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Lycodon and *Dinodon*: One genus or two? Evidence from molecular phylogenetics and morphological comparisons

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ABSTRACT

Based on a molecular phylogeny and a comparison of maxillary dentition and morphology, the relationship between the genera *Lycodon* and *Dinodon* was investigated. Bayesian Inference and Maximum Likelihood analysis of two mitochondrial genes (cyt b and ND4) and two nuclear genes (c-mos and Rag1) suggested that the two genera shared a most recent common ancestor. However, *Dinodon* was paraphyletic and *Lycodon* was polyphyletic, each with respect to the other. The results from counts of maxillary teeth indicated that the diagnostic characters used by previous authors to separate *Dinodon* and *Lycodon* were not reliable. Taking the molecular and morphological evidence together, we synonymized *Dinodon* with *Lycodon*. In addition, the validity of the species *L. futsingensis* was confirmed to be distinctly different from the other species of *Dinodon* and *Lycodon*.

1. Introduction

Traditionally, species have been described and classified on the basis of morphological traits, without regard to phylogenetic relationships with other taxa. For many species, selective or developmental constraints either prevent morphological divergence (e.g. Colborn et al., 2001) or promote convergence (e.g. Wake, 1991), complicating our understanding of group composition based on evolutionary relationships inferred from morphology. In such cases, molecular studies are invaluable. The increased availability of molecular systematic techniques and robust analytical methods now allow phylogenies to be inferred independent of phenotype. Furthermore, ongoing studies have repeatedly demonstrated that general morphological resemblance is not a reliable method for phylogeny and taxonomies, particularly in snakes (Burbrink and Lawson, 2007; Guo et al., 2009b, 2012; Pyron and Burbrink, 2009; Pyron et al., 2011). However, the ability of gene trees to resolve complex relationships also depends on obtaining an adequate genetic and taxonomic sampling.

A good example is *Lycodon,* one of the most diverse genera of Asiatic colubrids (sensu stricto, see Pyron et al., 2011), currently containing 43 species (Reptile Database; http://reptile-database.reptarium.cz) ranging from central Asia and eastern Iran to southern China, the Indo-Australian Archipelago, Japan and the Philippines (Lanza, 1999). Of these species, 10 have been described within the last few years (e.g. Vogel and David, 2010; Vogel and Luo, 2011; Zhang et al., 2011a,b). Within Colubridae, *Lycodon* appears to be closely related to *Dinodon* (Smith, 1943; Pyron et al., 2011), which is composed of eight species found from India in the west, to Japan in the east, China (Taiwan) in the south and Russia in the north (Reptile Database; http://reptile-database.reptarium.cz). Interestingly, some species within *Lycodon* have been placed in *Dinodon* and vice versa. For example, *Lycodon futsingensis* was first described as *Dinodon futsingensis* (Pope, 1928) and subsequently placed in *Lycodon* (Pope, 1935), whereas *Dinodon gammiei* was assigned to *Lycodon* by Boulenger (1893). Externally, no differences between the genera have been diagnosed and color pattern is similar among most species, sharing a typical cross-banded body pattern. The main differences separating the genera are their dentition and the shape of the maxillary bone (Smith, 1943). For example, in *Dinodon* the maxillary teeth are arranged into three groups, whereas they are arranged into two groups in *Lycodon*.

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In this study, we used multilocus method to construct a phylogeny of both genera. Additionally, we also conducted a morphological comparison of the maxillary of several representatives of two genera, particularly focusing on the dentition. Our main goal is to explore the validity of the two common Asian snake genera.

2. Materials and methods

2.1. Molecular phylogeny

Seventeen individuals representing five species of *Lycodon* and two species of *Dinodon* were sequenced here (GP series; Table 1). The remaining sequences from six individuals (belonging to four species and two genera) were retrieved from GenBank (Table 1). To investigate the relationship and monophyly of both genera, several representatives of their close relatives were also included and *Thrasops jacksonii* was chosen as outgroup based on previous study (Pyron et al., 2011).

Total DNA was extracted from liver or muscle tissues preserved in 85% alcohol, using standard methods (Sambrook and Russell, 2002). The entire gene sequences for the mitochondrial cytochrome *b* (cyt b), the partial gene sequences of NADH dehydrogenase subunit 4 (ND4) and two nuclear gene c-mos and Rag1 were amplified by the polymerase chain reaction (PCR) using primers L14910/H16064 (Burbrink et al., 2000), ND4/Leu (Arèvalo et al., 1994), S77/S78 (Lawson et al., 2005) and R13/R18 (Groth and Barrowclough, 1999), respectively. The cycling parameters were identical to those described in the studies mentioned above. Prior to sequencing, PCR products were purified using various commercial kits. The double-stranded product was sequenced using an ABI 3730 Genetic Analyzer (Applied Biosystems) following manufacturer's protocols.

