



## Phylogenetic relationships and classification of the Malagasy pseudoxyrhophiine snake genera *Geodipsas* and *Compsophis* based on morphological and molecular data

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### Abstract

Based on a specimen found at Montagne d'Ambre in northern Madagascar morphologically agreeing with *Compsophis albiventris* Mocquard, 1894, we report on the rediscovery of this enigmatic snake genus and species and its molecular phylogenetic relationships. *Compsophis albiventris*, considered to be the only representative of its genus and unreported since its original description, bears strong morphological similarities to species of *Geodipsas* Boulenger, 1896. A molecular phylogeny based on DNA sequences of three mitochondrial and nuclear genes (complete cytochrome *b*, fragments of 16S rRNA and *c-mos*) in *Compsophis albiventris* and three *Geodipsas* species corroborated close relationships between *C. albiventris* and *Geodipsas boulengeri*, and showed that the genera *Compsophis* and *Geodipsas* together form a monophyletic unit. Despite the general similarities, morphological data and chromatic features support the existence of two species groups, corresponding to *Compsophis* and *Geodipsas*. We consequently consider *Geodipsas* as a subgenus of *Compsophis* and transfer all species currently in *Geodipsas* into the genus *Compsophis*.

**Key words:** Squamata, Serpentes, Lamprophiidae, Pseudoxyrhophiinae; *Compsophis*; *Geodipsas* syn. nov.; *Compsophis albiventris*; *Compsophis boulengeri* comb. nov.; *Compsophis fatsibe* comb. nov.; *Compsophis infralineatus* comb. nov.; *Compsophis laphystius* comb. nov.; *Compsophis vinckei* comb. nov.; *Compsophis zeny* comb. nov.

### Introduction

The caenophidian snakes of Madagascar, except the psammophiine genus *Mimophis*, belong to a large radiation considered as subfamily Pseudoxyrhophiinae which also contains the Socotran endemic genus *Ditypophis* as most basal lineage (Nagy *et al.* 2003), and possibly also the southern African slug eaters, genus *Duberria*, in a phylogenetically nested position (Lawson *et al.* 2005). Pseudoxyrhophiines have classically been included in the family Colubridae which has recently been demonstrated to be paraphyletic, and thus its taxa have been rearranged over various families (e.g., Lawson *et al.* 2005; Vidal *et al.* 2007). We here follow the proposal of Vidal *et al.* (2007) to include the Pseudoxyrhophiinae in a family Lamprophiidae which is phylogenetically sister to the Elapidae, but it seems clear that further changes will be necessary in caenophidian family-level classification as results from more and more comprehensive datasets keep becoming available. Taxonomy of pseudoxyrhophiines has been summarized by Cadle (2003), and three new species have been described since then (Glaw *et al.* 2005a, b; Mercurio & Andreone 2005). Malagasy pseudoxyrhophiines currently contain 17 genera and ca. 72 species, although additional species have already been identified and are currently awaiting description.

The genus *Compsophis* was erected by Mocquard (1894) to accommodate a new species of snake from the Montagne d'Ambre massif in far northern Madagascar, *Compsophis albiventris* Mocquard, 1894. This species was described based on a single probably juvenile male specimen and the original characterization of its dentition was very short ("dentition diacrantérienne; dents mandibulaires antérieures plus longues que les postérieures"). Two years after Mocquard's description of the genus *Compsophis*, Boulenger (1896) erected in his snake catalogue the genus *Geodipsas* to accommodate the two Malagasy species *Geodipsas infralineata* (Günther, 1882) and *G. boulengeri* (Peracca, 1892). In the same catalogue he also listed the genus *Compsophis*, in the "Addenda and Corrigenda to Volume I" (which includes aglyphous snakes). Boulenger (1896: 609–610) provided the following information on the dentition of *Compsophis*: "Posterior maxillary teeth largest, separated from the rest by an interspace; anterior mandibular teeth longer than the posterior." As *Compsophis* has not been described as opisthoglyphous, he apparently overlooked the similarities to his opisthoglyphous genus *Geodipsas* ("maxillary teeth 14 or 15, equal, followed, after an interspace, by a pair of enlarged grooved fangs"). Guibé (1958) classified *Compsophis* as aglyphous and described a new detail of the maxillary dentition indicating that he had studied the dentition by himself ("dents maxillaires au nombre de 18, inégales, les 2 dernières fortement allongées et séparées des précédentes par un intervalle").

