

**You are what your ancestors ate: retained bufadienolide resistance in the piscivorous water cobra *Naja annulata* (Serpentes: Elapidae)**

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**Herpetological Journal**

Published: 01/07/2023

Peer reviewed version

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*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Fletcher, J., Malhotra, A., & Wüster, W. (2023). You are what your ancestors ate: retained bufadienolide resistance in the piscivorous water cobra *Naja annulata* (Serpentes: Elapidae). *Herpetological Journal*, 33(3), 83-87.

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**You are what your ancestors ate: retained bufadienolide resistance in the piscivorous water cobra *Naja annulata* (Serpentes: Elapidae)**

**Abstract**

Predators exploiting chemically defended prey are generally resistant to prey toxins. However, toxin resistance usually incurs a fitness cost and is therefore often lost when no longer needed. Bufonid toads are a frequently abundant food resource, but chemically defended by a group of cardiotonic steroids, bufadienolides. Bufophagous predators have evolved a specific and near-universal mechanism of resistance to these toxins, consisting of two amino acid substitutions in the Na<sup>+</sup>/K<sup>+</sup>-ATPase H1–H2 extracellular domain. The dynamics of loss or retention of this adaptation in secondarily non-bufophagous lineages remain inadequately understood. Here we explore this topic by showing that the piscivorous banded water cobra (*Naja annulata*) retains the bufadienolide-resistant genotype of the otherwise toad-eating cobra clade. This confirms a trend for secondarily non-toad-eating snakes to retain bufadienolide resistance.

**Keywords:** Antipredator adaptation, cardiotonic steroid, cardiac glycoside, evolution, piscivory

Cardiotonic steroids, also known as cardiac glycosides, are a common chemical defence among many plant and animal taxa. These toxins bind to and disable the ubiquitous and vital animal enzyme Na<sup>+</sup>/K<sup>+</sup>-ATPase, causing potentially lethal poisoning. However, many animals

23 have evolved resistance to cardiotoxic steroids. The main mechanism of resistance, which has  
24 evolved multiple times across the animal kingdom, consists of replacements of two of the  
25 amino acids comprising the Na<sup>+</sup>/K<sup>+</sup>-ATPase H1–H2 extracellular domain (Ujvari et al., 2015).  
26 This single, near-universal mechanism has made it possible to assess the likely susceptibility  
27 of a wide variety of animals to cardiac glycosides by simply sequencing the short segment of  
28 the Na<sup>+</sup>/K<sup>+</sup>-ATPase gene containing the H1–H2 extracellular loop (Ujvari et al., 2013, 2014;  
29 Mohammadi et al., 2016; Marshall et al., 2018).

30 Bufonid toads are abundant components of many freshwater and terrestrial ecosystems, and  
31 hence a potentially valuable food source for predators. However, most species are chemically  
32 defended by the group of cardiac glycosides known as bufadienolides, which make them  
33 lethal to unadapted predators (Shine, 2010). However, amphibian predators likely to  
34 encounter toads, including multiple snake lineages (Ujvari et al., 2015; Mohammadi et al.,  
35 2016), have evolved resistance to these toxins, allowing them to exploit this food source.

36 Since most antitoxin defences carry a cost, there may be selection against their retention  
37 when the drivers of their initial evolution are no longer present, as may have happened in  
38 Australo-Papuan varanid lizards (Ujvari et al., 2013). On the other hand, in snakes,  
39 Mohammadi et al. (2016) found that many species that have secondarily switched away from  
40 preying on bufonid toads nevertheless retain their ancestral resistance to bufadienolides. This  
41 suggests that these mutations either carry a very limited cost, or provide other selective  
42 advantages, or that reversal would be costly, perhaps due to epistatic intramolecular effects  
43 or pleiotropic interactions with other, possibly co-evolved, traits.

