



## Dissecting the major African snake radiation: a molecular phylogeny of the Lamprophiidae Fitzinger (Serpentes, Caenophidia)

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### Abstract

The Elapoidea includes the Elapidae and a large (~60 genera, 280 sp.) and mostly African (including Madagascar) radiation termed Lamprophiidae by Vidal *et al.* (2007), that includes at least four major groups: the psammophiines, atractaspidines, lamprophiines and pseudoxyrhophiines. In this work, we reviewed the recent taxonomic history of the lamprophiids, and built a data set including two nuclear protein-coding genes (*c-mos* and *RAG2*), two mitochondrial rRNA genes (12S and 16S rRNA) and two mitochondrial protein-coding genes (cytochrome *b* and ND4) for 85 species belonging to 45 genera (thus representing about 75% of the generic diversity and 30% of the specific diversity of the radiation), in order to clarify the phylogenetic relationships of this large and neglected group at the subfamilial and generic levels. To this aim, 480 new sequences were produced. The vast majority of the investigated genera fall into four main monophyletic clusters, that correspond to the four subfamilies mentioned above, although the content of atractaspidines, lamprophiines and pseudoxyrhophiines is revised. We confirm the polyphyly of the genus *Stenophis*, and the relegation of the genus name *Dromophis* to the synonymy of the genus name *Psammophis*. *Gonionotophis brussauxi* is nested within *Mehelya*. The genus *Lamprophis* Fitzinger, 1843 is paraphyletic with respect to *Lycodonomorphus* Fitzinger, 1843. *Lamprophis swazicus* is the sister-group to *Hormonotus modestus*, and may warrant generic recognition. Molecular data do not support the traditional placement of *Micrelaps* within the Atractaspidinae, but its phylogenetic position, along with that of *Oxyrhabdium* (previously considered to belong to the Xenodermatidae), requires additional molecular data and they are both treated as Elapoidea *incertae sedis*. The interrelationships of Psammophiinae, Atractaspidinae, Lamprophiinae, Pseudoxyrhophiinae, *Prosymna* (13 sp.), *Pseudaspis* (1 sp.) and *Pythonodipsas* (1 sp.), *Buhoma* (2 species), and *Psammodynastes* (1 sp.) remain unresolved. Finally, the genus *Lycognathophis*, endemic to the Seychelles, does not belong to the African radiation, but to the Natricidae.

**Key words:** Alethinophidia, Atractaspidinae, *c-mos*, cytochrome *b*, *Dromophis*, Elapoidea, *Gonionotophis*, *Hormonotus*, Lamprophiinae, *Lamprophis*, *Lycodonomorphus*, *Lycognathophis*, *Mehelya*, *Micrelaps*, ND4, *Oxyrhabdium*, Psammophiinae, *Psammophis*, Pseudoxyrhophiinae, *RAG2*, *Simocephalus*, *Stenophis*, 16S rRNA, 12S rRNA

## Introduction

Eighty per cent of the approximately 3150 living species of snakes are placed in the taxon Caenophidia (advanced snakes) (Uetz *et al.* 2008). Recent molecular studies have helped to clarify interfamilial relationships within Caenophidia (Vidal & Hedges 2002a; Kelly *et al.* 2003; Lawson *et al.* 2005; Vidal *et al.* 2007). In particular, a clade named Elapoidea by Vidal *et al.* (2007) was shown to include elapids (cobras, mambas, coral snakes, sea snakes) and a large and mostly African (including Madagascar) radiation there named Lamprophiidae. Although based on a restricted taxonomic sampling, all phylogenies using nuclear protein-coding genes only (genes suited for resolving higher-level snake phylogenetic relationships) have found the lamprophiids *sensu* Vidal *et al.* (2007) to be monophyletic (Vidal & Hedges 2002a, 2004; Vidal *et al.* 2007, 2009; Alfaro *et al.* 2008), and we therefore use Lamprophiidae in that sense here. The lamprophiids (~60 genera, 280 sp.) include four major groups: the psammophiines (~7 genera, 42 sp.), atractaspidines (~12 genera, 70 sp.), lamprophiines (~19 genera, 88 sp.) and pseudoxyrhopiines (~20 genera, 80 sp.) (Vidal 2002; Vidal & Hedges 2002a; Vidal *et al.* 2007). Following Vidal *et al.* (2007, 2009), Fry *et al.* (2008), and Vonk *et al.* (2008), we treat these groups as subfamilies of the African lamprophiid radiation, although others have afforded them family status, including Lamprophiidae, Psammophiidae, Pseudoxyrhopiidae (Kelly *et al.* 2008) and Atractaspididae (Branch 1998; Zaher 1999; Shine *et al.* 2006), while additional families, Prosymnidae (genus *Prosymna*) and Pseudaspididae (genera *Pseudaspis* and *Pythonodipsas*), have recently been proposed (Kelly *et al.* in press).

The psammophiines (genera *Dipsina*, *Hemirhagerrhis*, *Malpolon*, *Mimophis*, *Psammophis*, *Psammophylax*, *Rhamphiophis*) are distributed throughout Africa including Madagascar, the Middle East, south-central Asia, and southern Europe (Branch 1998; Kelly *et al.* 2008). *Dromophis* was recently synonymized with *Psammophis* (Kelly *et al.* 2008). Most psammophiines are diurnal, fast-moving terrestrial snakes that actively hunt their prey (Branch 1998), and their monophyly is supported by morphological and molecular data (Cadle 1994; Brandstätter 1995; Zaher 1999; Vidal & Hedges 2002a; Kelly *et al.* 2008).

A suite of genera have usually been assigned to the atractaspidines (*Amblyodipsas*, *Aparallactus*, *Atractaspis*, *Brachyophis*, *Chilorhinophis*, *Elapotinus*, *Homoroselaps*, *Hypoptophis*, *Macrelaps*, *Micrelaps*, *Poecilopholis* (?), *Polemon*, *Xenocalamus*) (McDowell 1968, 1986; Underwood & Kochva 1993; Branch 1998; Spawls & Branch 1995) which are distributed broadly in Africa, with a limited occurrence in the Middle East (Underwood & Kochva 1993). They are fossorial and/or nocturnal snakes that lack a loreal, and have smooth shiny scales, slender bodies, relatively small heads with indistinct necks, small eyes, and short tails (Shine *et al.* 2006). The monophyly of atractaspidines is supported both by morphological (McDowell 1968, 1986; Underwood & Kochva 1993; Zaher 1999) and molecular data (Vidal & Hedges 2002a; Nagy *et al.* 2005), although inclusion of the rarer genera (e.g. *Brachyophis*, *Chilorhinophis*, *Elapotinus*, *Hypoptophis*, *Micrelaps*, and *Poecilopholis*) has not been rigorously assessed.

