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# Genital morphology and systematics of *Geodipsas* Boulenger, 1896 (Reptilia: Serpentes: Colubridae), with description of a new genus

Thomas ZIEGLER, Miguel VENCES, Frank GLAW & Wolfgang BÖHME
Zoologisches Forschungsinstitut und Museum Alexander Koenig,
Adenauerallee 160, D-53113 Bonn.

**Genital morphology and systematics of *Geodipsas* Boulenger, 1896 (Reptilia: Serpentes: Colubridae), with description of a new genus.** - Hemipenes of the African colubrid snakes *Geodipsas depressiceps*, *G. procterae* and *G. vauerocegae*, and of the Malagasy species *Geodipsas heimi*, *G. infralineata* and *Alluaudina bellyi* are described. Moreover data on lepidosis and morphometry of these taxa are provided. By means of genital morphology, close affinities could clearly be demonstrated among the Malagasy *Geodipsas* species on the one hand, and among the African taxa on the other. In contrast to this, Malagasy *Geodipsas* spp. show distinct differences in hemipenis morphology as compared with the African species. We consider the deeply bifurcate sulcus spermaticus of the latter as derived; and suggest a monophyletic origin of the African taxa, which are transferred here to a new genus *Buhoma*. The Malagasy *Geodipsas* rather resemble hemipenially the externally different *Alluaudina*, but their relationships are still to be clarified.

**Key-words:** Reptilia - Serpentes - Colubridae - *Geodipsas* - *Alluaudina* - *Buhoma* gen. n. - genital morphology - systematics.

## INTRODUCTION

The colubrid genus *Geodipsas* Boulenger, 1896 is presently regarded to contain the four Malagasy snake species *G. infralineata* (Günther, 1882), *G. boulengeri* (Peracca, 1892), *G. heimi* Angel, 1936, and *G. vinckei* Domergue, 1988, as well as the four taxa *Geodipsas depressiceps depressiceps* (Werner, 1897), *G. d. martieri* Laurent, 1956, *G. procterae* Loveridge, 1922, and *G. vauerocegae* Tornier, 1902 from the African mainland (GLAW & VENCES 1994, RASMUSSEN *et al.* 1995). The genus was erected by BOULENGER (1896) for the Malagasy species *G. infralineata* and *G. boulengeri*; *G. infralineata* was later designated as the type species of the genus (LOVERIDGE 1957).

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Malagasy *Geodipsas* are inhabitants of the eastern rainforest; *G. infralineata* is arboreal and nocturnal, whereas *G. heimi* and *G. vinckei* seem to be more terrestrial (GLAW & VENCES 1994, 1996 and unpublished observations). Of the African species, *G. vauerocegae* and *G. procterae* are restricted to mountain ranges in Tanzania (RASMUSSEN *et al.* 1995), whereas *Geodipsas depressiceps* inhabits forested regions of western central Africa (GUIBE 1958).

Next to marine snakes and the typhlopid genera *Typhlops* (9 endemic Malagasy species) and *Ramphotyphlops* (1 cosmopolitan species occurring in Madagascar), *Geodipsas* is the only snake genus which includes species from Madagascar as well as taxa from the African mainland. The remaining 19 genera occurring on Madagascar are endemic to the Malagasy region; they belong to the Colubridae (17 genera with 70 species) and to the Boidae (2 genera with 3 species; but see KLUGE 1991).

BRYGOO (1982) did not exclude the possibility that the monotypic Malagasy *Mimophis* represents actually a synonym of the Afro-Asiatic genus *Psammophis*. The problem of *Mimophis* relationships has not yet been satisfyingly resolved (see CADLE 1994). BRANDSTÄTTER (1995) discussed the available evidence regarding the status of *Mimophis*, and concluded that similarities to *Psammophis* may partly be due to parallel evolution of Malagasy and African snakes. He emphasized dentition (two instead of three diastemae), shape of loreal (not broader than high) and hemipenis length (relatively longer) as important differences between *Mimophis* and *Psammophis*.

In many groups of squamate reptiles, morphology and ornamentation of the hemipenes play an important role in diagnosing species and reconstruction of phylogenetic relationships (e.g. BÖHME 1988). At present, the hemipenial morphology of the following Malagasy colubrid species is known in detail: *Dromicodryas bernieri*, *Leioheterodon madagascariensis* (as *Anomalodon madagascariensis*) and *Langaha madagascariensis* (as *Langaha nasuta*) (COPE 1900); *Liopholidophis lateralis* and *Mimophis mahfalensis* (DOMERGUE 1962); *Liopholidophis infrasignatus* (as *L. thieli*) and *L. lateralis* (DOMERGUE 1972); *Liophidium apperti*, *L. trilineatum*, *L. therezieni* and *L. vaillanti* (DOMERGUE 1983); *Ithycyphus goudoti*, *I. miniatus*, *I. perineti* and *I. oursi* (DOMERGUE 1986); *Madagascarophis meridionalis*, *M. colubrinus septentrionalis*, *M. ocellatus* (DOMERGUE 1987); *Micropisthodon ochraceus* (DOMERGUE 1991); *Liopholidophis dolicocercus*, *L. epistibes*, *L. grandidieri*, *L. infrasignatus*, *L. lateralis*, *L. pinguis*, *L. rhadinaea*, *L. sexlineatus* and *L. stumpffi* (CADLE 1996) and *Liophidium torquatum* (ZIEGLER *et al.* 1996). Some data on hemipenial morphology are also known for the African species *Geodipsas depressiceps* (BOGERT 1940), *G. procterae* and *G. vauerocegae* (RASMUSSEN *et al.* 1995; also briefly mentioned in LOVERIDGE 1957).

In the present paper we describe the hemipenes of two Malagasy *Geodipsas* species (*G. infralineata* and *G. heimi*) in comparison with the African species up to now included in the genus (*depressiceps*, *vauerocegae* and *procterae*), and with the Malagasy *Alluaudina bellyi*. Additionally, external morphology and lepidosis of the involved taxa will be compared with each other, and with other Malagasy colubrid genera which we consider to be possibly related to *Geodipsas* (i. e. *Brygophis*, *Compsophis*). Our aim is to clarify the relationships between the African and Malagasy taxa currently assigned to *Geodipsas*. Throughout this paper, also in tables and figures, we follow the current use of generic names; taxonomic changes will be proposed in the chapter "Taxonomic conclusions".



## MATERIAL AND METHODS

Specimens included in the present study are held in the collections of the following museums: MHNG - Muséum d'histoire naturelle, Geneva; SMF - Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; ZFMK - Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZMUC - Zoological Museum, University of Copenhagen. Additional museum acronyms used are BM - The Natural History Museum, London; MRAC - Musée Royal de l'Afrique Centrale, Tervuren; ZMB - Zoologisches Museum der Universität, Berlin.