44 Cobras (*Naja* and relatives - Kazandjian et al., 2021) are common predators of toads (Luiselli  
45 et al., 2002; Shine et al., 2007), and all members of the clade tested to date display the

bufadienolide-resistant genotype of the alpha 3 isoform of the Na<sup>+</sup>/K<sup>+</sup>-ATPase H1–H2 domain (Mohammadi et al., 2016). The main exception to the generalisation of toad-eating in cobras appear to be the water cobras: these consist of a clade of three species of the subgenus *Boulengerina*, *Naja annulata*, *N. christyi* and *N. nana*, and are phylogenetically nested deep within the genus *Naja* (Wüster et al., 2007; Wallach et al., 2009; Kazandjian et al., 2021). Water cobras are generally regarded as exclusively piscivorous (Chirio & LeBreton, 2007; Pauwels & Vande weghe, 2008; Collet & Trape, 2020; Spawls & Branch, 2020), although systematic studies of their diet are lacking (Grundler, 2020). Captive specimens of *Naja annulata* have been reported to consume a *Rana temporaria* and a *Lycodonomorphus bicolor* (Kratzer, 1965; Madsen & Osterkamp, 1982), and there has been speculation that the species may eat amphibians, but there are no confirmed records of this occurring in the wild (Spawls et al., 2002). In keeping with much of the available literature, we therefore treat *N. annulata* as more or less exclusively piscivorous in nature.

The apparent loss of bufophagy in *N. annulata* raises the question whether this species has retained the resistance to bufadienolides that arose during the initial divergence of the cobra clade (Mohammadi et al., 2016), or whether, in the absence of selection for cardiac glycoside resistance, this species has reverted to the sensitive genotype. To add to our understanding of the dynamics of gain and loss of this adaptation in cobras and their relatives, we here report on additional sequences of the Na<sup>+</sup>/K<sup>+</sup>-ATPase H1–H2 domain in elapid snakes, with particular focus on *N. annulata*.

Our methods largely follow Mohammadi et al. (2016) and Marshall et al. (2018). We extracted DNA from tissue samples collected from pet trade specimens or by colleagues at Liverpool School of Tropical Medicine in the course of other work (Kazandjian et al., 2021), using Qiagen

69 Dneasy Blood and Tissue Kits following the manufacturer's instructions. The alpha 3 isoforms  
 70 of the Na<sup>+</sup>/K<sup>+</sup>-ATPase H1–H2 domain were amplified using the primers ATP1a3Fwd (CGA GAT  
 71 GGC CCC AAT GCT CTC A) and ATP1a3Rvs (TGG TAG TAG GAG AAG CAG CCG GT) (Mohammadi  
 72 et al., 2016). For details of PCR conditions and the cleaning of PCR products, see Marshall et  
 73 al. (2018). PCR products were sent to Macrogen (Seoul, South Korea) for sequencing using  
 74 both forward and reverse primers.

75 The sequence trace files were checked for errors and aligned in MEGA 11 (Tamura et al.,  
 76 2021). We then aligned them with the relevant sequences from Mohammadi et al. (2016),  
 77 and used Genome BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to obtain corresponding  
 78 sequences from the published genomes of *Bungarus multicinctus*, *Laticauda colubrina*, *L.*  
 79 *laticaudata*, *Naja naja* and *Ophiophagus hannah* (Vonk et al., 2013; Kishida et al., 2019;  
 80 Suryamohan et al., 2020; Zhang et al., 2022). The coding sequences for the Na<sup>+</sup>/K<sup>+</sup>-ATPase  
 81 H1–H2 domain were translated into amino acid sequences in MEGA 11 and checked for the  
 82 key Q111L and G120R substitutions that confer resistance to cardiac glycosides (Ujvari et al.,  
 83 2015; Mohammadi et al., 2016).

84 We obtained new sequences of *Aspidelaps scutatus*, *Hemachatus haemachatus*, *Naja*  
 85 *annulata*, *N. kaouthia*, *N. naja*, *N. nigricollis*, *N. nivea* and *N. subfulva*. With existing  
 86 sequences, we aligned a total of 19 sequences of 16 species (Table 1). The translated amino  
 87 acid sequences show that all members of the cobra clade share the resistance-conferring  
 88 Q111L and G120R substitutions. This includes the piscivorous *Naja annulata* as well as the  
 89 most basal lineage of the group, *Aspidelaps*. All other elapids analysed lack these resistance-  
 90 conferring mutations, except that *Bungarus multicinctus* has Q111L but not G120R. The  
 91 amino-acid sequences of the H1–H2 domain mapped onto the phylogeny of the Elapidae are

shown in Fig. 1. All new sequences were deposited in GenBank (Accession numbers OQ338149-OQ338156 – Table 1)

Our results shed new light on the dynamics of the evolution of cardiac glycoside resistance in elapid snakes. With increasing phylogenetic breadth and depth (i.e., representation of *Aspidelaps* and the subgenus *Uraeus* through inclusion of *Naja nivea*) and additional species of the other subgenera of *Naja* (Wallach et al., 2009), our results strongly support the inference that bufadienolide resistance most likely evolved once at the base of the cobra radiation (Mohammadi et al., 2016). Virtually all members of this clade are occasional or frequent toad predators (Luiselli et al., 2002; Shine et al., 2007; Grundler, 2020), including its most basal lineage, *Aspidelaps* (Broadley & Baldwin, 2006). For the most part, bufadienolide resistance is thus restricted to toad-feeding elapid snakes.