The pseudoxyrhopiines *sensu* Zaher (1999), Nagy *et al.* (2003) and Lawson *et al.* (2005) include the genera *Alluaudina*, *Brygophis*, *Compsophis*, *Ditytophis*, *Dromicodryas*, *Duberria*, *Exallodontophis*, *Geodipsas*, *Heteroliodon*, *Ithycyphus*, *Langaha*, *Leioheterodon*, *Liophidium*, *Liopholidophis*, *Lycodryas*, *Madagascarophis*, *Micropisthodon*, *Pararhadinaea*, *Pseudoxyrhopus*, *Stenophis*, and *Thamnosophis*. *Geodipsas* has recently been placed in the synonymy of *Compsophis* (Glaw *et al.* 2007a), and *Bibilava* in the synonymy of *Thamnosophis* (Glaw *et al.* 2007b; Cadle & Ineich 2008). All genera of Malagasy caenophidian snakes, with the exception of the psammophiine *Mimophis* (Vidal & Hedges 2002a; Kelly *et al.* 2008), belong to a single radiation (Nagy *et al.* 2003). A few pseudoxyrhopiines are also found in the Comoros, *Ditytophis* is endemic to Socotra, and *Duberria* endemic to Africa. Pseudoxyrhopiines have a broad variety of lifestyles including terrestrial and arboreal, as well as nocturnal and diurnal snakes.

The content of Lamprophiinae remains problematic. In a list of African genera placed in the families Atractaspididae and 'Colubridae', Zaher (1999) included in his 'Boodontinae' many of the genera listed by

previous authors (e.g. Dowling & Duelman 1978; Dowling *et al.* 1996), i.e. *Boaedon*, *Bothrolycus*, *Bothrophthalmus*, *Chamaelycus*, *Cryptolycus*, *Dendrolycus*, *Dipsina*, *Dromophis*, *Gonionotophis*, *Grayia*, *Hormonotus*, *Lamprophis*, *Lycodonomorphus*, *Lycophidion*, *Macroprotodon*, *Mehelya*, *Pseudaspis*, *Pseudoboodon*, *Pythonodipsas* and *Scaphiophis*. In a further category ('Boodontinae' *incertae sedis*) Zaher placed the genera *Buroma*, *Dromicodryas*, *Duberria* and *Montaspis*. At the time, the affinities of a number of these genera were already thought to lie elsewhere; *Dipsina* and *Dromophis* were included within psammophiines (Branch 1988, Brandstätter 1995), while *Macroprotodon* and *Scaphiophis* can be allied with colubrines by virtue of their simple hemipenes with undivided sulcus spermaticus. In addition, *Boaedon* had already been synonymised with *Lamprophis* (Broadley 1966) and *Cryptolycus* with *Lycophidion* (Broadley 1996). *Duberria* has subsequently been shown to fall within the pseudoxyrhophiines (Lawson *et al.* 2005). The genera *Amplorhinus*, *Natriciteres*, *Limnophis* and *Psammodynastes* were placed by Zaher (1999) in his *Natricinae incertae sedis*, while *Poecilopholis* was placed *incertae sedis* within the 'Colubridae', and *Prosymna* seemingly overlooked.

Subsequent molecular studies have indicated that the enigmatic large African water snakes of the genus *Grayia* (4 species) are not lamprophiids, but rather group with calamariines and colubrines (Vidal & Hedges 2002a; Nagy *et al.* 2005; Lawson *et al.* 2005; Vidal *et al.* 2007). *Grayia* was recently placed in the subfamilial Grayiinae within a restricted Colubridae (Vidal *et al.* 2007).

The remaining genera assigned to the Lamprophiidae are all African, with the exception of the single Asian genus *Psammodynastes* (Vidal & Hedges 2002a). They form a species-rich and ecologically diverse group. It is the affinities and inter-relationships of these snakes that form the basis of this study.

## Material and methods

In order to investigate higher-level (familial) relationships, we first built a nuclear data set (*c-mos* and RAG2) for 31 species covering all major caenophidian lineages (Acrochordidae, Xenodermatidae, Paretidae, Viperidae, Homalopsidae, Pseudoxenodontidae, Colubridae, Natricidae, Dipsadidae, and Elapoidea). Among Elapoidea, we sampled at least one representative of each of the lineages recently identified by Kelly *et al.* (in press). Opportunity was taken to also include the enigmatic genus *Lycognathophis* from the Seychelles.

We then focused on Elapoidea and built a data set including two nuclear protein-coding genes (*c-mos* and RAG2), two mitochondrial rRNA genes (12S and 16S rRNA) and two mitochondrial protein-coding genes (cytochrome *b* and ND4) for five elapid species and 85 lamprophiid species belonging to 45 genera (thus representing about 75% of the generic diversity and 30% of the specific diversity of the radiation), in order to clarify the phylogenetic relationships of the group at the subfamilial and generic levels.

DNA extraction was performed using Winnepenninckx *et al.*'s (1993) protocol, or the NucleoSpin Tissue kit from Macherey-Nagel, or the DNeasy Tissue Kit from Qiagen. Samples used for this work, with corresponding localities and voucher numbers of the specimens, are listed in Appendix 1. Primers used for amplification and sequencing (sources cited in parentheses) are: two overlapping fragments of *c-mos* (Lawson *et al.* 2005; Vidal *et al.* 2007), RAG2 (Vidal *et al.* 2007), 12S rRNA (Vidal & Hedges 2002b), 16S rRNA (Palumbi *et al.* 1991), cytochrome *b* (de Queiroz *et al.* 2002; Nagy *et al.* 2003), and ND4 (Vidal & Hedges 2002a). Both strands of the PCR products were sequenced using the CEQ 2000 DNA Analysis System (Beckman), the ABI Prism 3100 Avant Genetic Analyser (Applied Biosystems), the MegaBACE 1000 DNA sequencer (Amersham), or at Genoscope (<http://www.genoscope.fr>), or Genoscreen (<http://www.genoscreen.fr>).

The two strands obtained for each sequence were aligned using the BioEdit Sequence Alignment Editor program (Hall 1999). The 480 sequences generated for this work have been deposited in GenBank under accession numbers beginning AY61, FJ404, and FJ387 (Appendix 2).

Sequence entry and alignment were performed manually with the MUST2000 software (Philippe 1993).

Alignment was straightforward for the protein-coding genes (*c-mos*, RAG2, cytochrome *b*, and ND4). For the 12S and 16S rRNA sequences, ambiguous sites were deleted from analyses, and the remaining few gaps were treated as missing data. Alignments can be obtained from Nicolas Vidal.