Collecting localities and related data of specimens used for hemipenial descriptions are given in the text; locality data of specimens studied for morphology and scalation are as follows. *G. depressiceps*: MHNG 1513.85 and 151389 Foulassi/Sangmelima, Cameroon; MHNG 1513.94 Kondémeyol, Cameroon; MHNG 1513.98 Djoum/Sangmelima, Cameroon; MHNG 1514.1 Kala/Yaoundé, Cameroon; 1514.3 Otomoto, Cameroon; 2031.81 A-D Territoire de Dekese, Kasai, Zaire. *G. infralineata*: ZFMK 62292 between Vohiparara and Ranomafana, eastern Madagascar; SMF 19572 Moramanga, eastern Madagascar. *G. vinckei*: ZFMK 59789 An'Ala near Andasibe, eastern Madagascar (juvenile specimen, possibly an immature female). Colour pictures of *G. vinckei* (ZFMK 59789) and *G. heimi* (ZFMK 59783) have recently been published by GLAW & VENCES (1996).

The recent development of a new technique (PESANTES 1994, ZIEGLER 1996) has made it possible to evert and study the hemipenes not only of fresh material, but also of specimens previously preserved in alcohol or even in formalin.

Abbreviations used in the text are as follows. SVL: snout vent length, from snout tip to beginning of cloaca; TaL: tail length, from end of cloaca to tail tip; HPL: hemipenis length, from apex to cloacal base point. Terminology of genital morphology follows KLAVER & BÖHME (1986) and BÖHME (1988). Other abbreviations in caption of table 1. We did not compare the total number of infralabials, since we had the impression that these were counted differently in the literature, and thus a reliable comparison with published data would not have been possible.

## RESULTS

### DESCRIPTION OF HEMIPENES

**Geodipsas heimi** Angel, 1936

ZFMK 59783 (SVL: 22; TaL: 4; HPL: 1 cm; freshly everted) from Andasibe (= Périnet, ca. 900 m above sea level), central eastern Madagascar, collected by F. Glaw 14. 1. 1995 (Fig. 1)

Fully everted hemipenes elongate. The pedicel, mainly on the upper asulcate surface, is covered with tiny spines. The apex is densely covered with small and

slender spines that become stronger towards the truncus. The strong and elongate spines of the truncus form a broad ring which is on the asulcate surface medially interrupted by tiny spines. Two strong and elongate spines of different sizes can be found asymmetrically placed medially on the asulcate surface of the pedicel. The spineless and largely closed sulcus spermaticus is slightly bifurcate, the "branches" terminating in a heart-shaped configuration on the sulcate surface below the tip of the hemipenis.

**Geodipsas infralineata** (Günther, 1882)

SMF 32614 (SVL: 36,5; TaL: 12; HPL: 1 cm; everted after fixation) from Col Pierre Radama, near Maroantsetra, eastern Madagascar, collected by H. Bluntschli (Fig. 2).

There are only modest differences between the available hemipenial preparations of *G. infralineata* and *G. heimi*. The "branches" of the slight bifurcation of the sulcus spermaticus appear to be slightly longer in the hemipenis of *G. infralineata*. Also, the hemipenis of *G. infralineata* lacks distinct tiny spines on the asulcate surface of the pedicel, and, in relation to the snout vent length, the hemipenis of *G. heimi* is distinctly longer than that of *G. infralineata*.

**Geodipsas depressiceps** (Werner, 1897)

SMF 32613 (SVL: 22,5; TaL: 3,8; HPL: 0,8 cm; everted after fixation) from Victoria, Cameroon, collected by F. v. Bormann (Fig. 3).

Hemipenis, elongate and covered with sharp and partly strongly recurved spines. At the lower truncus a single ring consisting of enlarged spines, only interrupted by the sulcus spermaticus, separates the densely arranged and medium-sized spines of apex and truncus from the tiny spines of the pedicel. Not discernible from Fig. 3 there exist longitudinal truncal ridges of tissue (between fields of medium sized spines) that extend to the lower apex, covered with somewhat smaller spines (see also BOGERT 1940). The spineless sulcus spermaticus is bifurcate for about 2/3 of its length, with its slender branches leading straightly to the apex and terminating laterally just below the tip of the hemipenis.

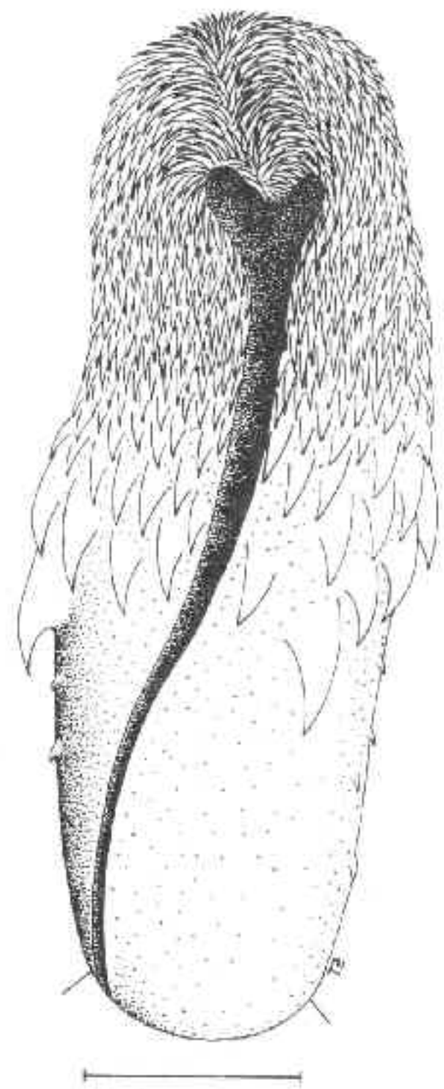
The hemipenes of SMF 32613 correspond to those of MHNG 1513.85 from Foulassi, Sangmelima, Cameroon (SVL: 21,5 TaL: 3,9; HPL: 0,7 cm) and to the only partly preserved organs of MHNG 2031.81A from Dekese, Kasai, Zaire (SVL: 20,5; TaL: 4 cm), which also have been everted from previously preserved specimens.

**Geodipsas procterae** Loveridge, 1922

ZMUC R631174 (SVL: 32; TaL: 9; HPL: 1,4 cm; everted after fixation) from Udehuva, Mount Nyumbanitu, Uzungwa mountains, Tanzania (Fig. 4).

Hemipenis elongate, slightly curved towards the central axis of the snake. The pedicel is covered with tiny spines, truncus and apex are densely covered with strong and stout spines of approximately the same length. The largely closed and spineless sulcus spermaticus is bifurcate for about 1/2 of its length, with the branches terminating laterally below the tip of the hemipenis (see also RASMUSSEN *et al.* 1995).