The notable exception to this pattern is *Naja annulata*, which appears to be a highly specialised fish predator, but is nested deep within the bufophagous cobra clade and retains the resistant genotype. This species therefore appears to follow the pattern identified by Mohammadi et al. (2016), that while bufadienolide resistance evolves readily in toad-eating lineages, it is often retained in descendant lineages that no longer feed on bufonids. This provides additional impetus to the study of the costs and benefits of bufadienolide resistance in snakes.

Another point of interest in our results is that the many-banded krait, *Bungarus multicinctus*, a member of a largely snake-eating clade, displays one, but not both, of the two substitutions associated with cardiac glycoside resistance. It is questionable whether substitution Q111L alone confers significant resistance against cardiac glycosides, so the functional consequences of this mutation in *B. multicinctus* remain unknown (Mohammadi et al., 2016). The topic of

bufadienolide resistance in kraits may repay further investigation, as there are several records of one species, *B. caeruleus*, eating bufonids (Slowinski, 1994). In addition, it is worth noting that ophiophagous snakes are potentially at risk of secondary cardiac glycoside poisoning through the consumption of recently-fed bufophagous snakes, especially if the latter sequester bufadienolides (Hutchinson et al., 2007). However, there are virtually no documented observations of such encounters, except that Hesed (2006) observed a non-resistant king cobra (*Ophiophagus hannah*) feeding on a *Rhabdophis nigrocinctus*, a species known to sequester bufadienolides in specialised nuchal glands (Takeuchi et al., 2018). Unfortunately, the king cobra was not followed after the event, so any ill-effects would have remained undocumented. In any case, the risk of secondary bufadienolide poisoning may provide a selective explanation for the retention of resistance in some of the non-bufophagous snake-eating species, such as *Clelia clelia*, *Erythrolamprus aesculapii* and *E. bizonus*, noted by Mohammadi et al. (2016). It should also be noted that only the alpha 3 isoform of the Na<sup>+</sup>/K<sup>+</sup>-ATPase H1–H2 domain has been sequenced for most snakes: resistance-conferring mutations in other isoforms are found in other clades (Ujvari et al., 2015), and could potentially also occur in squamates, providing additional pathways to resistance.

In conclusion, our results have shed new light on the dynamics of the evolution of bufadienolide resistance in the family Elapidae: they confirm the single origin of this adaptation at the base of the clade of cobra-like elapids, and the tendency for resistance to be retained in snakes descended from toad-eating ancestors, in this instance the water cobra *Naja annulata*, and highlight the potential interest of the genus *Bungarus* for further research on this phenomenon. Taxonomically fine-grained studies of clades with variable diets, as here, are particularly helpful to better understand the selective advantages and costs of

bufadienolide resistance in snakes, and whether retention of this adaptation is better explained by a low cost of resistance, or a high cost of reversal due to factors such as intramolecular epistasis (Mohammadi et al., 2021) or potential pleiotropic links to co-evolved physiological adaptations.

## ACKNOWLEDGEMENTS

We thank Katie Coburn for support in the laboratory, and Nick Casewell, Paul Rowley, Edouard Crittenden, Chris Wild and the late Luke Yeomans for help with sample acquisition. This work took place with approval from the Bangor University Animal Welfare and Ethics Review Board. No other permits were required: our samples came from specimens that were either housed at Liverpool School of Tropical Medicine for previous work (Kazandjian et al., 2021) or were non-invasive samples from captive-bred animals in private collections in the UK. We thank two anonymous reviewers and the editors of the *Herpetological Journal* for their constructive comments that have led to an improved manuscript.

## REFERENCES

- Broadley, D.G. & Baldwin, A.S. (2006). Taxonomy, natural history, and zoogeography of the Southern African shield cobras, genus *Aspidelaps* (Serpentes: Elapidae). *Herpetological Natural History*, 9, 163–176.
- Buehler, M.D. (2020). The Evolutionary History of Sea Kraits (Genus *Laticauda*). Unpublished MSc thesis, Villanova University. 76 p.