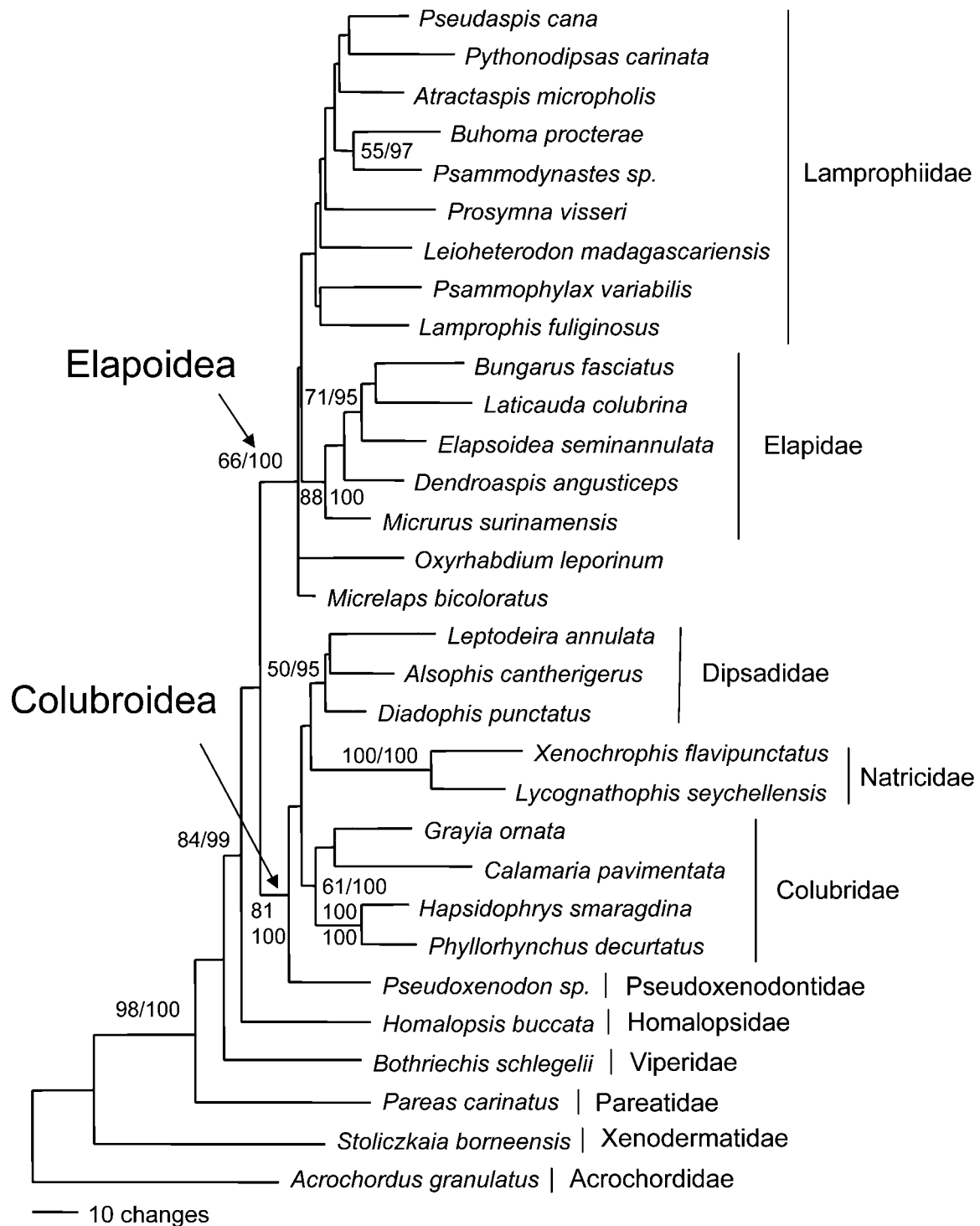
We estimated phylogenies using Maximum Likelihood (ML) and Bayesian methods of inference. ML analyses were performed with PAUP\* 4 (Swofford 2002) for the nuclear data set (31 taxa) and RAxML 7.0.4 (Stamatakis 2006; Stamatakis *et al.* 2008) for the combined data set (90 taxa). All Bayesian analyses were performed with MrBayes 3.1 (Ronquist & Huelsenbeck 2003). As separate analyses showed no significant topological incongruence (no conflicting nodes supported by ML BP values above 70% or Bayesian PP values above 95%), we performed combined analyses, which are considered to be our best estimates of phylogeny. Bayesian combined analyses were run with model parameters estimated as part of the Bayesian analyses, with three partitions corresponding to each codon position for the nuclear protein-coding genes, three partitions corresponding to each codon position for the mitochondrial protein-coding genes, and two partitions for the two mitochondrial rRNA genes. Bayesian analyses were performed by running 5,000,000 generations in four chains, saving the current tree every 100<sup>th</sup> generations. The first 2,000 trees (burn-in phase) were discarded, and the last 48,000 trees were used to construct a 50% majority rule consensus tree. For the nuclear ML analysis (31 taxa), we used a global model (GTR) as inferred by Modeltest using the AIC criterion (Posada & Crandall 1998) and performed 1000 bootstrap replicates with PAUP\* 4 (NJ starting trees and NNI branch swapping). For the combined ML analysis (90 taxa), we used the same partitions as in the Bayesian analysis, and performed 1000 bootstrap replicates using RAxML 7.0.4. P-distances were calculated using MEGA4 (Tamura *et al.* 2007).

## Results and discussion

**Phylogenetic relationships based on the nuclear data set (Fig. 1).** Our alignment resulted in 1263 sites (558 *c-mos* and 705 RAG2 sites). Outside Elapoidea, the interfamilial relationships are similar to those recently obtained by Vidal *et al.* (2007). One significant result is the position of *Lycognathophis* that strongly clusters with *Xenochrophis*, a well-established natricid (ML BP and Bayesian PP values of 100%), and that is therefore unrelated to the African lamprophiid radiation. The Elapoidea appears to be monophyletic, with two enigmatic genera in a basal position: *Micrelaps*, previously considered to be an atractaspidine, and *Oxyrhabdium*, previously considered to be a xenodermatid. It should nevertheless be stressed that RAG2 was not sequenced for *Micrelaps*, and that its position may be due to an artefact of missing data. This fossorial genus has been consistently allied to atractaspidines (McDowell 1968; Underwood & Kochva 1993; Rasmussen 2002) due to numerous morphological, trophic, and behavioural similarities, but the single species (*M. bicoloratus*) studied here did not group with the atractaspidines or with any other lamprophiid subfamily, and we therefore treat *Micrelaps* as *incertae sedis* among Elapoidea. Resolution of its relationships awaits further studies. As has been mentioned in Vidal *et al.* (2007), a basal position of xenodermatids (all Asian) among Caenophidia has been obtained for three out of the six extant genera (*Achalinus*, *Stoliczkaia*, and *Xenodermus*). In contrast, the fourth xenodermatid sampled, *Oxyrhabdium leporinum* from the Philippines, here appears to belong to the Elapoidea, as previously found by Lawson *et al.* (2005) and Kelly *et al.* (in press). Nevertheless, the sample from which the sequences have been obtained/used is the same in all three studies, and the position of *Oxyrhabdium* should therefore be further investigated using DNA from other specimens and the sister species, *O. modestum*. If their inclusion within the Elapoidea is confirmed it would suggest an additional caenophidian lineage of familial rank.