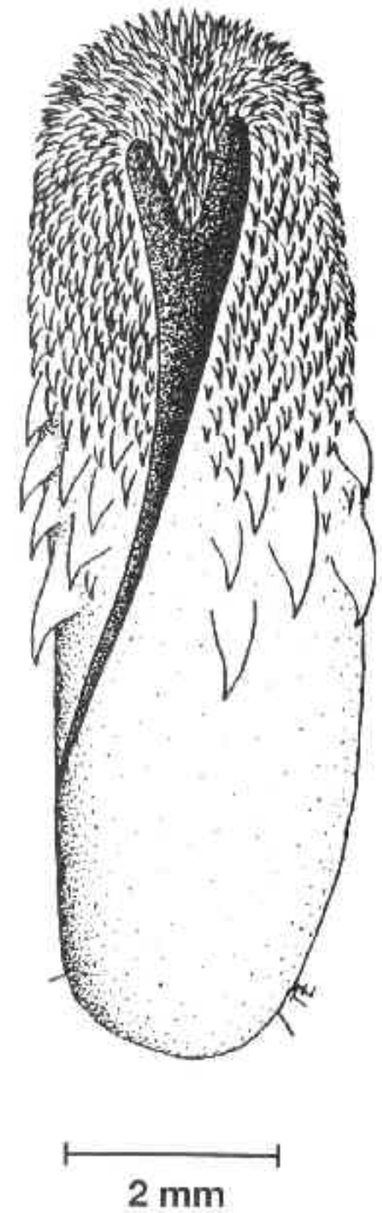
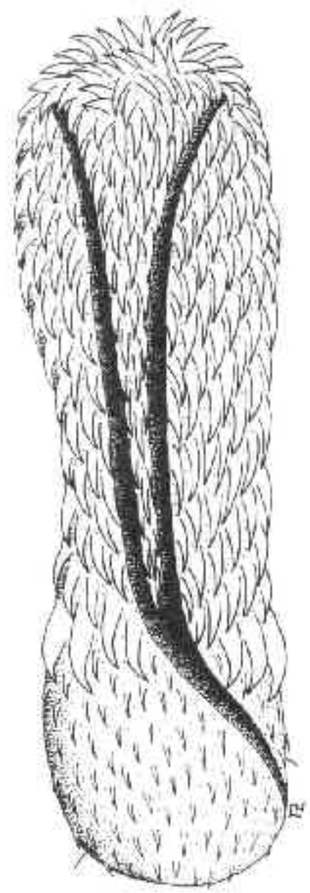




FIG. 1: Sulcal view of the left hemipenis of *Geodipsas heimi* (ZFMK 59783). – FIG. 2: Sulcal view of the left hemipenis of *Geodipsas infralineata* (SMF 32614).

**Geodipsas vauerocegae** Tornier, 1902

ZMUC R63907 (SVL: 23; TaL 4,5; HPL: 0,8 cm; everted after fixation) from Amani, east. Usambara mountains, Tanzania.

There is a strong similarity between the hemipenis of *G. procterae* and the smaller ones of *G. vauerocegae* (see also RASMUSSEN *et al.* 1995), but in *G. vauerocegae* the tiny spines of the pedicel are somewhat stronger and more elongate than in *G. procterae*.



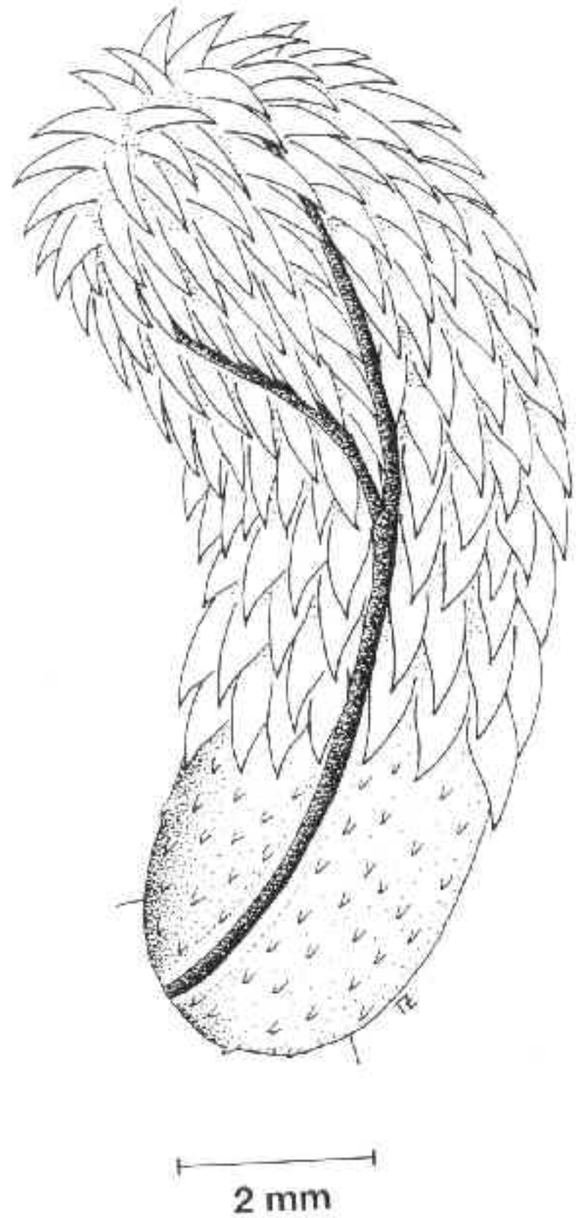




FIG. 3: Sulcal view of the right hemipenis of *Geodipsas depressiceps* (SMF 32613). - FIG. 4: Sulcal view of the left hemipenis of *Geodipsas procterae* (ZMUC R631174).

**Alluaudina bellyi** Mocquard, 1894

ZFMK 59799 (SVL: 26,5; TaL: 10; HPL: 0,6 cm; freshly everted) from Strict Nature Reserve ("Reserve naturelle Integrale") Marojejy, Camp 1 (ca. 300 m above sea level), north-eastern Madagascar, collected by F. Glaw 22.2.1995 (Fig. 5).



Fully everted hemipenes slightly elongate, terminally curved towards the sulcate surface. Apex and truncus are densely covered with slightly recurved and delicate spines, which also surround the sulcus spermaticus on the pedicel. On the lower truncus the spines become stronger and more elongate, only on the asulcate surface medially there is a spineless area, which is at a time laterally restricted by two broad and strong spines which are connected to each other. Not discernible from Fig. 5 are the laterally slightly lengthwise folded apex and upper truncus. The spineless