Alignment of protein coding genes was trivial as there were no indels and all sequences were in reading frame. Phylogenetic analyses were performed using two different methods including Bayesian Inference (BI) and Maximum Likelihood (ML). For the Bayesian analyses, the sequence data was partitioned by nuclear genes (c-mos and Rag1), and by codon position for mitochondrial coding genes (cyt b, ND4), to give a total of eight partitions (c-mos, Rag1, cyt b and ND4 codon position 1, pos. 2, pos. 3). Heterozygous sequences were phased using Phase (Stephens et al., 2001) and Seqphase (Flot, 2010). The best-fit substitution model was assigned to each partition using AIC in MrModeltest 2.3 (Nylander, 2004). We used MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) to estimate trees with three independent runs, each initiated with random trees. All searches consisted of four Markov chains (three heated chains and a single cold chain) estimated for 5 million generations and sampled every 1000 generations with 20% initial samples discarded as burn-in. Substitution parameters were unlinked and rates were allowed to vary across partitions. Stationarity was confirmed by plotting the likelihood against generation in the program Tracer v1.4 (Drummond and Rambaut, 2007). After confirming that three analyses reached stationarity at a similar likelihood score and the topologies were similar, the resultant trees were combined to calculate posterior probabilities (PPs) for each node in a 50% majority-rule consensus tree. The ML tree and bootstrap support (1000 non-parametric bootstrap replicates) were obtained using the same partitioning strategy in BI in RAxML, (Stamatakis et al., 2008).

2.2. Maxillary comparison

Seven individuals representing three species from both genera were examined, including four specimens of *Dinodon rufozonatum*

Table 1
Samples used in this study.

Taxon	Voucher numbers	Locality	GenBank access numbers			
			cyt b	ND4	c-mos	Rag1
Lycodon flavozonatum	GP 1939	Guangxi, China	KC733199	KC733232	KC733216	KC733184
Lycodon flavozonatum	GP 2279	Guangdong, China	KC733210	KC733243	KC733226	KC733193
Lycodon rufozonatum	GP 133	Sichuan, China	KC733194	KC733227	KC733211	KC733179
Lycodon rufozonatum	GP 625	Liaoning, China	KC733196	KC733229	KC733213	KC733181
Lycodon fasciatus	GP 2094	Guangdong, China	KC733201	KC733234	KC733218	KC733186
Lycodon fasciatus	GP 2097	Guangdong, China	KC733202	KC733235	KC733219	KC733187
Lycodon futsingensis	GP 1627	Guangdong, China	KC733198	KC733231	KC733215	KC733183
Lycodon futsingensis	GP 2214	Guangdong, China	KC733205	KC733238	KC733222	KC733190
Lycodon futsingensis	GP 2216	Zhejiang, China	KC733206	KC733239	–	–
Lycodon futsingensis	GP 2226	Guangdong, China	KC733207	KC733240	KC733223	–
Lycodon futsingensis	GP 2245	Guangdong, China	KC733209	KC733242	KC733225	KC733192
Lycodon ruhstrati	GP 285	Sichuan, China	KC733195	KC733228	KC733212	KC733180
Lycodon ruhstrati	GP 991	Guangxi, China	KC733197	KC733230	KC733214	KC733182
Lycodon ruhstrati	GP 2049	Guangdong, China	KC733200	KC733233	KC733217	KC733185
Lycodon ruhstrati	GP 2243	Guangdong, China	KC733208	KC733241	KC733224	KC733191
Lycodon subcinctus	GP 2191	–	KC733203	KC733236	KC733220	KC733188
Lycodon synaptor	GP 2188	Yunnan, China	KC733204	KC733237	KC733221	KC733189
Lycodon rufozonatum	LSUMZ 44977	–	AF471063	–	AF471163	AY662611
Lycodon rufozonatum	–	–	JF827672	JF827649	JF827695	–
Lycodon semicarinatus	–	–	D86118	–	–	–
Lycodon semicarinatus	–	–	AB008539	AB008539	–	–
Lycodon aulicus	–	–	HQ735416	–	HQ735418	–
Lycodon zawi	CAS 210323	–	AF471040	–	AF471111	–
Boiga dendrophila	–	–	AF471089	U49303	AF471128	–
Crotaphopeltis tornieri	–	–	AF471093	–	AF471112	–
Dipsadoboa unicolor	CAS 201660	–	AF471062	–	AF471139	–
Dispholidus typus	–	–	AY188012	U49302	AY187973	–
Dasypeltis atra	CAS 201641	–	AF471065	–	AF471136	–
Dasypeltis scabra	–	–	AY235729	–	–	–
Thelotornis capensis	LSUMZ 22073	–	AF471042	–	AF471109	–
Thrasops jacksoni	LSUMZ H-6819	–	AF471044	–	DQ112084	–
Toxicodryas pulverulenta	CAS 220642	–	AF471047	–	AF471118	–
Telescopus fallax	LSUMZ H696t	–	AF471043	–	AY188000	–