161 Chirio, L. & LeBreton, M. (2007). Atlas des Reptiles du Cameroun. Paris: Publications  
 162 Scientifiques du Muséum National d'Histoire Naturelle IRD. 686 p.

163 Collet, M. & Trape, J.-F. (2020). Une nouvelle et remarquable espèce de naja semi-aquatique  
 164 (Elapidae, sous-genre *Boulengerina* Dollo, 1886) de la République Démocratique du Congo.  
 165 *Bulletin de la Société Herpétologique de France*, 173, 41–52.

166 Grundler, M. (2020). SquamataBase: a natural history database and R package for  
 167 comparative biology of snake feeding habits. *Biodiversity Data Journal*, 8, e49943.

168 Hesed, K. (2006). Natural History Notes. *Ophiophagus hannah*. Diet. *Herpetological Review*  
 169 37, 480.

170 Hutchinson, D.A., Mori, A., Savitzky, A.H., Burghardt, G.M., Wu, X., Meinwald, J. &  
 171 Schroeder, F.C. (2007). Dietary sequestration of defensive steroids in nuchal glands of the  
 172 Asian snake *Rhabdophis tigrinus*. *Proceedings of the National Academy of Science of the*  
 173 *USA*, 104, 2265–2270.

174 Kazandjian, T.D., Petras, D., Robinson, S.D., Thiel, J. van, Greene, H.W., Arbuckle, K., Barlow,  
 175 A., Carter, D.A., Wouters, R.M., Whiteley, G., Wagstaff, S.C., Arias, A.S., Albulescu, L.-O.,  
 176 Plettenberg Laing, A., Hall, C., Heap, A., Penrhyn-Lowe, S., McCabe, C.V., Ainsworth, S., Silva,  
 177 R.R. da, Dorrestein, P.C., Richardson, M.K., Gutiérrez, J.M., Calvete, J.J., Harrison, R.A.,  
 178 Vetter, I., Undheim, E.A.B., Wüster, W. & Casewell, N.R. (2021). Convergent evolution of  
 179 pain-inducing defensive venom components in spitting cobras. *Science*, 371, 386–390.

180 Kishida, T., Go, Y., Tatsumoto, S., Tatsumi, K., Kuraku, S. & Toda, M. (2019). Loss of olfaction  
 181 in sea snakes provides new perspectives on the aquatic adaptation of amniotes. *Proceedings*  
 182 *of the Royal Society B: Biological Sciences*, 286, 20191828.

183 Kratzer, H. (1965). Über die Tanganyika-Wasserkobra (*Boulengerina annulata stormsi*).  
 184 *Salamandra*, 1, 61–67.

185 Luiselli, L., Angelici, F. & Akani, G.C. (2002). Comparative feeding strategies and dietary  
 186 plasticity of the sympatric cobras *Naja melanoleuca* and *Naja nigricollis* in three diverging  
 187 Afrotropical habitats. *Canadian Journal of Zoology*, 80, 55–63.

188 Madsen, T. & Osterkamp, M. (1982). Notes on the biology of the fish-eating snake  
 189 *Lycodonomorphus bicolor* in Lake Tanganyika. *Journal of Herpetology*, 16, 185–188.

190 Marshall, B.M., Casewell, N.R., Vences, M., Glaw, F., Andreone, F., Rakotoarison, A., Zancolli,  
 191 G., Woog, F. & Wüster, W. (2018). Widespread vulnerability of Malagasy predators to the  
 192 toxins of an introduced toad. *Current Biology*, 28, R654–R655.

193 Mohammadi, S., Gompert, Z., Gonzalez, J., Takeuchi, H., Mori, A. & Savitzky, A.H. (2016).  
 194 Toxin-resistant isoforms of Na<sup>+</sup>/K<sup>+</sup>-ATPase in snakes do not closely track dietary  
 195 specialization on toads. *Proceedings of the Royal Society B: Biological Sciences*, 283,  
 196 20162111.

197 Mohammadi, S., Yang, L., Harpak, A., Herrera-Álvarez, S., del Pilar Rodríguez-Ordoñez, M.,  
 198 Peng, J., Zhang, K., Storz, J.F., Dobler, S., Crawford, A.J. & Andolfatto, P. (2021). Concerted  
 199 evolution reveals co-adapted amino acid substitutions in Na<sup>+</sup>K<sup>+</sup>-ATPase of frogs that prey  
 200 on toxic toads. *Current Biology* 31, 2530-2538.e10.