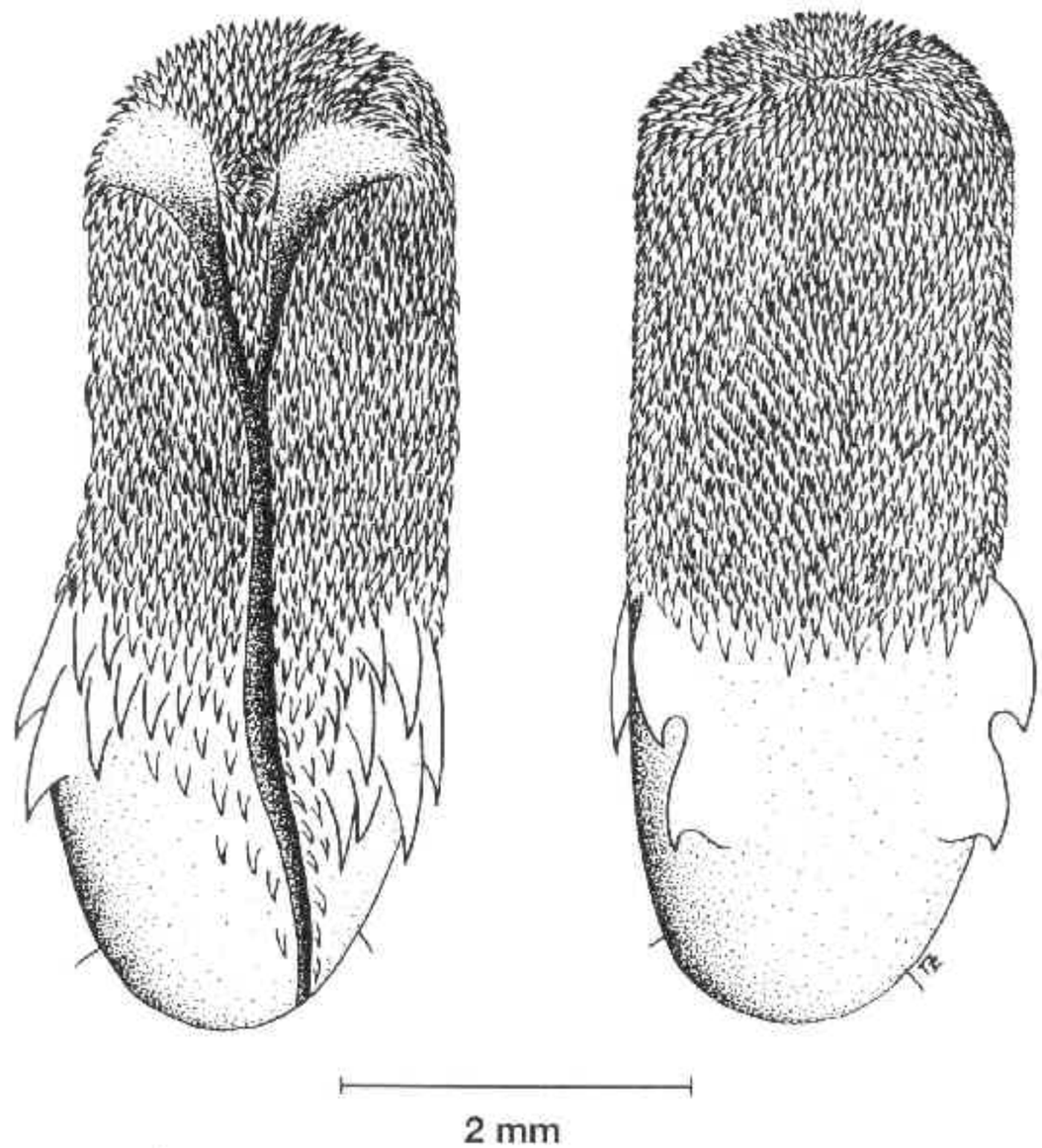



FIG. 5: Sulcal (left) and asulcal (right) view of the right hemipenis of *Alluaudina bellyi* (ZFMK 59799).

and largely closed sulcus spermaticus is slightly bifurcate for about 1/3 of its length, with the branches terminating laterally in spineless extensions on the sulcate surface far below the tip of the hemipenis.

## SCALATION AND MORPHOLOGY – COMPARISON BETWEEN AFRICAN AND MALAGASY SPECIES

Table 1 gives measurements and scale counts of the specimens examined in the present study, compared with the respective type descriptions. Table 2 summarizes metric and meristic data of all species considered. A direct comparison between African and Malagasy taxa gives the following results:

*Size.*- African species included in *Geodipsas* are relatively small snakes (up to 520 mm total length). The same is true for all Malagasy *Geodipsas* except *G. infralineata* (ca. 790 mm total length in the type).

*Relative tail length.*- The tail is relatively short (less than 20% of total length) in all African taxa assigned to *Geodipsas*. The same is true for Malagasy *Geodipsas* except *G. infralineata*.

*Number of ventral scales.*- African *Geodipsas* have a rather low number of ventrals in common (122-163), with clear differences between some taxa. In Madagascar, most species have a low number of ventrals but a higher number (up to 191) is found in *G. infralineata*.

*Number of dorsal scales.*- Most of the African taxa (*proterne, vauerocegue* and *marlieri*) have 17 rows of dorsal scales, whereas *depressiceps* has 19 rows (17 in one specimen). All Malagasy *Geodipsas* have 19 rows.

*Pre- and postoculars.*- African *Geodipsas* have 2 preoculars (1 in *vauerocegue*). All Malagasy species have only 1 preocular (2 preoculars on one side of the head in one specimen of *G. infralineata*). Most African and Malagasy taxa have 2 postoculars (the upper postocular is mostly larger than the lower), but single specimens of several species have 3 postoculars.

*Temporals.*- The configuration of the temporals can be used to distinguish the African species from all Malagasy snake species considered, although the distinction is not as consistent as would be necessary for a diagnostic or phylogenetically valuable character. The African species have mostly 1+2 temporals (1+3 in some *G. depressiceps*), and the upper temporal scale of the second row is mostly longer (and thus reaching further posteriorly), often about twice as long as the lower scale. This was observed (at least on one head side) in 10 out of 12 *G. depressiceps*, and can be seen in the pictures of the holotypes of *G. vauerocegue* and *G. proterne* shown by RASMUSSEN *et al.* (1995).

A similar character state was not observed in any Malagasy specimen. These have either 1+1 (*G. vincke*), 2+2 (one head side of one *G. heimi* and one *G. infralineata*), or 1+2 temporals with the lower scale in the second row reaching further than the upper scale. The latter situation is observed in one *G. heimi* in table 1 and in *G. infralineata*: two specimens in table 1 as well as the drawing in the original



TABLE 1: Measurements and lepidosis of the studied specimens. For a better comparison, data of the corresponding type descriptions are also given. These are taken out of WERNER (1897) for *Geodipsas depressiceps*, of DOMERGUE (1988) for *Geodipsas vincke*, of ANGEL (1936) for *G. heimi* and of GUIBE (1958) for *Alluaudina bellyi*. Question marks: Values not given in the original description, or values not recognizable due to bad preservation of specimen.
Abbreviations used are: **Sex**: Sex of the specimen, either F (female) or M (male). **SVL**: length of head and body in mm. **TaL**: length of tail in mm. **D**: number of dorsal scale rows counted at midbody. **V**: number of ventral scales. **SC**: number of subcaudals. **SC div.**: Subcaudals divided (= in pairs), yes/no. A: anal scale single (1) or divided (2). **PreOc**: number of preocularis. **PostOc**: number of postoculars. **Temp**: formula for first two rows of temporal scales. **Temp config**: refers to the second row of temporal scales; mentioned is which of the temporals in this row reaches furthest posteriorly (in most cases the furthest reaching scale is also the longest); + means that the corresponding scale is much longer than the other scale(s) (generally about twice as long); l/r refers to left and right side of the head. Values are only given with Temp formulas 1+2 or 1+3. **SupLab**: number of supralabials. **SupLab (eye)**: supralabials entering the eye. **InfLab (Subl)**: number of infralabials in contact with anterior pair of sublinguals. **Sublin (large)**: number of regular pairs of large sublingual scales. **Sublin (small)**: number of irregular small scales interposed between large sublinguals and ventrals.