Table 2
Results of AIC model selection conducted in MrModeltest for partitions of the dataset.

Partition	AIC model
Cyt b	HKY + I + G
Cyt b, position 1	GTR + I + G
Cyt b, position 2	GTR + I + G
Cyt b, position 3	GTR + G
ND4	HKY + I + G
ND4, position 1	GTR + I + G
ND4, position 2	HKY + I
ND4, position 3	HKY + G
c-mos	HKY
Rag1	GTR + I

(the type species of *Dinodon*. YBU S1201–S1204), one specimen of *Lycodon futsingensis* (YBU S1205) and two specimens of *Lycodon ruhstrati* (YBU 11287 and YBU 11270). All specimens were adults without anomalies or injuries to the head. The main differences between the genera are the arrangement and number of maxillary teeth, thus we only examined and compared the maxillary teeth for these specimens. Accurate tooth counts can be obtained by counting the sockets and the teeth present, rather than by just only counting the teeth present. Line drawings of skulls were prepared from photographs and skull samples. All skull samples are deposited in the Yibin University, Sichuan, China. For comparison, the maxillary of three species of *Lycodon* and *Dinodon* (*L. aulicus*, *L. faciatus*, *D. flavozonatum*) were also included (Smith, 1943).

3. Results

3.1. Phylogenetic relationship reconstruction

The final alignment of four gene fragments consisted of a total of 3361 aligned base pairs: 1104 from cyt b, 694 from ND4, 1012 from Rag1, and 551 from c-mos. The concatenated dataset contained 907 variable sites (including outgroups), of which 653 were phylogenetically informative under MP criteria. No deletions, insertions or stop codons were detected in mitochondrial protein coding genes, indicating that unintentional amplification of pseudogenes was unlikely. For sequences of Rag1, there were 18 bp deletions in two samples (GP 2049 and GP 2094). Base frequencies were estimated by the program MrModeltest as $A = 0.3055$, $C = 0.2758$, $G = 0.1484$, $T = 0.2704$. New sequences generated for this project were deposited in GenBank (Table 1, accession nos. KC733179–KC733243).

The best-fit model indicated by MrModeltest varied among data partitions. The optimal models of sequence evolution of each