The remaining elapoids are divided into elapids and lamprophiids and are the subject of the next section. Our choice of rooting our trees with elapids may be criticized in the case that it were later demonstrated that lamprophiids do not form a monophyletic group. However, this is not of consequence because the following

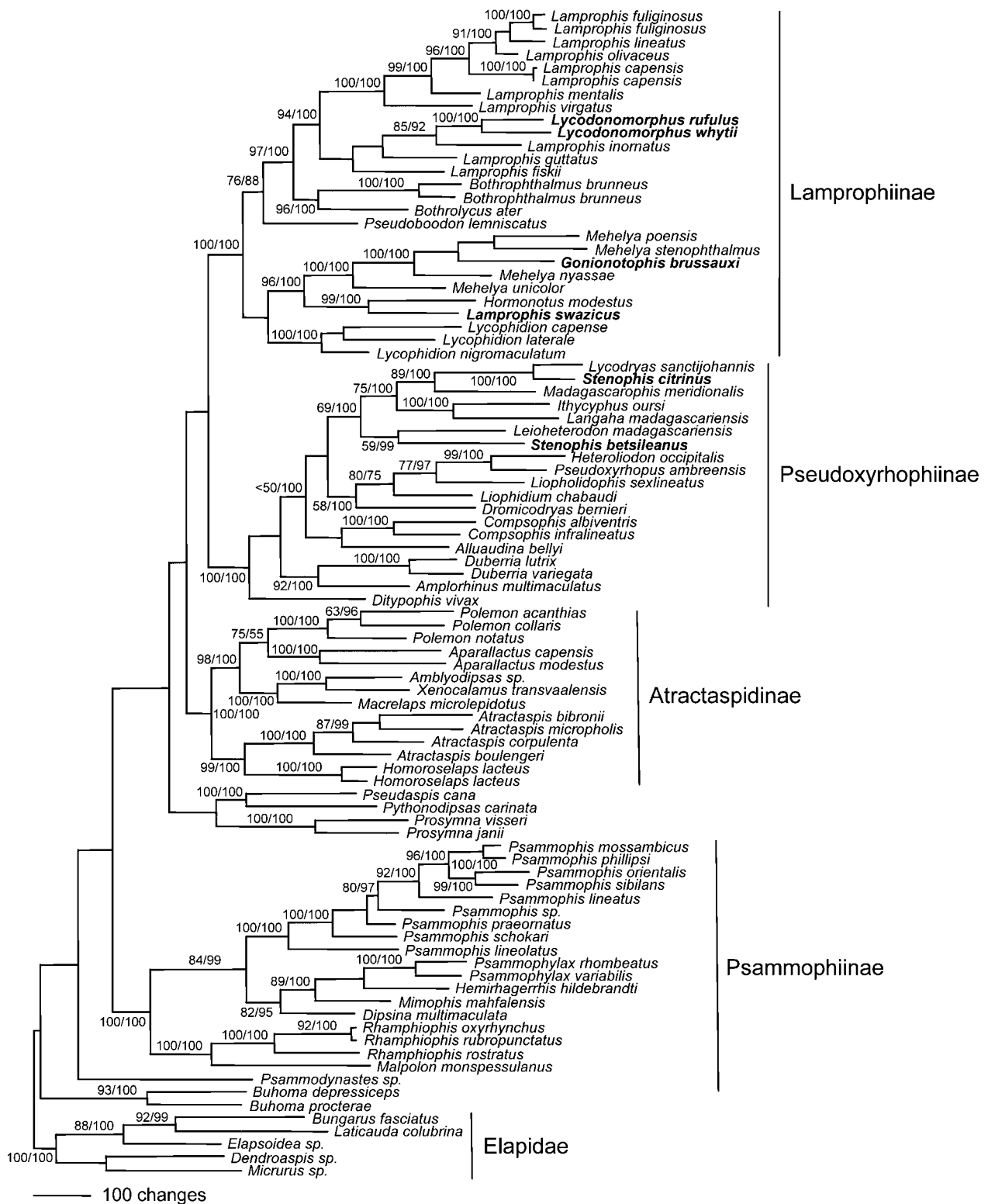
discussion is limited to relationships only within the identified clades due to a lack of phylogenetic resolution between them.



**FIGURE 1.** Bayesian tree obtained from the nuclear data set (c-mos and RAG2; 31 taxa, 1263 sites). Nodes with values are supported by ML bootstrap values above 70% (first value) and/or by Bayesian posterior probabilities above 95% (second value).

**Phylogenetic relationships based on the combined data set (Fig. 2).** Our alignment resulted in 3950 sites: 696 c-mos, 714 RAG2, 320 12S rRNA, 453 16S rRNA, 1107 cytochrome *b*, and 660 ND4. Nearly all of the 45 genera fall into four main clusters, treated here as subfamilies that correspond to the Psammophiinae, Pseudoxyrhopiinae, Lamprophiinae, and Atractaspidinae. Although the monophyly of each of those subfam-

ilies and relationships within them are strongly supported, relationships among them remain weakly resolved. The allocation of a small number of genera to the four recognized subfamilies was not possible. Zaher (1999) treated *Buhome* as *incertae sedis* with respect to his 'Boodontinae'. In this study both species of *Buhome* group together (albeit with deep divergence; mitochondrial p-distance: 15.6%, nuclear p-distance: 3.3%), but



**FIGURE 2.** Bayesian tree obtained from the combined data set (c-mos, RAG2, 12S & 16S rRNA, cytochrome b and ND4; 90 taxa, 3950 sites). Nodes with values are supported by ML bootstrap values above 70% (first value) and/or by Bayesian posterior probabilities above 95% (second value). The genera *Stenophis* and *Lamprophis* are each polyphyletic. The genus *Mehelya* is paraphyletic with respect to *Gonionotophis*.

their affinities within the Lamprophiidae remain unresolved. The southern African monotypic genera *Amplorhinus*, *Pythonodipsas*, and the recently described *Montaspis* (Bourquin 1991) have been treated as *incertae sedis* in general accounts (Branch 1988, 1998), although Zaher (1999), following Dowling & Duellman's (1978) classification, included *Amplorhinus* with natricids. *Montaspis* shares many external features of scalation with *Amplorhinus*, as well as a mesic habitat association. The latter has here been shown to belong to the pseudoxyrhophiines (sister-group to *Duberria*, BP ML value: 92, Bayesian PP value: 100), and *Montaspis* may have similar affinities. The genera *Pseudaspis* and *Pythonodipsas* are sister-groups (BP ML and Bayesian PP values: 100%), but the affinities of *Prosymna*, *Psammodynastes*, *Pseudaspis* and *Pythonodipsas* within the Lamprophiidae remain unclear, and we remain cautious about assigning them to existing or new families or subfamilies pending further studies.

Among the sampled psammophiines, the clade formed by the genera *Malpolon* and *Rhamphiophis* is the sister-group to the remaining psammophiines (*Dipsina*, *Mimophis*, *Hemirhagerrhis*, *Psammophylax* and *Psammophis*). Kelly *et al.* (2008) transferred *Rhamphiophis acutus* to *Psammophylax*, and also recorded deep divergence between the species *M. monspessulanus* and *M. moilensis*. The latter supports the recent transfer of *moilensis* to *Scutophis* (Brandstätter 1995), although Broadley (2005) noted that the name may not have been adequately diagnosed by Brandstätter (1995). We also affirm the specific status of *Rhamphiophis rostratus* (Kelly *et al.* 2008), at one time a subspecies of *Rhamphiophis oxyrhynchus*, because it appears to be the sister-group to *R. rubropunctatus* and *R. oxyrhynchus*. The remaining psammophiines are divided into two main groups: one including *Dipsina*, *Mimophis*, *Hemirrhagerrhis* and *Psammophylax*, and the other including *Psammophis* and *Dromophis*. Our trees are consistent with the relegation of *Dromophis* to the synonymy of *Psammophis* by Kelly *et al.* (2008) because the two species of the former genus *Dromophis* (*lineatus* and *praeornatus*) do not cluster together and are embedded within *Psammophis*.