| No. | Sex | SVL | TaL | D | V | SC | SC div. | A | PreOc | PostOc | Temp | Temp config | SupLab | SupLab (eye) | InfLab (Subl) | Sublin (large) | Sublin (small) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. depressiceps* | | | | | | | | | | | | | | | | | |
| type description | | 287-243 | 34-44 | 19 | 144-151 | 35 | ? | 1 | 2 | 2 | 1+2 | ? | 7 | 3,4 | 4 | ? | ? |
| MHNG 2031.81A | | ? | ? | 19 | ? | ? | ? | ? | ? | ? | 1+2 | r:upper+; l:equal | 7 | 3,4 | 4 | 3 | 0 |
| MHNG 2031.81B | | 209 | 36 | 19 | 147 | 33 | Yes | 1 | 2 | 2 | 1+2 | r:upper+; l:upper | 7 | 3,4 | 4 | 3 | 0 |
| MHNG 2031.81C | | 193 | 32 | 19 | 147 | 34 | Yes | 1 | 2 | 2 | 1+2 | r:upper+; l:upper | 7 | 3,4 | 4 | 3 | 0 |
| MHNG 2031.81D | | 220 | 39 | 17 | 141 | 33 | Yes | 1 | 2 | 2 | 1+2 | upper+ | 7 | 3,4 | 4 | 3 | 0 |
| MHNG 1513.85 | M | 213 | 40 | 19 | 143 | 33 | Yes | 1 | 3 | 2 | 1+3 | not upper | 7 | 3,4 | 4 | 3 | 0 |
| MHNG 1513.89 | F | 193 | 37 | ? | 143 | 36 | Yes | ? | ? | ? | | | ? | ? | | ? | ? |
| MHNG 1513.94 | M | 186 | 34 | 19 | 143 | 40 | Yes | 1 | 3 (right) | ? | 1+2 | l:upper | ? | 3,4 | 4 | 3 | 0 |
| MHNG 1513.98 | M | 220 | 44 | 19 | ca. 135 | 37 | Yes | 1 | 2 | 2 | 1+3 | l:upper | 7 | 3,4 | 4 | | |
| MHNG 1514.1 | F | 222 | 37 | 19 | ca. 147 | 32 | Yes | 1 | 2 | 2 | 1+2 | upper+ | 7 | 3,4 | 4 | 3 | 0 |
| MHNG 1514.3 | M | 177 | 33 | 19 | 134 | 34 | Yes | 1 | ? | ? | 1+3 | not upper | | | | 2 | 1 |
| ZFMK 5824 | F | 254 | 40 | 19 | 142 | 31 | Yes | 1 | 2 | 2 | 1+2 | upper+ | 7 | 3,4 | 4 | 3 | 0 |
| SMF 19574 | | 225 | 44 | 19 | 144 | 38 | Yes | 1 | 2 | 2 | 1+2 | upper+ | 7 | 3,4 | 4 | 3 | 0 |
| SMF 32613 | M | 218 | 39 | 19 | 138 | ca.36 | Yes | ? | 2 | 2 | 1+2 | upper+ | 7 | 3,4 | | | |
| *G. infralineata* | | | | | | | | | | | | | | | | | |
| type description | | 635 | 152 | 19 | 186 | 62 | ? | 1 | 1 | 2 | 1+2 | lower | 7 | 3,4 | | ? | ? |
| ZFMK 62292 | F | 398 | 108 | 19 | 177 | 63 | Yes | 1 | 2/1 | 2 | 1+2 | lower | ? | 3,4 | 4 | 2 | ca. 5 |
| SMF 32614 | M | 345 | 121 | 19 | 185 | 80 | Yes | ? | 1 | 2 | 2+2 | | 7 | 3,4 | 3 | 2 | ca. 5 |
| SMF 19572 | F | 540 | 131 | 19 | 189 | 66 | Yes | 1 | 1 | 2 | 1+2 | lower | 7 | 3,4 | 4 | 2 | 2 |
| *G. vincke* | | | | | | | | | | | | | | | | | |
| type description | | 411 | 84 | 19 | 163 | 45 | Yes | 1 | 1 | 3 | 1+1 | | 7 | 3,4 | 4 | 2 | 5 |
| ZFMK 59789 | F? | 172 | 31 | 19 | 152 | 38 | Yes | 1 | 1 | 2 | 1+1 | | 7 | 3,4 | 4 | 2 | 2 |
| *G. heimi* | | | | | | | | | | | | | | | | | |
| type description | ? | 280 | 55 | 19 | 134 | 34 | ? | 1 | 1 | 2 | 1+2 | | 7 | 3,4 | ? | ? | ? |
| ZFMK 59783 | M | 220 | 40 | 19 | 133 | 30 | Yes | 1 | 1 | 2 | 2+2/1+2 | lower | 7 | 3,4 | 4 | 2 | ca. 6 |
| *Alluaudina bellyi* | | | | | | | | | | | | | | | | | |
| type description | | 293 | 73 | 25 | 161 | 68 | No | 1 | 2 | 3 | many | | 8 | 4,5 | 4-5 | ? | ? |
| ZFMK 59799 | M | 269 | 98 | 25 | 163 | 78 | No | 1 | 2 | 3 | many | | 8 | 4,5 | 6 | 3 | 3 |

description and two specimens pictured by GLAW & VENCES (1994: plate 336 and fig. 515). Also the other Malagasy genera considered differ from the African taxa. In *Alluaudina* no regular temporals can be identified; the corresponding place is made up by numerous small scales. *Compsophis* has a configuration of 2+3; and *Brygophis*, following the drawing of DOMERGUE (1988) has the lower scale in the second row reaching further than the upper scale.

*Supralabials.*- *G. depressiceps*, *G. d. marlieri* and *G. vauerocegae* have 7 supralabials, whereas *G. procterae* has 8 supralabials (third, fourth, and fifth entering the eye). All Malagasy *Geodipsas* have 7 supralabials, of which the third and fourth enter the eye. *Alluaudina* has 8 supralabials, but only fourth and fifth are entering the eye, the state is thus possibly not homologous to the state in the African *procterae*.

Infralabials.- A difference is found in the number of infralabials that contact the first pair of sublinguals. These are 4 in most taxa, but 3 in *G. d. marlieri* and in most *G. vauerocegae*. 5-6 infralabials contact the first sublinguals in *Alluaudina*.

*Sublingual scales.*- The configuration of the sublingual scales can be used to separate most African specimens from the Malagasy taxa. In 9 out of 10 *G. depressiceps* there are three regular pairs of longish sublingual scales; behind these the ventral scales immediately begin. The same situation can be observed in the holotype of *G. vauerocegae*, whereas the holotype of *G. procterae* has some (rather large) scales irregularly interposed between the two pairs of large sublinguals and the beginning of the regular ventral scales (figs. in RASMUSSEN *et al.* 1995). In contrast, the Malagasy *Geodipsas* have only two large pairs of sublinguals, and a varying number of small irregular scales are interposed between these and the beginning of the ventrals. A similar situation is also found in *Brygophis* and *Alluaudina*.

*Other scalation characters.*- Several other characters exhibit variation within the snake species considered in the present study. *Alluaudina* has strongly keeled dorsal scales, a character shared with *G. depressiceps* from Africa. However, scale ultrastructures of these species are completely different (own unpublished data), indicating that the keeled states are not homologous. *G. boulengeri* is unique in having two loreal scales. *G. procterae* has undivided subcaudals, a character state shared with *Alluaudina*.