201 Pauwels, O.S.G. & Vande weghe, J.P. (2008). Reptiles du Gabon. Washington, D.C.:  
202 Smithsonian Institution. 272 p.

203 Shine, R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia.  
204 *The Quarterly Review of Biology*, 85, 253–291.

205 Shine, R., Branch, W.R., Webb, J.K., Harlow, P.S., Shine, T. & Keogh, J.S. (2007). Ecology of  
206 cobras from southern Africa. *Journal of Zoology*, 272, 183–193.

207 Slowinski, J.B. (1994). The diet of kraits (Elapidae: *Bungarus*). *Herpetological Review*, 25, 51–  
208 53.

209 Spawls, S. & Branch, B. (2020). The Dangerous Snakes of Africa. London: Bloomsbury. 336 p.

210 Spawls, S., Howell, K., Drewes, R. & Ashe, J. (2002). A field guide to the reptiles of East  
211 Africa: Kenya, Tanzania, Uganda, Rwanda and Burundi. San Diego: Academic Press. 543 p.

212 Suryamohan, K., Krishnankutty, S.P., Guillory, J., Jevit, M., Schröder, M.S., Wu, M.,  
213 Kuriakose, B., Mathew, O.K., Perumal, R.C., Koludarov, I., Goldstein, L.D., Senger, K., Dixon,  
214 M.D., Velayutham, D., Vargas, D., Chaudhuri, S., Muraleedharan, M., Goel, R., Chen, Y.-J.J.,  
215 Ratan, A., Liu, P., Faherty, B., Rosa, G. de la, Shibata, H., Baca, M., Sagolla, M., Ziai, J., Wright,  
216 G.A., Vucic, D., Mohan, S., Antony, A., Stinson, J., Kirkpatrick, D.S., Hannoush, R.N., Durinck,  
217 S., Modrusan, Z., Stawiski, E.W., Wiley, K., Raudsepp, T., Kini, R.M., Zachariah, A. & Seshagiri,  
218 S. (2020). The Indian cobra reference genome and transcriptome enables comprehensive  
219 identification of venom toxins. *Nature Genetics*, 52, 106–117.

220 Takeuchi, H., Savitzky, A.H., Ding, L., Silva, A. de, Das, I., Nguyen, T.T., Tsai, T.-S., Jono, T.,  
221 Zhu, G.-X., Mahaulpatha, D., Tang, Y. & Mori, A. (2018). Evolution of nuchal glands, unusual

222 defensive organs of Asian natricine snakes (Serpentes: Colubridae), inferred from a  
 223 molecular phylogeny. *Ecology and Evolution*, 8, 10219–10232.

224 Tamura, K., Stecher, G., Kumar, S. (2021). MEGA11: Molecular Evolutionary Genetics  
 225 Analysis Version 11. *Molecular Biology and Evolution*, 38, 3022–3027.

226 Ujvari, B., Casewell, N.R., Sunagar, K., Arbuckle, K., Wüster, W., Lo, N., O’Meally, D.,  
 227 Beckmann, C., King, G.F., Deplazes, E. & Madsen, T. (2015). Widespread convergence in  
 228 toxin resistance by predictable molecular evolution. *Proceedings of the National Academy of*  
 229 *Science of the USA*, 112: 11911–11916.

230 Ujvari, B., Mun, H., Conigrave, A.D., Bray, A., Osterkamp, J., Halling, P. & Madsen, T. (2013).  
 231 Isolation breeds naivety: island living robs Australian varanid lizards of toad-toxin immunity  
 232 via four base pair mutation. *Evolution*, 67, 289–294.

233 Ujvari, B., Mun, H.-C., Conigrave, A.D., Ciofi, C. & Madsen, T. (2014). Invasive toxic prey may  
 234 imperil the survival of an iconic giant lizard, the Komodo dragon. *Pacific Conservation*  
 235 *Biology*, 20, 363.

236 Vonk, F.J., Casewell, N.R., Henkel, C.V., Heimberg, A.M., Jansen, H.J., McCleary, R.J.R.,  
 237 Kerkkamp, H.M.E., Vos, R.A., Guerreiro, I., Calvete, J.J., Wüster, W., Woods, A.E., Logan,  
 238 J.M., Harrison, R.A., Castoe, T.A., Koning, A.P.J. de, Pollock, D.D., Yandell, M., Calderon, D.,  
 239 Renjifo, C., Currier, R.B., Salgado, D., Pla, D., Sanz, L., Hyder, A.S., Ribeiro, J.M.C., Arntzen,  
 240 J.W., Thillart, G.E.E.J.M. van den, Boetzer, M., Pirovano, W., Dirks, R.P., Spaink, H.P.,  
 241 Duboule, D., McGlinn, E., Kini, R.M. & Richardson, M.K. (2013). The king cobra genome  
 242 reveals dynamic gene evolution and adaptation in the snake venom system. *Proceedings of*  
 243 *the National Academy of Science of the USA*, 110, 20651–20656.