The atractaspidines are divided into two main groups: one including the genera *Homoroselaps* and *Atractaspis* (Atractaspidini), and the other including *Amblyodipsas*, *Macrelaps*, *Xenocalamus*, *Aparallactus* and *Polemon* (Aparallactini). These relationships are identical to those obtained by Nagy *et al.* (2005). We note that De Witte & Laurent (1947), in the last formal revision of species here assigned to *Polemon*, included the species *acanthias*, *collaris* and *notatus* in different genera (*Miodon*, *Polemon* and *Cynodontophis*, respectively). Although a more complete study of the genus is needed before revising its status, we note large genetic divergences between the three species (mitochondrial p-distances from 12 to 13.1 %). We found deep divergence (mitochondrial p-distance of 16.3%) between the two species of *Aparallactus* included in this study, and note that *A. modestus* in both its dentition ('aglyph') and trophic behaviour (feeding on soft-bodied invertebrates) is divergent from other centipede eaters. The genera *Brachyophis*, *Chilorhinophis*, *Elapotinus*, *Hypoptophis* and probably *Poecilopholis* (regarded as *incertae sedis* by Zaher 1999) ally with the Aparallactini on morphological grounds, but their molecular affinities await fresh material.

The pseudoxyrhophiines are distributed mostly in Madagascar, and have previously been shown to include the Socotran endemic *Ditytophis* (Nagy *et al.* 2003) and the African *Duberria* (Lawson *et al.* 2005). Here we show that another genus from mainland Africa, *Amplorhinus*, also belongs to this assemblage and not with natricids (Zaher 1999), because it clusters strongly with *Duberria*. It should be noted that *Ditytophis*, *Amplorhinus* and *Duberria* are basal to the Malagasy genera. Another interesting result is the polyphyly of the arboreal genus *Stenophis*, with *S. betsileanus* recovered as the sister-group to *Leioheterodon*, and *S. citrinus* as the sister-group to *Lycodryas* (further studies are in progress).

The final large clade corresponds to the lamprophiines, although the content of the subfamily is revised because it excludes the genera *Buhoma*, *Prosymna*, *Psammodynastes*, *Pseudaspis* and *Pythonodipsas*. Among lamprophiines, we identify a basic division between *Lycophidion*, *Hormonotus*, 'Lamprophis' *swazicus*, *Mehelya* and *Gonionotophis* on the one hand and *Pseudoboodon*, *Bothrolycus*, *Bothrophthalmus*, *Lamprophis* and *Lycodonmorphus* on the other. *Gonionotophis brussauxi* is nested within *Mehelya*, suggesting that taxonomic action will be required to maintain monophyletic genera. Beyond additional taxonomic sampling in

future phylogenetic analyses, one nomenclatural issue that will need to be considered is that although *Gonionotophis* Boulenger, 1893 has priority over *Mehelya* Csiki, 1903, the name *Simocephalus* Günther, 1858 is also potentially available (Williams & Wallach 1989). A formal revision of file snakes is currently underway by D. G. Broadley and C. M. R. Kelly, and we leave the nomenclatural tangle for others to unravel.

The genus *Lamprophis* Fitzinger, 1843 is paraphyletic with respect to *Lycodonomorphus* Fitzinger, 1843 (ML BP value: 85%, Bayesian PP value: 92%). Nevertheless, sequences from four to five species of *Lycodonomorphus* and a possible six species of *Lamprophis* remain unavailable. Given these gaps in taxon sampling, and the relatively deep divergence within the two clades that currently contain the majority of *Lamprophis* sampled (excluding the obvious exception of *L. swazicus*, see below), we caution against formal taxonomic action at this stage. There are indications that the *L. fuliginosus-lineatus-capensis* complex contains cryptic taxa (C. M. R. Kelly pers. comm). In this study, one specimen of *Lamprophis* with morphological features that are consistent with the ‘*mentalis*’ phase (see discussion in Broadley 1990), shows significant genetic divergence from other *L. capensis* (mitochondrial p-distance: 9.3%) suggesting that it deserves specific recognition. However, genetic relationships within the *L. fuliginosus-lineatus-capensis* complex do not easily correlate with morphology and require more detailed studies (C. Kelly, pers. comm.). In addition, the recent confusion over species boundaries in the *Lycodonomorphus whytii-mlanjensis-obscuriventris* complex also cautions against premature taxonomic action, considering the potential for unnecessary synonyms and overlooked homonyms.

A further issue is the position of ‘*Lamprophis*’ *swazicus* because it is not closely related to the other members of the genus, but instead strongly clusters with the monotypic genus *Hormonotus* (BP ML value: 99%, Bayesian PP value: 100%). Superficially, they are both uniform brown attenuated long-tailed snakes, and there is little difference in the head shields, dorsal scale rows 15-15-13 (vertebral row enlarged) in *modestus* versus 17-17-13 in *swazicus*; ventrals 221-244 versus 199-208; subcaudals 81-100 versus 75-91; maxillary teeth 5 to 6 + 11 to 15 versus 7 + 10 to 12. The hemipenes are also similar, although more spinose basally in *modestus*. Nevertheless, their habitats are different: forest for *modestus*, rocky areas in montane grassland for *swazicus*, and the two taxa are separated by a gap of around 1900 km. Additionally, the genetic divergence is large (mitochondrial p-distance: 19.2%, nuclear p-distance: 2.3%), and generic recognition may be warranted for *swazicus*.

Finally, two families (here considered as putative subfamilies), Prosymnidae (genus *Prosymna*) and Pseudaspidae (genera *Pseudaspis* and *Pythonodipsas*), have recently been proposed (Kelly *et al.* in press). Nevertheless, before giving familial rank names to lineages with unresolved affinities (*Prosymna*, *Pseudaspis* and *Pythonodipsas*, *Buhoma*, *Psammodynastes*, *Micrelaps*, *Oxyrhabdium*), we suggest that additional sequencing of nuclear protein-genes allowing better higher-level phylogenetic resolution is required.

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## Appendix 1

Samples used for this work, with corresponding localities and voucher numbers of the specimens. Institutional abbreviations for voucher specimens as follows: AMB, Aaron M. Bauer field collection; CAS, California Academy of Sciences, San Francisco, USA; FN, William R. Branch field collection; IPMB, Institute of Pharmacy and Molecular Biotechnology, University of Heidelberg, Germany; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; HLMD, Hessisches Landesmuseum Darmstadt, Germany; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; MRSN, Museo Regionale di Scienze Naturali, Turin, Italy; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; PEM, Port Elizabeth Museum, Port Elizabeth, South Africa; SURC, Silliman University Reference Collection, Philippines; TP, Ted Papenfuss field collection; UADBA, Université d'Antananarivo, Département de Biologie Animale, Madagascar; ZSM, Zoologische Staatssammlung München, Germany.

### ELAPIDAE

*Dendroaspis polylepis*, South Africa, Durban (tissue sample: IPMB 28651)

### LAMPROPHIIDAE

#### Atractaspidinae:

*Homoroselaps lacteus*, South Africa, Pretoria (IPMB 28676); *Homoroselaps lacteus*, PEM R17097; Port Elizabeth, Eastern Cape, South Africa; *Atractaspis bibronii*, PEM R15835; Lac Ngonaya, Chibuto, Central Mozambique; *Atractaspis boulengeri*, FN R156; Rabi, Gabon; *Atractaspis corpulenta*, FN R168; Rabi, Gabon; *Atractaspis micropholis*, Togo; *Macrelaps microlepidotus*, no locality data (IPMB 28666); *Xenocalamus transvaalensis*, PEM R12103; Kosi Bay trench, Maputaland, South Africa; *Amblyodipsas polylepis*, PEM R15626; Moma, N. Mozambique; *Aparallactus capensis*, South Africa (IPMB 28675); *Aparallactus modestus*, PEM R5304; Rabi (Shell Gabon), Ogoúé-Maritime Province, Gabon; *Polemon acanthias*, PEM R1479; Haute Dodo, Côte d'Ivoire; *Polemon collaris*, PEM R5383; Rabi, Gabon; *Polemon notatus*, PEM R5404; Rabi, Gabon.