*Maxillary teeth.*- Number of maxillary teeth is 17-19+II in *G. vauerocegae* and *G. procterae* (mean 18.1 and 17.8, N = 38 and 13, respectively; RASMUSSEN *et al.* 1995, Rasmussen pers. comm.), 15-18+II in *G. depressiceps* and *G. infralineata* (mean 16.2 and 16.3, N = 13 and 4, respectively; Rasmussen, pers. comm.), and 12+II in *G. vinckei* (DOMERGUE 1988).

## DISCUSSION

### HEMIPENIS MORPHOLOGY

A comparison of the hemipenes described in the present study indicates that the affinities between the African taxa *Geodipsas depressiceps*, *G. procterae*, and *G. vauerocegae* are much closer than those of any of these taxa to the Malagasy species.



TABLE 2: Differential characters between the species considered in the present study. Data of *Geodipsas vauerocegae* and *G. procterae* from RASMUSSEN et al. (1995); details of sublinguals and temporal conformation from pictures of *vauerocegae* and *procterae* holotypes in RASMUSSEN et al. (1995). Data of *G. d. depressiceps* from table 1 and LAURENT (1956). Data of *G. d. marlieri* from table 1 and GUIBÉ (1958). Data of *G. boulengeri* from PERACCA (1892); details of temporal conformation from the corresponding drawing of the holotype. Data of *Compsophis albiventris* from MOCQUARD (1894) and drawings of GUIBÉ (1958). Data of *Brygophis coulangesi* from DOUMERGUE (1988). Data of *Alluaudina mocquerisi* from GLAW & VENCES (1994). Other data from table 1. Abbreviations as in table 1 except for **Tl.**, (maximum total length in mm), **Tal.%**, and **SC** are given separately for males (M) and females (F) when data were available. For **Tal%**, **V**, and **SC** we give the range of observed values. For other characters we give the value which was most often observed, followed (in brackets) by other observed values (except **Temp config**). The **Temp** formula of *Compsophis albiventris* could not be ascertained since the drawing of GUIBÉ (1958) differs from the formula 1+2 given in the description. Several character states of *G. d. marlieri* (**PreOc**, **PostOc**, **Temp**, **SupLab**) are not totally reliable since LAURENT (1956) only mentioned characters which are distinct to *G. d. depressiceps*.

| | Tl. | Tal.% | V | SC | SC div. | D | Pre-Oc | Post Oc | Temp | Temp config | Sup Lab | SupLab (eye) | InfLab (subl) | SublIn (large) | SublIn (small) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *G. d. depressiceps* | 278 (M) 333 (F) | 16-19 (M) 12-15 (F) | 134-148 | 37-40 (M) 31-37 (F) | Yes | 19 (17) | 2 (3) | 2 | 1+2 (1+3) | upper | 7 | 3,4 | 4 | 3 (2) | 0 (1) |
| *G. d. marlieri* | 433 (M) 443 (F) | 15-18 (M) 13-14 (F) | 150-164 | 37-44 (M) 35-37 (F) | Yes | 17 | 2 (?) | 2 (?) | 1+2 (?) | ? | 7 (?) | 3,4 (?) | 3 | ? | ? |
| *G. vauerocegae* | 320 (M) 410 (F) | ? | 122-133 | 38-48 (M) 35-41 (F) | Yes | 17 | 1 (2) | 2 (1) | 1+2 | upper | 7 (8) | 3,4 (4,5) | 3 (4) | 3 | 0 |
| *G. procterae* | 440 (M) 520 (F) | ? | 143-154 | 43-50 (M) 33-39 (F) | No | 17 | 2 (3) | 2 (3) | 1+2 | upper | 8 | 3,4,5 | 4 | 2 | 3 |
| *G. infralineata* | 787 | 20-26 | 159-191 | 43-81 | Yes | 19 | 1 (3) | 2 | 1+2 | lower (2+2) | 7 | 3,4 | 4 | 2 (3) | 2-5 |
| *G. heimi* | 335 | 15-16 | 133-134 | 30-34 | Yes | 19 | 1 | 2 | 1+2 | lower (2+2) | 7 | 3,4 | 4 | 2 | ca. 6 |
| *G. vinckei* | 495 | 15-17 | 152-163 | 38-45 | Yes | 19 | 1 | 2-3 | 1+1 | only one present | 7 | 3,4 | 4 | 2 | 2-5 |
| *G. boulengeri* | 348 | ? | 137 | 31 | Yes | 19 | 1 | 2-3 | 1+2 | lower | 7 | 3,4 | ? | ? | ? |
| *Compsophis albiventris* | 167 | ? | 148 | 41 | Yes | 19 | 1 | 2 | 1+2? | equal? 2+X? | 7 | 3,4 | | ? | ? |
| *Brygophis coulangesi* | 1203 | 19 | 204 | 73 | Yes | 19 | 1 | 3 | 1+2 | lower | 7 | 3,4 | 4 | 2 | 6 |
| *Alluaudina bellyi* | 447 | 27 | 153-163 | 57-78 | No | 25 | 2 | 3 | many (3+3?) | too many present | 8 | 4,5 | 6 | 3 | 3 |
| *Alluaudina mocquerisi* | 510 | 22-25 | 202-205 | 91-98 | No | 24-25 | 3 | 4 | many (3+3?) | too many present | 8 | 4,5 | 5 | 3 | 2 |

Within the African species (except for *Geodipsas depressiceps*), as well as within the Malagasy *Geodipsas*, it is quite difficult to distinguish species relying solely on genital morphology; on the contrary, there are clear distinctive features between the hemipenes of the African and the Malagasy snakes considered.

One of the most important differences between the African and Malagasy taxa is the deeply bifurcate sulcus spermaticus of the former. In colubrid snakes divided sulci and bilobed hemipenes are often considered as plesiomorphic condition (e.g. UNDERWOOD 1967; MYERS & CADLE 1994). However, arguments exist also to consider simple organs with undivided sperm grooves as primitive compared with divided ones (e.g. BÖHME 1988; BÖHME & SIFLING 1993). The deep bifurcation found in African *Geodipsas* may therefore be a synapomorphic trait.

On the other hand, we regard the more heterogeneous spine ornamentation on the hemipenes of the Malagasy *Geodipsas* as derived. The spines of the pedicel are reduced to a large extent, or partially existing as tiny spines. The small and slender spines of the apex gradually become larger towards the lower truncus. The latter contrasts with the state in *G. depressiceps*, which (also concerning the deeply bifurcate sulcus and the truncal ridges of tissue) seems to be the most derived of the African taxa, and in which there is only a single and continuous ring of elongate spines on the truncus. The hemipenes of *G. procterae* and *G. vauerocegae* are characterized by a largely plesiomorphic, nearly complete spine ornamentation, only differentiated in tiny spines of the pedicel and stronger ones of truncus and apex.

Furthermore, and contrasting with the African species, the asulcate surface of the lower truncus of the hemipenes of the Malagasy *Geodipsas* species bears an interruption of the elongate, strong spines, which is filled up by tiny spines. Just medially at the pedicel there are two isolated strong spines on the asulcate surface, absent in the African species.