Subsequent descriptions of Malagasy *Geodipsas* were those of *G. heimi* Angel, 1936 and *G. vinckei* Domergue, 1988. Loveridge (1957) designated *infralineata* as type species of *Geodipsas*. More recently, Ziegler *et al.* (1997) excluded the three species from continental Africa (*G. depressiceps*, *G. procterae*, and *G. vauerocegae*) that had previously been placed in *Geodipsas* and transferred them into the new genus *Buhoma*, and Cadle (1996) described two new species from Madagascar, *G. laphystia* and *G. zeny*, and placed *G. heimi* into the synonymy of *G. boulengeri*. After the latest description of *G. fatsibe* by Mercurio & Andreone (2005), *Geodipsas* is currently a genus endemic to Madagascar containing six described species: *Geodipsas boulengeri*, *G. fatsibe*, *G. infralineata*, *G. laphystia*, *G. vinckei*, and *G. zeny*.

Since the original description by Mocquard (1894) no other snake specimens have been assigned to *Compsophis albiventris*. Here we report on the discovery of an adult snake at Montagne d'Ambre which is assignable to this species by external morphology and colouration. Based on novel molecular data we found this specimen, that had already been included in the phylogenetic study of Nagy *et al.* (2003), to be phylogenetically very close to *Geodipsas* and therefore propose nomenclatural consequences.

## Material and methods

Snakes were anesthetized, fixed in formalin, and stored in 70% ethanol. Muscle tissue samples were taken from freshly killed specimens in the field and preserved in 98% ethanol. Meristic and mensural terminology follows Cadle (1996). Snout-vent length (SVL) and tail length (TL) were measured to the nearest millimeter with a caliper. Counts of ventral scales are ventrals without preentrals. Museum acronyms used are: Hessisches Landesmuseum, Darmstadt, Germany (HLMD); Muséum National d'Histoire Naturelle, Paris, France (MNHN); Museo Regionale di Scienze Naturali, Torino, Italy (MRSN); Université d'Antananarivo, Département de Biologie Animale, Madagascar (UADBA); National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM); Zoological Museum, University of Amsterdam, The Netherlands (ZSM); and Zoologische Staatssammlung, München, Germany (ZMA).

DNA was extracted using standard protocols (Sambrook *et al.* 1989). The complete mitochondrial gene cytochrome *b* as well as a fragment of the mitochondrial gene 16S rRNA and a fragment of the nuclear protooncogene *c-mos* were amplified in PCRs using the same primers as in Nagy *et al.* (2003). PCR products were directly sequenced on different ABI Prism Genetic Analyzer automated sequencers (Applied Biosystems, Foster City, USA). Sequences were checked for quality and aligned by hand or using ClustalX 1.83 (the latter for 16S rDNA sequences only, Thompson *et al.* 1997).

In all phylogenetic analyses, the single Socotran endemic pseudoxyrhophiine snake, *Ditypophis vivax*, was used as the outgroup. Parsimony analyses were carried out using the computer program PAUP\*, version 4b10 (Swofford 2002). We calculated 2000 bootstrap replicates as a measure of branch support. Bayesian analyses of phylogenetic inference were carried out running  $2 \times 10^6$  generations in four chains in the program MrBayes (Ronquist & Huelsenbeck 2003) under substitution models selected by the software MrModeltest (Nylander 2004). Newly obtained DNA sequences were deposited in GenBank; voucher specimens and accession numbers are listed in Table 1.

**TABLE 1.** Voucher specimens and GenBank accession numbers of specimens used in molecular analysis.

Species	Voucher specimen	Locality	GenBank accession number, cytochrome <i>b</i>	GenBank accession number, 16S rRNA	GenBank accession number, c-mos
<i>Compsophis albiventris</i>	ZSM 497/2000	Mt. d'Ambre	AY188011	AY188050	AY187972
<i>Compsophis boulengeri</i>	ZSM 77/2005	Andasibe	EF203995	EF204007	EF204001
<i>Compsophis infralineatus</i>	ZSM 378/2000	Manjakatempo	AY188017	AY188056	AY187978
<i>Compsophis infralineatus</i>	ZSM 78/2005	Andohahela, 1550 m alt.	EF203994	EF204006	EF204000
<i>Compsophis infralineatus</i>	UADBA 20989	Vohiparara/Ranomafana	EF203990	EF204002	EF203996
<i>Compsophis infralineatus</i>	ZMA 20217	Vohiparara/Ranomafana	EF203993	EF204005	EF203999
<i>Compsophis laphystius</i>	UADBA 24490	Vohiparara/Ranomafana	EF203991	EF204003	EF203997
<i>Compsophis laphystius</i>	UADBA 24499	Vohiparara/Ranomafana	EF203992	EF204004	EF203998
<i>Alluaudina bellyi</i>	MRSN R1836	Berara	AY188005	AY188044	AY187966
<i>Ditypophis vivax</i>	HLMD RA-2972	Socotra (Yemen)	AY188013	AY188052	AY187974
<i>Ithycyphus miniatus</i>	MRSN R1924	Berara	AY188019	AY188058	AY187980
<i>Langaha madagascariensis</i>	ZSM 636/2000	no locality data	AY188020	AY188059	AY187981