#### Lamprophiinae:

*Hormonotus modestus*, PEM R5408; Rabi, Gabon; *Gonionotophis brussauxi*, IRSNB 16266; Mount Iboundji, Offoué-Onoy Dpt, Ogooué-Lolo Prov., Gabon; *Mehelya nyassae*, PEM R15462; Marrameu, Zambezi Delta, N. Mozambique; *Mehelya poensis*, PEM R5435, Rabi (Shell Gabon), Ogoúé Maritime Province, Gabon; *Mehelya stenophthalmus*, FN R101; Rabi, Gabon; *Mehelya unicolor*, Kenya; *Lycophidion capense*, PEM R13512; Port Elizabeth, Eastern Cape Province, South Africa; *Lycophidion laterale*, IRSNB 16295; Moudouma, Boumi-Louetsi Dpt., Ngounié Prov., Gabon; *Lycophidion nigromaculatum*, PEM R17867; Draw River, Ghana; *Bothrolycus ater*, IRSNB 16298; Moudouma, Boumi-Louetsi Dpt., Ngounié Prov., Gabon; *Bothrophthalmus brunneus*, PEM R5409; Rabi, Gabon; *Bothrophthalmus brunneus*, IRSNB 16248; Itsiba, Boumi-Louetsi Dpt., Ngounié Prov., Gabon; *Lycodonomorphus rufulus*, PEM R8042; Port Elizabeth, Eastern Cape Province, South Africa; *Lycodonomorphus whytii*, sample kindly donated by Peter Gravlund; *Lamprophis capensis*, PEM R15002; Lacerdonia, Zambezi Delta, Mozambique; *Lamprophis capensis*, PEM R16201, Niassa Game Reserve, Mozambique; *Lamprophis fiskii*, PEM R5764; 18 km W. Steinkopf, Northern Cape, South Africa; *Lamprophis fuliginosus*, Burundi; *Lamprophis fuliginosus*, CAS 168909; Tanga Region, Tanzania; *Lamprophis guttatus*, AMB 6058; N.E. Cape, South Africa; *Lamprophis inornatus*, AMB 6135; Mogoebaskloof, Tzanan District, N. Province, South Africa; *Lamprophis lineatus*, Cameroun; *Lamprophis 'mentalis'*, captive born; *Lamprophis olivaceus*, PEM R5337; Rabi (Shell Gabon), Ogoúé Maritime Province, Gabon; *Lamprophis virgatus*, MRAC 2001-102-R-7; Diyanga, Ogoulou Dpt., Ngounié Prov., Gabon.

#### Pseudoxyrhophiinae:

*Ditytophis vivax*, HLMD RA-2972; Socotra, Yemen; *Compsophis albiventris*, ZSM 497/2000; Mt. d'Ambre, Madagascar; *Compsophis infralineatus*, ZSM 378/2000; Manjakatempo, Madagascar; *Amplorhinus multimaculatus*, PEM R5490; Natal Midlands; *Duberria lutrix*, PEM R5411; Coega Salt works, East bank, Port Elizabeth; *Duberria variegata*, PEM R9729; Dukuduku Forest, Mtubatuba, KwaZulu-Natal, South Africa; *Dromicodryas bernieri*, PEM FN440; Tuliara, Madagascar; *Liophidium chabaudi*, MVZ 238844; *Liopholidophis sexlineatus*, UADBA FG/MV 2000.38; Mandraka, Madagascar; *Pseudoxyrhopus ambreensis*, Mt. d'Ambre, Madagascar; *Heteroliodon occipitalis*, PEM FN439; 10 km S. Basibasy, Madagascar; *Alluaudina bellyi*, MRSN FAZC 10622; Berara, Madagascar; *Stenophis betsileanus*, Madagascar; *Stenophis citrinus*, Madagascar; *Leioheterodon madagascariensis*, Madagascar; *Langaha madagascariensis*, Madagascar; *Ithycyphus oursi*, PEM FN436; Ranobe, Tuliara Dist., S.W. Madagascar; *Madagascarophis meridionalis*, MVZ 238848; *Lycodryas sanctijohannis*, ZSM321/2002; Comoros.

Psammophiinae:

*Malpolon monspessulanus*, HLMD RA2606; Polidrassi, Greece; *Rhamphiophis oxyrhynchus*, MNHN 1990.4336; Dielmo, close to Toubakouta, 15 km from the Gambia border, Senegal; *Rhamphiophis rostratus*, FN 1400; N. Moebase Village, N. Mozambique; *Rhamphiophis rubropunctatus*, captive animal; *Mimophis mahfalensis*, Madagascar; *Hemirrhagerrhis hildebrandtii*, PEM R9700; 70 km S.S.E. Dodoma, Tanzania; *Psammophylax rhombeatus*, PEM R9727; Suikersbosrand Nature Reserve, Gauteng, South Africa; *Psammophylax variabilis*, Burundi; *Psammophis lineatus*, captive animal; *Psammophis lineolatus*, Kazakhstan, Charyn Canyon (IPMB 28601); *Psammophis mossambicus*, PEM R15488; Zambezi Delta, Mozambique; *Psammophis orientalis*, PEM R16132; Nyassa; *Psammophis phillipsi*, PEM R5451; Loango National Park, Gabon; *Psammophis praeornatus*, Ghana; *Psammophis schokari*, Tunisia, Bou Hedma (IPMB 28602); *Psammophis sibilans*, Niger; *Psammophis sp.*, TP28431; Somalia.

Lamprophiidae incertae sedis:

*Buroma procterae*, no locality data; *Buroma depressiceps*, IRSNB 16404; Itsiba, Boumi-Louetsi Dpt., Ngounié Prov., Gabon; *Prosymna janii*, PEM R12072; Warden's House, Kosi Bay Nature Reserve, KwaZulu-Natal, South Africa; *Prosymna visseri* CAS 214753; Namibia, Sesfontein, *Psammodynastes sp.*, sample kindly donated by Peter Gravlund; *Pythonodipsas carinata*, PEM R8234; Namibia, Kaokoveld; *Pseudaspis cana*, PEM R17084; 5 km before Malmesbury on N7 from Cape Town, Western Cape, South Africa.

ELAPOIDEA incertae sedis

*Oxyrhabdium leporinum*, SURC, no number, sample kindly donated by Robin Lawson.

NATRICIDAE

*Lycognathophis seychellensis*, Parc du Morne Seychellois, Mahé, Seychelles.