Since the hemipenes of a representative of the genus *Alluaudina* are available for the first time in detail, first hypotheses on possible affinities can be drawn. There are several hemipenial features which *A. bellyi* has in common with *Geodipsas heimi* and *G. infralineata*: (a) the small and reduced spines of apex and upper truncus, (b) the enlarged spines of the lower truncus, which are medially interrupted on the asulcate surface; and (c) the only slightly bifurcate sulcus, with its short branches terminating far below the tip of the hemipenis. Thus it can be stated that regarding hemipenis morphology Malagasy *Geodipsas* exhibit closer affinities to *Alluaudina bellyi* than to the externally more similar African taxa.

### SCALATION

Scale characters do not unequivocally differentiate the African from the Malagasy *Geodipsas*. Nevertheless, some character states (configuration of temporals and sublinguals) similar within all or most African taxa are not or seldom found in Malagasy species, which on the other hand are rather heterogeneous regarding these characters. The number of dorsal scale rows, on the contrary, is not variable in Madagascar (except the rather distinct *Alluaudina*), but different in three African taxa (and in one specimen of the remaining African taxon *depressiceps*). Three out of four African taxa have 2 preoculars, a situation not found in Malagasy *Geodipsas* (only in *Alluaudina*).



No set of characters could be identified which would clearly disrupt the uniformity of the African taxa by grouping one of them nearer to the Malagasy taxa than the others: *depressiceps* has 19 dorsal scale rows as the Malagasy species, but has very distinctly the "African" state of temporals and sublinguals; *procterae*, which has (in the holotype) a sublingual conformation similar to the "Malagasy" state and 8 supralabials (similar but not identical to the Malagasy *Alluaudina*), has 17 dorsal scale rows and an "African" temporal configuration; *vauerocegae* which has only one preocular like the Malagasy *Geodipsas* has 17 dorsals and "African" configurations of temporals and sublinguals.

We did not undertake a phylogenetic polarization of the character states identified in lepidosis; this would have been clearly premature in such variable characters without a more extensive analysis of colubrid snakes to identify suited outgroups. Nevertheless we conclude that phenetically there are obvious relationships between the four African taxa, and that data from lepidosis do not contradict the hypothesis that they represent a monophyletic unit.

## TAXONOMIC CONCLUSIONS

### DESCRIPTION OF A NEW GENUS

The distinct differences in hemipenis morphology indicate generic distinctness of the Malagasy *Geodipsas* from the African taxa so far included in the genus. Similar arguments have previously proved to be useful for splitting several heterogeneous snake genera into units that reflect more correctly phylogenetic relationships, e. g. ROSSMANN & EBERLE (1977) of the genus *Natrix*, DOWLING & FRIES (1987) and DOWLING & PRICES (1988) of the genus *Elaphe*, GLOYD & CONANT (1990) of the genus *Agkistrodon*, and MYERS & CADLE (1994) of the genus *Rhadinaea*; certainly some further revisions will follow (e.g. BÖHME & ZIEGLER in prep. regarding the genus *Coronella*).

Since the African taxa were all originally described as belonging to already named genera with defined type species (*Geodipsas: vauerocegae, procterae, marlieri; Tropidonotus: depressiceps*), no generic name is available to group the African taxa into a genus separate from *Geodipsas*; a new generic name is therefore needed and will be proposed below.

The separation of the African taxa from *Geodipsas* on the genus level is further corroborated by recent studies of WOLLBERG, KOCHVA & UNDERWOOD (in prep.) on rictal glands in *Atractaspis*, *Geodipsas*, and aparallactine snakes. Following this study (Underwood, pers. comm.), the taxa *depressiceps*, *vauerocegae* and *procterae* "have sequential supralabial, Duvernoy's and superior rictal glands and also inferior rictal glands like *Aparallactus*. [...] In this condition they contrast with *Geodipsas infralineata*, the type species of the genus. This suggests that the African species are 'aparallactines' and are wrongly assigned to the genus *Geodipsas*".

Based on these arguments we transfer the African species previously assigned to *Geodipsas* to a new genus, for which we coin the name

**Buhoma** gen. n.

Type species.- *Geodipsas vauerocegae* Tornier, 1902. We designate this taxon as type species since it was recently reviewed in detail, and its holotype illustrated (RASMUSSEN *et al.* 1995). The holotype is a male specimen collected by Dr. Küttner in East Usambara mountains; ZMB 17557; photographs of holotype in RASMUSSEN *et al.* (1995).

Etymology.- Buhoma is the vernacular name by which *B. depressiceps marlieri* is known in the Musigati region, Burundi (DERLEYN 1978); we here define its gender as feminine.

Diagnosis.- Distinguishable from *Geodipsas* by deep bifurcation of sulcus spermaticus, and by combination of configuration of (a) sublinguals and (b) temporals (see above). Following BOGERT (1940) a distinction from all other African colubrid genera is possible by combination of (a) presence of hypapophyses on the posterior vertebrae, (b) grooved posterior maxillary teeth, (c) sulcus spermaticus forked.

Description.- Small forest snakes (maximum known total length 520 mm) with round pupils. 17-19 dorsal scale rows; 122-163 ventrals; anal undivided; subcaudals single or in pairs, 31-50; 7 or 8 supralabials (third and fourth or fourth and fifth in contact with eye); generally one or two (exceptionally three) preoculars and two (exceptionally one or three) postoculars. Temporals 1+2; upper temporal of second row generally longest. 15-19+II maxillary teeth. Rictal gland configuration similar to that in *Aparallactus* (Underwood pers. comm.). For a detailed description of skull characters of *B. depressiceps* see BOURGEOIS (1968). Hemipenis simple and elongate. Pedicel covered with tiny respectively small and slender spines, truncus and apex densely covered with strong and stout resp. recurved spines, which can form a single ring of elongate spines at the lower truncus; there can exist longitudinal truncal ridges of tissue, covered with small spines. Sulcus spermaticus without spines, bifurcate for about 1/2 to 2/3 of its length, with the branches terminating laterally below the tip of the hemipenis.

Species included.- *Buhoma vauerocegae* (Tornier, 1902); *Buhoma procterae* (Loveridge, 1922); *Buhoma depressiceps* (Werner, 1897); *Buhoma depressiceps marlieri* (Laurent, 1956). The latter taxon may deserve specific status.

Distribution.- Central Africa. *B. vauerocegae* is known from the Usambara, Magrotto, and Uluguru mountain ranges, whereas *B. procterae* inhabits the Uluguru and Udzungwa mountain ranges, all in Tanzania (RASMUSSEN *et al.* 1995). The distribution map in RASMUSSEN *et al.* (1995) shows an additional locality of the latter species in the eastern Usambara mountain range: at this locality, as well as in the Uluguru mountain range, *B. vauerocegae* and *B. procterae* occur sympatrically. Type locality of *procterae* is 3 miles from Morogoro, Uluguru mountains (holotype BM 1946.1.248; photographs of holotype in RASMUSSEN *et al.* 1995). *B. d. depressiceps* has a wider distribution in western central Africa. Type locality is "Barombi-Station" in Cameroon (WERNER 1897; original description based on two syntypes, deposited in the ZMB). Other localities are in the People's Republic of Congo (Dimonika region; TRAPE 1985); Equatorial Guinea (Macias Nguema = Fernando Poo; CAPOCACCIA 1961); Cameroon (e. g. specimens in Tab. 1); Zaire (e. g. specimens in Tab. 1 and localities in LAURENT 1956). *B. d. marlieri* was described from Mwana, terr. de Mwenga (Kivu) in Zaire (LAURENT 1956) and is also known from other localities in Zaire (see LAURENT 1956); Burundi (Musigati, Bubanza province; DERLEYN 1978); Uganda (Kalinzu; PITMAN 1974 fide DERLEYN 1978).