## Results and discussion

### Redescription and morphological relationships of *Compsophis albiventris*

The relationships of *Compsophis* have long remained enigmatic due to the paucity of available material and its aglyphous dentition. For example, based on this character, the genus was assigned to the tribe Heteroiodontini by Meirte (1992), while *Geodipsas* was assigned to the Geodipsadini despite the overall morphological similarity of the two genera. Glaw & Vences (1994) noted that except for the aglyphous vs. opisthoglyphous condition, the differences in dentition were minimal (16 vs. 14–15 maxillary teeth followed after an interspace by two enlarged fangs that are either ungrooved or grooved), and hypothesized that future studies may show *Geodipsas* to be a junior synonym of *Compsophis*. Cadle (1996), too, recognized the similarity of these two taxa, and referred to a forthcoming study (not published so far to our knowledge) that would address the relationships of *C. albiventris* to *Geodipsas boulengeri*, which he considered to be complicated by the dentitional variation.

The present study mainly relies on one new snake specimen from Montagne d'Ambre (12°31'S, 49°10'E, ca. 1000 m elevation) that was collected on 18 March 2000 by M. Vences, F. Glaw and K. Glaw at night on a low bush near a relatively fast flowing stream, just a few hundred meters from the visitor's building ("Gite"). This new specimen (Figs. 1–3), probably an adult female (ZSM 497/2000), compares as follows to the holo-

type (data of holotype MNHN 1893.212 after Mocquard [1894] and Guibé [1958] in parentheses): Total length 504 mm (167 mm), snout-vent length 430 mm (139 mm); tail length 74 mm (28 mm); 19 dorsal scale rows at midbody (19); dorsal scales smooth and without apical pits (same state in the holotype); 149 ventrals (148); 38 subcaudals in two rows (41 in two rows); head distinct from neck (distinct from neck); 1 loreal scale (1); 1 preocular scale (1); 2 postocular scales (2); anal scale undivided (undivided); 7 supralabials on right side, third and fourth in contact with eye (7, third and fourth in contact with eye) [an exceptional state is present on the left side with only 6 well recognizable supralabials, of which only the third is in contact with the eye (see Fig. 3b)]; 9 infralabials, the first four in contact with anterior gular scales (9 infralabials, the first four in contact with anterior gular scales); ca. 15 ungrooved maxillary teeth on the right side, followed posteriorly after a distinct gap by two distinctly enlarged and clearly grooved teeth (18 ungrooved maxillary teeth, the two posteriormost distinctly enlarged and separated by an interval from the others according to Guibé); pupil almost round (round), actually a broad, prolate ellipse (see Fig. 1 and Cadle 1996: 66) although the shape of the contracted pupil is unknown; dorsum and flanks uniformly brown with a poorly recognizable dark vertebral line as visible in Fig. 1 (uniformly dark brown according to Mocquard, with a dark vertebral line according to Guibé); light stripes and circular whitish spots on the upper labials as visible in Fig. 1 (yellowish spots on the upper labials); a larger light spot on each side of the neck ("une tache blanc jaunâtre allongée aux niveau de l'os carre" according to Mocquard, these spots are not mentioned or shown in Guibé); venter bright white (whitish).



**Figure 1.** *Compsophis albiventris*, specimen from Montagne d'Ambre (ZSM 497/2000) in life.

Despite the apparent aglyphous state in the holotype of *Compsophis albiventris* we have no doubt that the new specimen is conspecific with this species (unfortunately, the holotype is in loan since over ten years and was therefore not available for our study). The almost perfect agreement of meristic characters which are not found in this combination in any other Malagasy snake, together with the full congruence in colour and pattern and the same collecting locality, are unambiguous in this respect. We therefore hypothesize that the agly-



phous dentition of the holotype of *Compsophis albiventris* may be a character of juveniles of this species or an abnormal individual state.