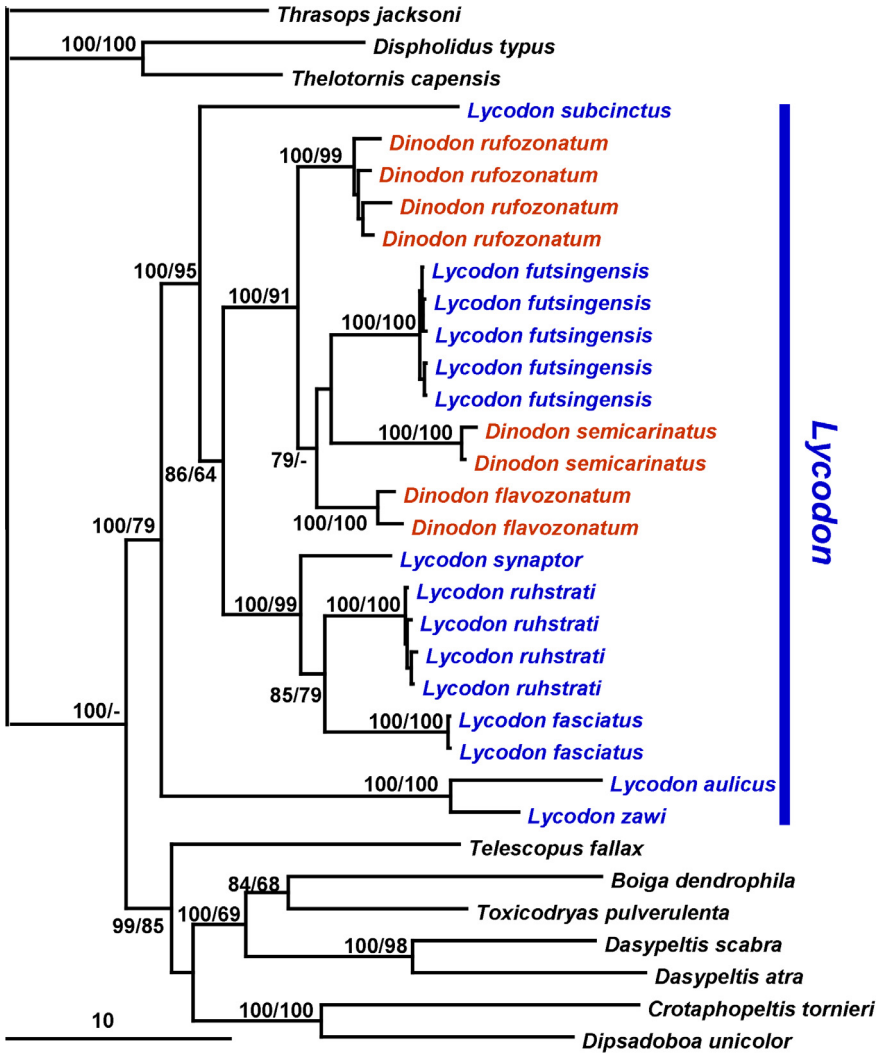

Fig. 1. Bayesian 50% majority-rule consensus tree inferred using 8-partition model from nuclear and mtDNA data in MrBayes. The values assigned to the internodes indicate posterior probability support (before the slash) and ML bootstrap (after the slash). A node with support value <50% was indicated by "–". Branch support indices are not given for some internodes to preserve clarity.

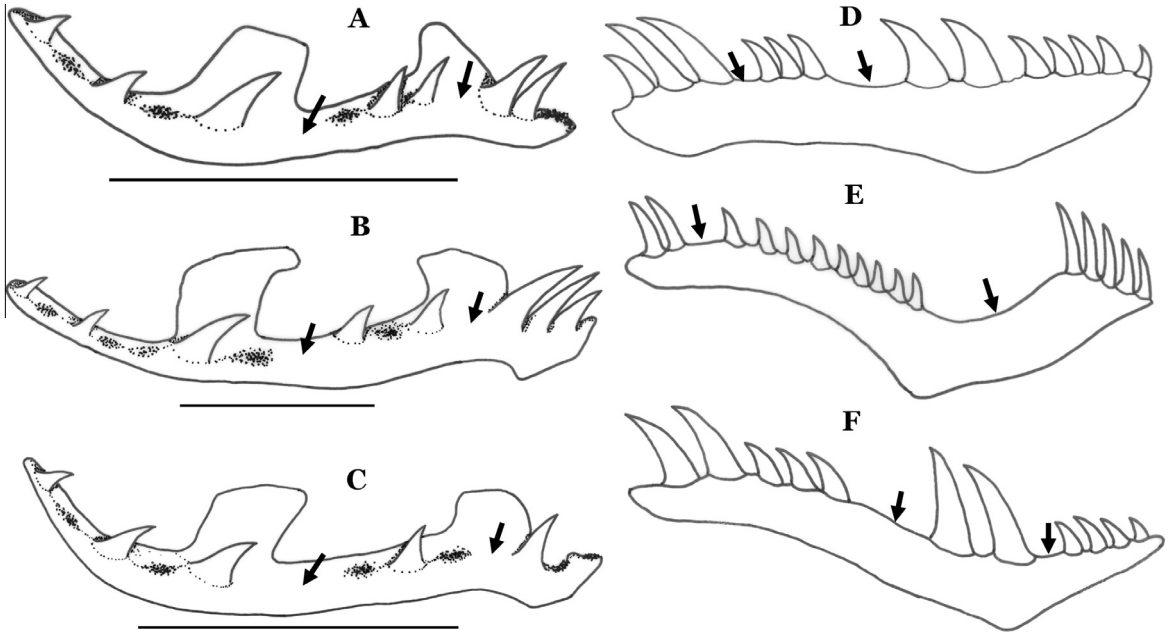

Fig. 2. Maxillary morphology of three species. (A) *Dinodon rufozonatum* (YBU S1202); (B) *Lycodon futsingensis* (YBU S1205); (C) *Lycodon ruhstrati* (YBU 11278); (D) *Dinodon flavozonatum*; (E) *Lycodon aulicus*; (F) *Lycodon faciatus*. The bar indicates 0.5 mm, the arrow represents the gaps of the maxillary teeth. (D–F) from Smith (1943).