**Appendix 2**

Sequences used with corresponding GenBank accession numbers. For a few taxa, DNA sequence data from different species of the same genus were combined (*Dendroaspis*, *Micrurus*, *Elapsoidea*, *Amblyodipsas*, and *Pseudoxenodon*). 'Missing' indicates that the corresponding gene fragment was not obtained.

	c-mos	Rag-2	cyt- <i>b</i>	ND4	12S rRNA	16S rRNA
Elapoidea						
Elapidae						
<i>Dendroaspis angusticeps/polylepis</i>	AF544735/ FJ387197	EF144099	FJ404295	AY058974	AF544764	FJ404194
<i>Bungarus fasciatus</i>	AF544732/ AY058924	EF144100	AF217830	U49297	U96793	Z46501
<i>Laticauda colubrina</i>	AF544702/ AY058932	EF144101	AF217834	AY058977	U96799	Keogh (1998)
<i>Micrurus surinamensis/fulvius</i>	AF544708/ AY058935	EF144102	AF217839	AF228444	AF544770	AF544799
<i>Elapsoidea nigra/semiannulata/ sundevalli</i>	AF544678/ AY187977	EF144098	AY188016	AY058975	AF544745	AY188055
Lamprophiidae						
Atractaspidinae						
<i>Homoroselaps lacteus 1</i>	FJ404240/ AY611901	FJ404410	AY611992	FJ404338	FJ404135	AY611809
<i>Homoroselaps lacteus 2</i>	FJ404241/ AY611935	FJ404411	AY612026	FJ404339	FJ404136	AY611843
<i>Atractaspis bibronii</i>	FJ404236/ AY611932	FJ404406	AY612023	FJ404333	FJ404131	AY611840
<i>Atractaspis boulengeri</i>	FJ404237/ AY611925	FJ404407	AY612016	FJ404334	FJ404132	AY611833

<i>Atractaspis corpulenta</i>	FJ404238/ AY611929	FJ404408	AY612020	FJ404335	FJ404133	AY611837
<i>Atractaspis micropholis</i>	AF544677/ AY611915	EF144105	AY612006	FJ404336	AF544740	AY611823
<i>Macrelaps microlepidotus</i>	FJ404242/ AY611902	FJ404412	AY611993	FJ404340	FJ404137	AY611810
<i>Xenocalamus transvaalensis</i>	FJ404246/ AY611934	FJ404416	AY612025	FJ404344	FJ404141	AY611842
<i>Amblyodipsas polylepis/dimidiata</i>	FJ404233/ AY611936	FJ404403	AY612027	DQ486322	FJ404128	AY611844
<i>Aparallactus capensis</i>	FJ404234/ AY187967	FJ404404	AY188006	FJ404331	FJ404129	AY188045
<i>Aparallactus modestus</i>	FJ404235/ AY611916	FJ404405	AY612007	FJ404332	FJ404130	AY611824
<i>Polemon acanthias</i>	FJ404243/ AY611940	FJ404413	AY612031	FJ404341	FJ404138	AY611848
<i>Polemon collaris</i>	FJ404244/ AY611938	FJ404414	AY612029	FJ404342	FJ404139	AY611846
<i>Polemon notatus</i>	FJ404245/ AY611939	FJ404415	AY612030	FJ404343	FJ404140	AY611847
Lamprophiinae						
<i>Hormonotus modestus</i>	FJ404261/ Missing	FJ404433	FJ404296	FJ404360	FJ404159	FJ404195
<i>Gonionotophis brussauxi</i>	FJ404258/ AY611952	FJ404430	AY612043	FJ404358	FJ404156	AY611861
<i>Mehelya nyassae</i>	FJ404283/ AY611987	FJ404453	AY612078	FJ404379	FJ404182	AY611896
<i>Mehelya poensis</i>	FJ404284/ AY611954	FJ404454	AY612045	FJ404380	FJ404183	AY611863
<i>Mehelya stenophthalmus</i>	FJ404286/ AY611927	FJ404456	AY612018	FJ404382	FJ404185	AY611835
<i>Mehelya unicolor</i>	FJ404285/ AF471099	FJ404455	AF471077	FJ404381	FJ404184	FJ404196
<i>Lycophidion capense</i>	FJ404279/ AY611984	FJ404450	AY612075	FJ404376	FJ404178	AY611893
<i>Lycophidion laterale</i>	FJ404280/ FJ387198	FJ404451	FJ404297	FJ404377	FJ404179	FJ404197
<i>Lycophidion nigromaculatum</i>	FJ404281/ Missing	Missing	FJ404298	Missing	FJ404180	Missing
<i>Pseudoboodon lemniscatus</i>	DQ486174	Missing	DQ486350	DQ486325	Missing	Missing
<i>Bothrolycus ater</i>	FJ404249/ AY611950	FJ404419	AY612041	FJ404347	FJ404144	AY611859
<i>Bothrophthalmus brunneus 1</i>	FJ404250/ AY611965	FJ404420	AY612056	FJ404348	FJ404145	AY611874
<i>Bothrophthalmus brunneus 2</i>	FJ404251/ FJ387199	FJ404421	AF471090	FJ404349	FJ404146	FJ404198
<i>Lycodonomorphus rufulus</i>	FJ404276/ FJ387200	FJ404448	FJ404299	FJ404374	FJ404175	FJ404199

<i>Lycodonomorphus whytii</i>	FJ404277/ FJ387201	FJ404449	FJ404300	FJ404375	FJ404176	FJ404200
<i>Lamprophis capensis 1</i>	FJ404263/ AY611986	FJ404435	AY612077	FJ404362	FJ404161	AY611895
<i>Lamprophis capensis 2</i>	FJ404264/ FJ387202	FJ404436	Missing	Missing	FJ404162	FJ404201
<i>Lamprophis fiskii</i>	FJ404265/ FJ387203	FJ404437	FJ404301	FJ404363	FJ404163	FJ404202
<i>Lamprophis fuliginosus 1</i>	AF544686/ FJ387204	EF144104	FJ404302	FJ404364	FJ404164	FJ404203
<i>Lamprophis fuliginosus 2</i>	FJ404266/ AF471143	FJ404438	AF471060	FJ404365	FJ404165	FJ404204
<i>Lamprophis guttatus</i>	FJ404267/ AY611981	FJ404439	AY612072	FJ404366	FJ404166	AY611890
<i>Lamprophis inornatus</i>	FJ404268/ AY611982	FJ404440	AY612073	FJ404367	FJ404167	AY611891
<i>Lamprophis lineatus</i>	FJ404269/ FJ387205	FJ404441	FJ404303	Missing	FJ404168	FJ404205
<i>Lamprophis 'mentalis'</i>	FJ404270/ FJ387206	FJ404442	FJ404304	FJ404368	FJ404169	FJ404206
<i>Lamprophis olivaceus</i>	FJ404271/ AY611953	FJ404443	AY612044	Missing	FJ404170	AY611862
<i>Lamprophis virgatus</i>	FJ404272/ AY611917	FJ404444	AY612008	FJ404369	FJ404171	AY611825
<i>Lamprophis swazicus</i>	DQ486180	Missing	DQ486356	DQ486331	Missing	Missing
<i>Pseudoxyrhopiinae</i>						
<i>Dityophis vivax</i>	FJ404255/ AY187974	FJ404424	AY188013	FJ404352	FJ404150	AY188052
<i>Compsophis albiventris</i>	FJ404254/ AY187972	Missing	AY188011	FJ404351	FJ404149	AY188050
<i>Compsophis infralineatus</i>	FJ404259/ AY187978	FJ404431	AY188017	FJ404359	FJ404157	AY188056
<i>Amplorhinus multimaculatus</i>	FJ404248/ AY611971	FJ404418	AY612062	FJ404346	FJ404143	AY611880
<i>Duberria lutrix</i>	Missing/ FJ387207	FJ404428	FJ404305	FJ404356	FJ404154	FJ404207
<i>Duberria variegata</i>	FJ404257/ FJ387208	FJ404429	FJ404306	FJ404357	FJ404155	FJ404208
<i>Dromicodryas bernieri</i>	Missing/ FJ387209	FJ404425	DQ979987	FJ404353	FJ404151	FJ404209
<i>Liophidium chabaudi</i>	FJ404274/ FJ387210	FJ404446	FJ404307	FJ404372	FJ404173	FJ404210
<i>Liopholidophis sexlineatus</i>	FJ404275/ AY187985	FJ404447	AY188024	FJ404373	FJ404174	AY188063
<i>Pseudoxyrhopus ambreensis</i>	FJ404289/ AY187996	FJ404459	AY188035	FJ404385	FJ404188	AY188074
<i>Heteroliodon occipitalis</i>	FJ404260/ FJ387211	FJ404432	FJ404308	Missing	FJ404158	FJ404211