244 Wallach, V., Wüster, W. & Broadley, D.G. (2009). In praise of subgenera: taxonomic status of  
 245 cobras of the genus *Naja* Laurenti (Serpentes: Elapidae). *Zootaxa*, 2236, 26–36.

246 Wüster, W., Crookes, S., Ineich, I., Mané, Y., Pook, C.E., Trape, J.-F. & Broadley, D.G. (2007).  
 247 The phylogeny of cobras inferred from mitochondrial DNA sequences: Evolution of venom  
 248 spitting and the phylogeography of the African spitting cobras (Serpentes: Elapidae: *Naja*  
 249 *nigricollis* complex). *Molecular Phylogenetics and Evolution*, 45, 437–453.

250 Zhang, Z.-Y., Lv, Y., Wu, W., Yan, C., Tang, C.-Y., Peng, C. & Li, J.-T. (2022). The structural and  
 251 functional divergence of a neglected three-finger toxin subfamily in lethal elapids. *Cell*  
 252 *Reports*, 40, 111079.

253

## 254 **Table legends**

255 **Table 1.** Taxa included in the analysis, origin of new material, GenBank accession numbers  
 256 and original reference

257

## 258 **Figure legends**

259 **Figure 1.** Amino acid sequences of the H1–H2 extracellular loop of all species analyzed in  
 260 this study mapped onto the phylogeny of the cobras and their relatives. Phylogeny redrawn  
 261 from Kazandjian et al. (2021); the timing of the divergence between *Laticauda colubrina* and  
 262 *L. laticaudata* is taken from Buehler (2020). Bold type on a yellow background indicates  
 263 amino-acids likely to confer bufadienolide resistance, bold red branches indicate inferred  
 264 bufadienolide-resistant lineages, and the bold blue branch indicates the origin of piscivory in  
 265 water cobras.

266

**Table 1.** Taxa included in the analysis, origin of new material, GenBank accession numbers and original reference

Species	GenBank Accession number	Origin of new material	Source
<i>Laticauda colubrina</i>	BLBF01000071		Kishida et al. (2019)
<i>Laticauda laticaudata</i>	BHFT01056349		(Kishida et al., 2019)
<i>Bungarus multicinctus</i>	CM042835		(Zhang et al., 2022)
<i>Ophiophagus hannah</i>	AZIM01007862		(Vonk et al., 2013)
<i>Dendroaspis angusticeps</i>	KU738076		(Mohammadi et al., 2016)
<i>Dendroaspis polylepis</i>	KU738077		(Mohammadi et al., 2016)
<i>Aspidelaps scutatus</i>	OQ338149	UK pet trade specimen, locality of origin unknown	This study
<i>Hemachatus haemachatus</i>	KU738087		Mohammadi et al. (2016)
<i>Hemachatus haemachatus</i>	OQ338153	LSTM Hem Hae ZAF003, South Africa	This study
<i>Naja (Uraeus) nivea</i>	OQ338155	LSTM Naj Niv ZAF001, South Africa	This study
<i>Naja (Naja) naja</i>	OQ338151	UK pet trade specimen, Sri Lanka	This study
<i>Naja (Naja) naja</i>	CM019160		Suryamohan et al. (2020)
<i>Naja (Naja) atra</i>	KU738098		Mohammadi et al. (2016)
<i>Naja (Naja) kaouthia</i>	OQ338152	UK pet trade specimen, Malaysia	This study
<i>Naja (Afronaja) nigricollis</i>	OQ338154	LSTM Naj Mos TZA004, Tanzania	This study
<i>Naja (Afronaja) nigricollis</i>	KU738100		Mohammadi et al. (2016)
<i>Naja (Boulengerina) subfulva</i>	OQ338156	LSTM Naj Mel CMR002, Cameroon	This study
<i>Naja (Boulengerina) melanoleuca</i>	KU738099		Mohammadi et al. (2016)
<i>Naja (Boulengerina) annulata</i>	OQ338156	UK pet trade specimen, locality of origin unknown	This study