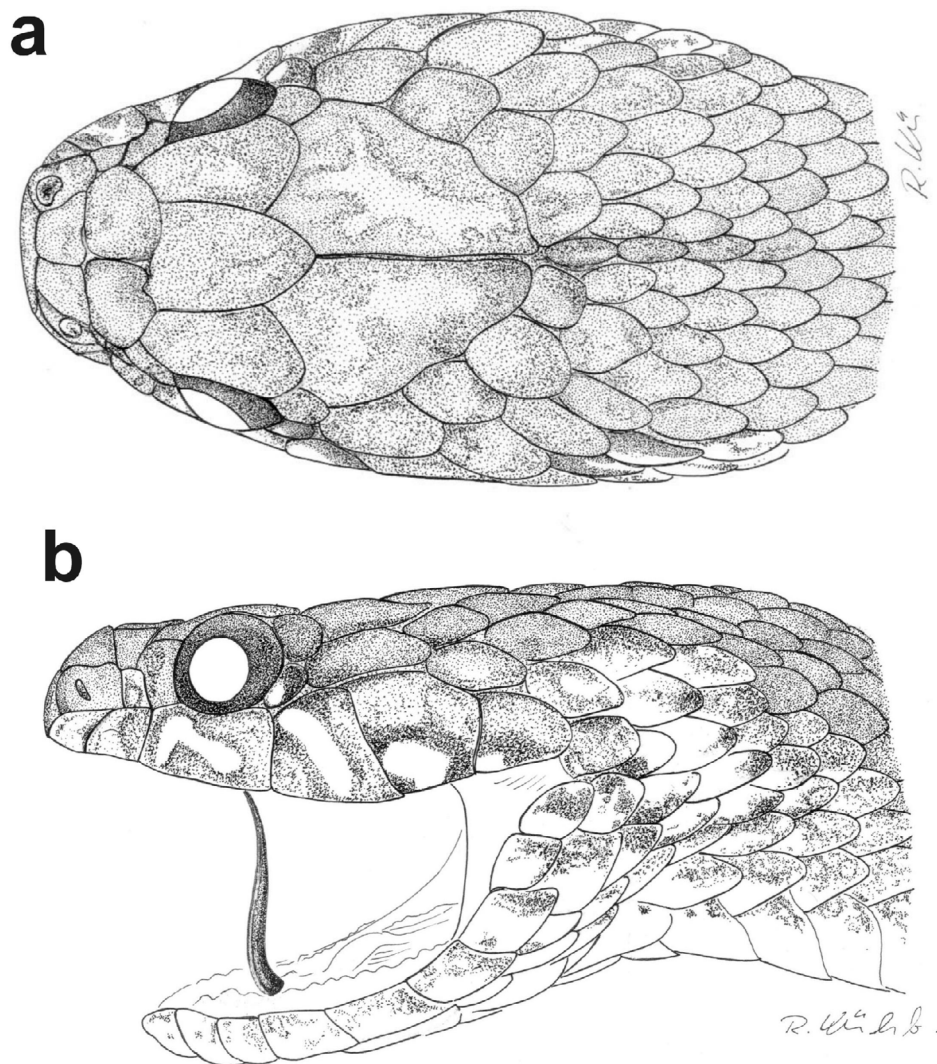
**Figure 2.** *Compsophis albiventris* (ZSM 497/2000) in life, showing the white venter which is emphasized in the species name.

The meristic characters of *Compsophis albiventris* remarkably agree with *Geodipsas boulengeri*. The latter species, according to the data in Cadle (1996) and Ziegler *et al.* (1997), has 19 dorsal scale rows, 131–137 ventrals, 24–36 subcaudals, and a maximum SVL of 298 mm. In addition, this species shares with *albiventris* the uniform brownish back colour, light spots on the upper labials, light neck spots behind the jaw angle, and a uniformly coloured venter which, however, is usually red in life (becoming yellowish in preservative). Cadle (1996) compared his specimens of *G. boulengeri* with five preserved specimens of "*Geodipsas species inquirenda*" from Montagne d'Ambre (the type locality of *Compsophis albiventris*) which were characterized by having 143–150 ventrals, an immaculate ventral region, larger supralabial spots, and neck spots behind the jaw angle. These characters agree with the holotype of *Compsophis albiventris*, and we therefore assume that these specimens (including the four vouchers MNHN 1978.2786, 1986.1379; 1986.1380; USNM 149836; not examined by us) are to be referred to this species, although their ventral colour was not mentioned by Cadle (1996). We also assume that the specimen records of *Geodipsas boulengeri* in Montagne d'Ambre (as *G. heimi*, now junior synonym of *G. boulengeri*) listed by Raxworthy & Nussbaum (1994) refer in fact to *Compsophis albiventris* which was not recorded in that paper.