<i>Alluaudina bellyi</i>	FJ404247/ AY187966	FJ404417	AY188005	FJ404345	FJ404142	AY188044
<i>Stenophis betsileanus</i>	Missing/ AY187998	FJ404461	AY188037	FJ404387	FJ404190	AY188076
<i>Stenophis citrinus</i>	FJ404291/ AY611956	FJ404462	AY612047	FJ404388	FJ404191	AY611865
<i>Leioheterodon madagascariensis</i>	AF544685/ AY187983	EF144103	AY188022	FJ404371	AF544768	AY188061
<i>Langaha madagascariensis</i>	FJ404273/ AY187981	FJ404445	AY188020	FJ404370	FJ404172	AY188059
<i>Ithycyphus oursi</i>	FJ404262/ FJ387212	FJ404434	FJ404309	FJ404361	FJ404160	FJ404212
<i>Madagascarophis meridionalis</i>	FJ404282/ AY187988	FJ404452	AY188027	FJ404378	FJ404181	AY188066
<i>Lycodryas sanctijohannis</i>	FJ404278/ AY611919	Missing	AY612010	Missing	FJ404177	AY611827
<b>Psammophiinae</b>						
<i>Malpolon monspessulanus</i>	Missing/ AY187990	FJ404390	AY188029	FJ404320	FJ404116	AY188068
<i>Rhamphiophis oxyrhynchus</i>	AF544710/ FJ387213	FJ404400	Missing	Missing	FJ404125	FJ404213
<i>Rhamphiophis rostratus</i>	FJ404231/ AY611988	FJ404401	AY612079	FJ404329	FJ404126	AY611897
<i>Rhamphiophis rubropunctatus</i>	FJ404232/ Missing	FJ404402	FJ404310	FJ404330	FJ404127	Missing
<i>Dipsina multimaculata</i>	DQ486181	Missing	DQ486357	DQ486332	Missing	Missing
<i>Mimophis mahfalensis</i>	AF544688/ AY187993	FJ404391	AY188032	FJ404321	AF544771	AY188071
<i>Hemirrhagerrhis hildebrandti</i>	FJ404239/ FJ387214	FJ404409	FJ404311	FJ404337	FJ404134	FJ404214
<i>Psammophylax rhombeatus</i>	FJ404230/ FJ387215	FJ404399	FJ404312	FJ404327	FJ404124	FJ404215
<i>Psammophylax variabilis</i>	AF544709/ AY611955	EF144107	AY612046	FJ404328	AF544774	AY611864
<i>Psammophis lineatus</i>	FJ404256/ Missing	FJ404426	FJ404313	FJ404354	FJ404152	FJ404216
<i>Psammophis lineolatus</i>	FJ404223/ AY187995	FJ404392	AY188034	DQ486286	FJ404117	AY188073
<i>Psammophis mossambicus</i>	FJ404224/ Missing	FJ404393	FJ404314	FJ404322	FJ404118	FJ404217
<i>Psammophis orientalis</i>	FJ404225/ Missing	FJ404394	FJ404315	DQ486295	FJ404119	FJ404218
<i>Psammophis phillipsi</i>	FJ404226/ AY611970	FJ404395	AY612061	FJ404323	FJ404120	AY611879
<i>Psammophis praeornatus</i>	Missing/ FJ387216	FJ404427	Missing	FJ404355	FJ404153	Missing
<i>Psammophis schokari</i>	FJ404227/ AY611943	FJ404396	AY612034	FJ404324	FJ404121	AY611852

<i>Psammophis sibilans</i>	FJ404228/ Missing	FJ404397	FJ404316	FJ404325	FJ404122	FJ404219
<i>Psammophis</i> sp.	FJ404229/ FJ387217	FJ404398	FJ404317	FJ404326	FJ404123	FJ404220
Lamprophiidae <i>incertae sedis</i>						
<i>Prosymna janii</i>	FJ404293/ FJ387219	FJ404464	FJ404319	FJ404389	FJ404193	FJ404222
<i>Prosymna visseri</i>	FJ404292/ AY187994	FJ404463	AY188033	Missing	FJ404192	AY188072
<i>Pythonodipsas carinata</i>	FJ404290/ AY187997	FJ404460	AY188036	FJ404386	FJ404189	AY188075
<i>Pseudaspis cana</i>	FJ404288/ AY611989	FJ404458	AY612080	FJ404384	FJ404187	AY611898
<i>Buhomea procterae</i>	FJ404253/ AY611910	FJ404423	AY612001	FJ404350	FJ404148	AY611818
<i>Buhomea depressiceps</i>	FJ404252/ AY611951	FJ404422	AY612042	Missing	FJ404147	AY611860
<i>Psammodynastes</i> sp.	FJ404287/ FJ387218	FJ404457	FJ404318	FJ404383	FJ404186	FJ404221
Elapoidea <i>incertae sedis</i>						
<i>Micrelaps bicoloratus</i>	DQ486173	Missing				
<i>Oxyrhabdium leporinum</i>	DQ112081	FJ404466				
Acrochordidae						
<i>Acrochordus granulatus</i>	AF544706	EF144093				
Xenodermatidae						
<i>Stoliczkaia borneensis</i>	AF544721	EF144094				
Pareatidae						
<i>Pareas carinatus</i>	AF544692	EF144096				
Viperidae						
<i>Bothriechis schlegelii</i>	AF544680	EF144095				
Homalopsidae						
<i>Homalopsis buccata</i>	AF544701	EF144097				
Pseudoxenodontidae						
<i>Pseudoxenodon karlschmidti/bambusicola</i>	AF471102	EF144111				
Colubridae						
<i>Phyllorhynchus decurtatus</i>	AF544728	EF144115				
<i>Hapsidophrys smaragdina</i>	AF544691	EF144114				
<i>Calamaria pavimentata</i>	AF471103	EF144116				
<i>Grayia ornata</i>	AF544684	EF144113				
Natricidae						
<i>Lycognathophis seychellensis</i>	FJ404294/ FJ387220	FJ404465				
<i>Xenochrophis flavipunctatus</i>	AF544714	EF144112				