus*, since intrageneric post-cloacal sac and bone variability is evidently very rare in the Gekkonidae. Osteological comparisons might supply the information needed for the justification of recognizing two genera (at least this method produced excellent results in the case of the erection of the genus *Asaccus*, whose species were formerly assigned to *Phyllodactylus* (Dixon & Anderson, 1973)).

According to Pasteur (1964b) the presence of post-cloacal sacs (and, as mentioned above, bones) in the subgenus *Domerguella* is to be regarded as a case of reappearance of these structures, in other words, as a case of evolutionary reversal.

Generally, the occurrence of evolutionary reversal is not regarded as a common phenomenon (Dollo's law), but as far as the situation in the genus *Lygodactylus* is concerned, Pasteur seems to be certain of his case. In the above-mentioned publication he presented, in addition to the occurrence of post-cloacal sacs (and bones), a series of eight characteristics of the subgenus *Domerguella* that should be regarded as indicative of a very advanced state of this subgenus (as compared to the subgenus *Lygodactylus*). Furthermore, during a recent conversation on this matter Pasteur assured me that he was "absolutely convinced" that the presence of sacs and bones in the subgenus *Domerguella* should be regarded as the result of evolutionary reversal.

Two possible explanations for the situation in the genus *Lygodactylus*, without necessitating use

of the concept of evolutionary reversal, suggest themselves:

- (1) within the genus, the subgenus *Domerguella* is the more primitive one (subgenus *Lygodactylus* advanced);
- (2) the situation within the genus is an example of the phenomenon of mosaic evolution: the subgenera *Domerguella* and *Lygodactylus* have diverged from a common ancestor which was in the possession of both post-cloacal sacs and bones. In the subgenus *Domerguella*, which attained a large number of derived character-states, sacs and bones were retained, while in the otherwise less divergent subgenus *Lygodactylus* they were lost.

Both explanations are in direct contradiction with Pasteur's views on the matter, especially so since Pasteur (1982) stated that the subgenus *Domerguella* is to be regarded as ultimately derived from the *Lygodactylus* (*L.*) *capensis* group, a species group already characterized by the absence of sacs and bones.

This is not the place to enter into an extended discussion of Pasteur's detailed and carefully compiled work. It should here be noted that a comparative histological investigation of gekkonid post-cloacal sacs and bones might shed more light on the exact nature of these structures in the subgenus *Domerguella*.

ABBREVIATIONS

BP: Collection C. P. Blanc/G. Pasteur.
 MNHNP: Muséum National d'Histoire Naturelle, Paris.
 ZMA: Zoölogisch Museum, Universiteit van Amsterdam.

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