#### Molecular phylogeny

A data set of DNA sequences comprising of 2197 nucleotide positions (aligned) was used in our phylogenetic analyses. Confirming the results of Nagy *et al.* (2003), the present, more detailed study proves the monophyly of the common *Compsophis-Geodipsas* branch in all analyses with very high support (Fig. 4). However, *Geodipsas* as currently understood turned out to be paraphyletic and to contain *Compsophis albiventris* in a

nested position. Within the *Compsophis-Geodipsas* clade, two subclades were found: The first of these contained *Compsophis albiventris* positioned sister to *Geodipsas boulengeri*, the second clade contained *Geodipsas infralineata* and *G. laphystia*.



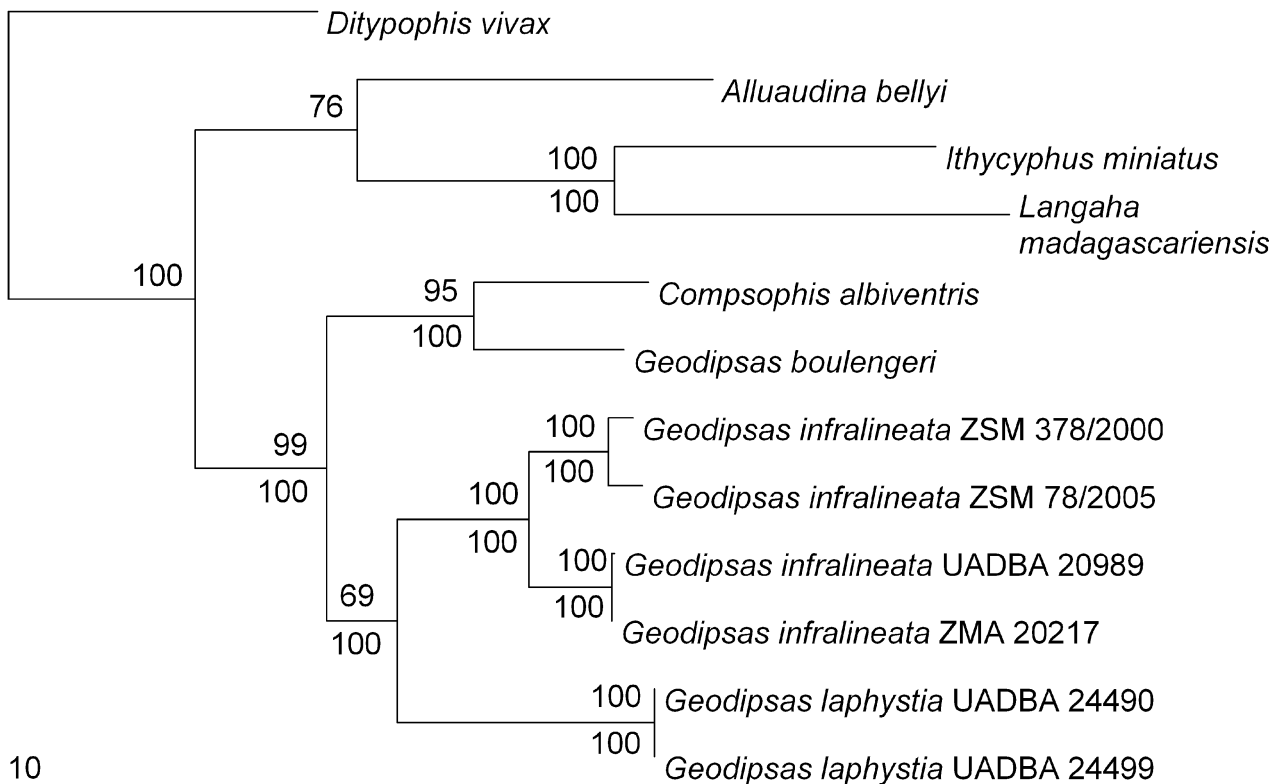
**Figure 3.** Dorsal (a) and lateral (b, left side) view of head scalation in *Compsophis albiventris* (ZSM 497/2000).