*B. vauerocegae* and *procterae* occur in mountain ranges; *B. procterae* occurs at least as high as 2140 m (RASMUSSEN *et al.* 1995). *B. d. marlieri* is also restricted to higher altitudes, and in Zaire is not known from altitudes lower than 1300 m (LAURENT 1956). *B. d. depressiceps*, on the other hand, is known from lower elevations: 500-600 m on Macias Nguema (Fernando Poo), but also seems to reach higher altitudes (up to 2000 m; specimen [not examined] MRAC 76003.0221 from Zaire; Meirte, pers. comm.).

Biology.- As far as known, *Buhoma* are terrestrial snakes (RASMUSSEN *et al.* 1995; TRAPE 1985). *B. vauerocegae* seems to prefer rainforest habitats. It was found on the forest floor, and was demonstrated to feed on anurans. *B. procterae* occurs in forest and thick bush country, and a frog specimen (*Hoplophryne*) was identified as prey. These two species seem to be oviparous. The respective data sources are found in RASMUSSEN *et al.* (1995); these authors suggest that *vauerocegae* and *procterae* may be predominantly diurnal species.

Following TRAPE (1985) also *B. depressiceps* is terrestrial. One frog (*Arthroleptis variabilis*) was found in the stomach of one *depressiceps* specimen according to WERNER (1899), remains of a *Phrynobatrachus* in another specimen according to LAURENT (1956). The latter author stated that *B. d. marlieri* lives under leaf litter and grass, in the vicinity of swamps and ponds. DERLEYN (1978) collected *B. d. marlieri* from Burundi near brooks in forest. The author pointed out that specimens were extremely fragile and did not accept amphibian prey in captivity.

## SYSTEMATIC RELATIONSHIPS OF *Buhoma*

The position of *Geodipsas* within the framework of African colubrid systematics has always been isolated. BOGERT (1940) placed the genus as only member into his phenetic group III. PARKER (1949), partly relying on BOGERT (1940), postulated close relationships with the monotypic Sokotran genus *Ditypophis*, but it seems that he confused hemipenial data attributing *Geodipsas* a bilobed hemipenis. In any case *Ditypophis* clearly differs in dentition from *Geodipsas* (see PARKER 1949). UNDERWOOD (1967) mentioned the similarity of *Geodipsas* with some opistoglyphe genera of BOGERT's group VII. All these authors understood *Geodipsas* as including the African taxa, and thus their considerations are also true for the new genus *Buhoma*. Several of BOGERT's genus groups have been corroborated by phylogenetic studies, but others do not seem to be monophyletic assemblages (see CADLE 1994). *Geodipsas* was not included in recent immunological studies (CADLE 1994), and thus the systematic relationships of *Geodipsas* s. str. and *Buhoma* remain enigmatic. New,

comprehensive studies are needed before their relationships with other African and Malagasy taxa can be clarified.

Our decision of anticipating the description of the new genus *Buhoma* to the urgently necessary further clarification of colubrid systematics is also based on the renewed interest in the herpetofauna of Madagascar and its biogeographic origins. We wish to emphasize that our data do not support any sistergroup relationships between African and Malagasy colubrid taxa below the genus level, and that no biogeographic conclusion should be based on the former classification - implying close relationships - of African and Malagasy taxa belonging to a single genus *Geodipsas*.

## Systematics of the Malagasy *Geodipsas*

Beside the generic partition of the African and Malagasy taxa until now assigned to *Geodipsas*, a nomenclatural problem exists regarding this generic name. The genus *Geodipsas* was created in 1896 by Boulenger for two species from Madagascar, namely *Tachymenis infralineatus* and *Tachymenis boulengeri*. Two years before, Mocquard (1894) had erected the genus *Compsophis* for a single specimen of a new snake species from Montagne d'Ambre (northern Madagascar), which he named *Compsophis albiventris*. In contrast to *Geodipsas* this genus was considered as aglyphous (Guibé 1958) and thus both genera were not thought to be related. Nevertheless, number and relative size of maxillary teeth of both, as given by Guibé (1958), seem to be similar (Glaw & Vences 1994), and by external morphology no characters are known which would allow a distinction of the single known *Compsophis* specimen from *Geodipsas heimi*, which was described by Angel in 1936. In fact, Raxworthy & Nussbaum (1994) found *G. heimi* at the *Compsophis* type locality Montagne d'Ambre. If, by future studies, *Compsophis albiventris* is found to to be congeneric to *Geodipsas*, or even to be a senior synonym of *Geodipsas heimi*, the generic name *Geodipsas* must be considered a junior synonym of *Compsophis*. On the other hand, the type species *G. infralineata* differs considerably from the remaining Malagasy *Geodipsas* species but is phenetically similar to *Brygophis* (Tab. 2). One specimen (ZFMK 17740) from Madagascar, which was not considered in the present paper, shows characters of *Brygophis coulangesi* and of *Geodipsas infralineata*. It possibly represents a new species which, at present, can not clearly be assigned to either *Geodipsas* or *Brygophis*. Recent descriptions of numerous new colubrids from Madagascar (e. g. Domergue 1995, Cadle 1996) as well as the existence of several undescribed species identified by us in the ZFMK collection (e.g. Glaw & Vences 1996) demonstrate the lack of knowledge regarding this group. Further studies are needed to assess the status of the genera *Geodipsas*, *Compsophis*, and *Brygophis*.

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## Note added in proof

While the present paper was in press, another extensive study on *Geodipsas* systematics was published [Cadle, J. E. 1996: Systematics of snakes of the genus *Geodipsas* (Colubridae) from Madagascar, with descriptions of new species and observations on natural history. Bulletin of the Museum of comparative zoology 155(2): 33-87]. Basically, Cadle's data are in accordance with ours, but he applies several taxonomic modifications at the species level which should be mentioned here: (1) He describes two new species from Madagascar (*G. laphystia* and *G. zeny*); the former is most similar to *G. infralineata*, what partly explains our observations on large intraspecific variability in that taxon. Of the specimens studied by us, ZFMK 62292 and probably SMF 32614 belong to *G. laphystia*. (2) He synonymizes *G. heimi* with *G. boulengeri*; throughout our paper, the name *G. heimi* should therefore be changed to *G. boulengeri*.

Cadle provides hemipenial data for additional specimens of all species studied by us, and for two additional Malagasy species (*G. laphystia*, *G. zeny*). His data strongly support our conclusions by corroborating the hemipenial differences between *Geodipsas* and *Buhoma*. Cadle himself concludes "that improved clarity of the uncertainty surrounding relationship of the Malagasy species of *Geodipsas* is best served by removing the African species to another genus (...)." However, he defers "specific nomenclatural action to a future report" since he considers the hemipenial features of the African species (largely divided sulcus) as not derived. He also emphasizes the hemipenial differences between *B. depressiceps* on one hand and *B. procterae* and *B. vauerocegae* on the other (e.g. ring of hooked basal spines in the former), which we regard as less relevant.

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