Genetic divergences of *Compsophis* to species of *Geodipsas* were relatively low. Comparing cytochrome *b* sequences only, uncorrected p-distances were 13.2% between *C. albiventris* and *G. infralineata*, and 12.1% between *C. albiventris* and *G. boulengeri*, which is similar to or even lower than other intrageneric divergences known from Malagasy snakes (e.g., 14.3% between the two species of *Dromicodryas*; see Nagy *et al.* 2003 for further details).

Another interesting finding is the surprisingly high genetic divergence within *Geodipsas infralineata*. According to the data presented here, specimens of *infralineata* are divided into two clades of relatively high genetic divergence (4.7–4.8% uncorrected pairwise distance in cytochrome *b*). These correspond to (1) specimens from the highland localities of Ankaratra and Andohahela, and (2) to the mid-altitude locality of Ranomafana National Park. Specimen UADBA 20989 from Ranomafana is an adult male of 465 mm SVL and 139 mm tail length, 183 ventrals and 76 subcaudals. ZSM 78/2005 from Andohahela is an adult male (with everted hemipenes) of 547 mm SVL and 147 mm tail length, 180 ventrals and 65 subcaudals. ZSM 378/

2000 from Manjakatempo (Ankaratra Massif) has a SVL of 465 mm, 178 ventrals and a mutilated tail.

Although obvious differences do not result from these data and Cadle (1996) did not mention morphological differences between high- and mid-altitude populations of *infralineata*, we consider the high genetic divergences as indicative of possible differentiation at the species level. To understand the distribution and differentiation of these candidate species, it will be necessary to screen a larger number of specimens for both molecular and morphological characters.



**Figure 4.** Molecular phylogenetic relationships based on multigene analyses of three species previously assigned to *Geodipsas*, and *Compsophis albiventris*. Parsimony bootstrap values in percent (based on 2000 replicates) are shown above the branches and Bayesian posterior probabilities (based on  $2 \times 10^6$  generations) under the branches. Scale represents ten (evolutionary) changes in sequences.

#### Relationships and classification of *Geodipsas* and *Compsophis*

As pointed out above, the morphological and chromatic characters and the agreement of the collecting locality leave no doubts that the specimen ZSM 497/2000, and very probably the specimens considered by Cadle (1996) as "*Geodipsas* species inquirenda", are to be assigned to *Compsophis albiventris*, and that the aglyphous dentition of the holotype of this species is a juvenile or abnormal condition. The alternative would imply that two species, identical in various meristic and chromatic characters which are otherwise unique among Malagasy pseudoxyrhophiines, and differing only in dentition, would coexist at an isolated rainforest site in northernmost Madagascar, a highly unlikely scenario.

The molecular data corroborated the hypothesis, based on morphological similarity and already proposed by Cadle (1996), that *Compsophis albiventris* is closely related to *Geodipsas boulengeri*. The clade containing these two species is sister to the remaining *Geodipsas* in our phylogenetic analysis. These two clades are also supported by meristic data and colouration:

Group 1: The three species *infralineata*, *fatsibe* and *laphystia* are larger, mainly arboreal and nocturnal snakes (maximum SVL 469–635 mm, max. tail length 135–153 mm) with 172–198 ventrals and 53–82 subcaudals. The head is very distinct from the neck. The upper lip is usually light with a dark stripe above the

supralabials from the eye to the neck (the supralabials are usually yellowish in *laphystia* and whitish with dark vertical lines at the border of the supralabials in *infralineata* and *fatsibe*). There is no light spot or collar in the neck (although dark neck spots can occur). In most cases a partial dark midventral line (which can be fragmented in a series of dots) can be found on venter and tail. The dorsal colour pattern mostly includes longitudinal (*laphystia*) or diagonal (*infralineata*, *fatsibe*) lines.

Group 2: The four species *albiventris*, *boulengeri*, *vinckei* and *zeny* are small, apparently more terrestrial and diurnal snakes (maximum SVL 228–411 mm, max. tail length 53–84 mm) with 131–163 ventrals and 24–45 subcaudals. The head is moderately distinct from the neck. These snakes, with the exception of *zeny*, share further similarities in colouration: the upper lip is dark with conspicuous distinct light spots on the supralabials (a pattern unknown from any other Malagasy snake), a light spot is present on each side of the neck (fused to a collar in *vinckei*), there is no dark midventral line (a few spots can be present), and the dorsum is uniformly dark without longitudinal or diagonal lines. The colouration of *zeny* with a distinct midventral line, a dorsal pattern of lines, the absence of a light neck spot, and the absence of distinct light spots on the supralabials resembles more strongly the pattern observed in species of group 1 but its morphological and meristic characteristics lead us to include this species in group 2.

These two groups appear to represent two monophyletic sister clades that could be recognized as different genera. In this case, the name *Geodipsas* would correspond to group 1 and *Compsophis* to group 2. However, the ambiguous position of *zeny* with respect to colouration, indicates that such a classification may be unstable and subject to further change once that more data on this enigmatic species become available. While no clear synapomorphies are known for the phenetic groups 1 and 2 as defined here, the constantly undivided anal scale is likely to constitute a synapomorphic trait for the clade of both groups. Furthermore, the genital morphology of these snakes, especially their nonbilobed hemipenis, the distally divided sulcus spermaticus, and general detailed similarity in form and ornamentation provide an important array of further possible synapomorphies (Cadle 1996; Ziegler *et al.* 1997), including *Compsophis* as "*Geodipsas* species inquirenda" (Cadle 1996:72), despite similarities to the hemipenes of *Alluaudina* (Ziegler *et al.* 1997). As an additional argument, the genetic divergence between the *albiventris*-*boulengeri* clade and the other sampled *Geodipsas* is relatively low (e.g., cytochrome *b* p-distance of 13.2% between *C. albiventris* and *G. infralineata*) in comparison to the divergence between other Malagasy pseudoxyrhophiine genera (recorded values of ca. 18–23%).

Finally, the mosaic-like distribution of colour features in *zeny* and the generally poor knowledge about variation and habits of most species concerned does not warrant a generic recognition at present. We therefore propose to include *Geodipsas* as a subgenus in *Compsophis*:

*Compsophis* Mocquard, 1894

Subgenus *Compsophis* Mocquard, 1894

(1) *Compsophis* (*C.*) *albiventris* Mocquard, 1894

(2) *Compsophis* (*C.*) *boulengeri* (Peracca, 1892) **new combination**

*Tachymenis boulengerii* Peracca, 1892

*Geodipsas heimi* Angel, 1936

(3) *Compsophis* (*C.*) *vinckei* (Domergue, 1988) **new combination**

*Geodipsas vinckei* Domergue, 1988

(4) *Compsophis* (*C.*) *zeny* (Cadle, 1996) **new combination**

*Geodipsas zeny* Cadle, 1996

Subgenus *Geodipsas* Boulenger, 1896

(5) *Compsophis* (*G.*) *fatsibe* (Mercurio & Andreone, 2005) **new combination**

*Geodipsas fatsibe* Mercurio & Andreone, 2005

(6) *Compsophis* (*G.*) *infralineatus* (Günther, 1882) **new combination**



*Tachymenis infralineatus* Günther, 1882

(7) *Compsophis* (*G.*) *laphystius* (Cadle, 1996) **new combination**

*Geodipsas laphystia* Cadle, 1996

**Diagnosis:** The genus *Compsophis* is distinguished from all other Malagasy caenophidian snakes by the following combination of characters: Opisthoglyphous snakes with two distinctly enlarged and clearly grooved fangs posteriorly. Pupil almost round; 19–21 dorsal scale rows at midbody which undergo posterior reduction to 17–19 rows; dorsal scales smooth and without apical pits; 131–198 ventrals, anal plate undivided, 24–82 subcaudals in two rows; head distinct from neck; 7 supralabials, the third and fourth in contact with eye; 9 infralabials; one loreal (exceptionally two), one preocular, two or three postocular scales; hemipenes simple (nonbilobed), with distal or terminal division of the sulcus spermaticus.

This conservative classification reflects the monophyly and the close relationships of *Compsophis* and *Geodipsas* on the one hand and also allows to address each of the two species groups by a nomenclaturally valid name. Future molecular studies including the species *fatsibe*, *vinckei* and especially *zeny* are necessary to test the assumed monophyly of the two clades. These studies should also investigate the relationships of the monotypic genus *Brygophis* Domergue & Bour, 1988 which is very similar to the subgenus *Geodipsas* by meristic data (Ziegler *et al.* 1997; Andreone & Raxworthy 1998) and therefore could turn out to be a junior synonym of *Geodipsas*.

## Acknowledgements

We wish to thank Kathrin Glaw, Meik Landsberger, and Angelun Razafimanantsoa for their help in the field, Ruth Kühbandner for preparing the line drawings, John Cadle for fruitful discussions, and the Malagasy authorities for research and export permits. The research of ZTN in Amsterdam was financially supported by the Synthesys program (EU FP6).

## References

- Andreone, F. & Raxworthy, C.J. (1998) The colubrid snake *Brygophis coulangesi* (Domergue 1988) rediscovered in north-eastern Madagascar. *Tropical Zoology*, 11, 249–257.
- Boulenger, G.A. (1896) Catalogue of the snakes in the British Museum (Natural History). Volume III. London, British Museum (Natural History), 727 pp. + 25 plates.
- 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, 33–87.
- Cadle, J.E. (2003) Colubridae, snakes, *In*: Goodman, S.M. & Benstead, J.P. (Eds.), *The Natural History of Madagascar*. The University of Chicago Press, Chicago and London, pp. 997–1004.
- Domergue, C.A. (1988) Notes sur les serpents de la région malgache. VIII. Colubridae nouveaux. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Ser. 4*, 10, 135–146.
- Glaw, F., Franzen, M. & Vences, M. (2005a) A new species of colubrid snake (*Liopholidophis*) from northern Madagascar. *Salamandra*, 41, 83–90.
- Glaw, F. & Vences, M. (1994) *A Fieldguide to the Amphibians and Reptiles of Madagascar*. Second edition. Vences & Glaw Verlag, Köln, 480 pp.
- Glaw, F., Vences, M. & Nussbaum, R.A. (2005b) A new species of *Heteroliodon* (Reptilia: Squamata: Colubridae) from Montagne des Français, far northern Madagascar. *Herpetologica*, 61, 275–280.
- Günther, A. (1882) Ninth contribution to the knowledge of the fauna of Madagascar. *Annals and Magazine of Natural History*, 1882 (April), 261–266.
- Guibé, J. (1958) Les serpents de Madagascar. *Memoires de l'Institut Scientifique de Madagascar*, 12, 189–260.
- Lawson, R., Slowinski, J.B., Crother, B.I. & Burbrink, F.T. (2005) Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, 37, 581–601.

- Loveridge, A. (1957) Check list of the reptiles and amphibians of East Africa (Uganda, Kenya, Tanganyika, Zanzibar). *Bulletin of the Museum of Comparative Zoology at Harvard College*, 117, 153–362.
- Meirte, D. (1992) Cles de détermination des serpents d'Afrique. *Annales Musée Royale de l'Afrique Centrale, Tervuren, Sci. Zoologie*, 267: 1–152.
- Mercurio, V. & Andreone, F. (2005) Description of a new *Geodipsas* snake from northern Madagascar (Squamata: Colubridae). *Zootaxa*, 1093, 61–68.
- Mocquard, F. (1894) Reptiles nouveaux ou insuffisamment connus de Madagascar. *Compte Rendu sommaire des Séances de la Société Philomathique de Paris*, 17, 1–8.
- Nagy, Z.T., Joger, U., Wink, M., Glaw, F. & Vences, M. (2003) Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mitochondrial gene phylogenies. *Proceedings of the Royal Society, London: Biological Sciences*, 270, 2613–2621.
- Nylander, J.A.A. (2004) MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Raxworthy, C.J. & Nussbaum, R.A. (1994) A rainforest survey of amphibians, reptiles and small mammals at Montagne d'Ambre, Madagascar. *Biological Conservation*, 69, 65–73.
- Ronquist, F., & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
- Sambrook, J., Fritsch, E.F. & Maniatis, T. (1989) *Molecular Cloning: A Laboratory Manual*. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory.
- Swofford, D.L. (2002) *PAUP\**. *Phylogenetic Analysis Using Parsimony (and other methods)*, v. 4b10. Sunderland, MA: Sinauer.
- Thompson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, 24, 4876–4882.
- Vidal, N., Delmas, A.-S., David, P., Cruaud, C., Couloux, A. & Hedges, S.B. (2007) The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein-coding genes. *Comptes Rendus Biologies*, 330, 182–187.
- Ziegler, T., Vences, M., Glaw, F. & Böhme, W. (1997) Genital morphology and systematics of *Geodipsas* Boulenger, 1896 (Reptilia: Serpentes: Colubridae), with description of a new genus. *Revue Suisse de Zoologie*, 104, 95–114.