partition are listed in Table 2. Both ML and BI analyses showed a consistent topology with slight disagreement in support values in some nodes (Fig. 2). BI and ML trees showed strong support (79% BS and 100% PP respectively) for the monophyly of *Lycodon* + *Dinodon* (Fig. 1). However, *Lycodon* is indicated to be polyphyletic with respect to *Dinodon*, while *Dinodon* is paraphyletic with respect to *Lycodon*. Within the clade including *Lycodon* and *Dinodon*, two species of *Lycodon* (*L. aulicus* and *L. zawi*) formed a strongly supported monophyletic group, which are themselves sister to the clade including the other five species of *Lycodon* and three species of *Dinodon,* with high support indices (95% BS and 100% PP). Another three species of *Lycodon* (*L. synaptor*, *L. ruhstrati* and *L. fasciatus*) also form a monophyletic group, with support values of 99% BS and 100% PP. Unexpectedly, *L. futsingensis* was found within *Dinodon* and these together formed a highly supported clade (91% BS and 100% PP).

3.2. Maxillary comparison

The seven specimens examined showed general morphological resemblance to other colubrids in skulls and maxillary characteristics (Cundall, 1981; Zhang, 1988; Guo et al., 2009a). In *Dinodon rufozonatum*, the maxillary bone is arched, and the three specimens agree in having 7 + 3 + 3 maxillary teeth on both sides, while the fourth (YBU S1202) has 6 + 3 + 3 on one side and 7 + 3 + 3 on the other side. The teeth of the anterior group (7 or 6) noticeably increase in size from front to rear and the last two are much enlarged. The middle group (3) are unequal in size and relatively small. The last one in the posterior group is much smaller than the other two (Fig. 2A–C). However, it should be pointed out that the second gap in two of the three specimens is very small, or not distinct. In *L. futsingensis* and *L. ruhstrati*, the maxillary bones are arched, and the maxillary teeth are divided into three groups by two gaps. The anterior group consist of 5 (*L. futsingensis*) and 6 (*L. ruhstrati*) teeth, gradually enlarging posteriorly, and the last two are much enlarged. The middle group is composed of 3 small teeth, while the posterior group consists of 2 enlarged and a much smaller posterior tooth (Fig. 2A–C).

4. Discussion

4.1. A revised taxonomy of Dinodon and Lycodon

Although our sampling was incomplete relative to the contents of *Dinodon* and *Lycodon*, multilocus phylogenetics indicated that all representatives from both genera formed a strongly supported group, and both genera were showed to be paraphyletic or polyphyletic (Fig. 1). The genera *Dinodon* and *Lycodon* were described in 1853 and 1826 respectively. The main diagnostic differences between the two genera are the arrangement of the maxillary teeth: in *Dinodon*, the teeth were considered to be divided into three groups by two distinct interspaces, while in *Lycodon* there are only two groups (Boulenger, 1894).

Wall (1911) stated that the generic characters used by Boulenger (1894) to separate *Dinodon* and *Lycodon* were questionable. The diagnostic maxillary teeth characters were also questioned by Pope (1935) and Smith (1943). Wall (1911) proposed a difference in the number of teeth in the posterior group of maxillaries of both genera (three in *Dinodon*, but only two in *Lycodon*). However, Pope (1935) argued that such a difference should not be considered of generic importance.

Pope (1935), Smith (1943) (Fig. 2D–F) and Vogel et al. (2009) described the maxillary teeth of several species of *Lycodon* and-or *Dinodon*, all of which exhibited three groups of maxillary teeth. The results presented here agree with the above two genera in maxillary teeth arrangement (three groups), although the actual number of teeth present is slightly variable. Evidently, the results from Pope (1935), Smith (1943), Vogel et al. (2009) and our present work strongly support Wall's (1911) conjecture that the generic diagnostic characters used by Boulenger (1894) to identify *Dinodon* and *Lycodon* are unreliable. Additionally, based on Vogel et al. (2009) and our work, the maxillary teeth numbers of the posterior group are variable (2 or 3), which is inconsistent with Wall (1911).

Thus we conclude that this character is also not useful for separating the two genera. It is clear that *Dinodon* and *Lycodon* cannot be identified and separated by maxillary teeth characterstics and maxillary bone.

Molecular phylogenetic analysis also indicated that neither *Dinodon* or *Lycodon* are monophyletic. Seven representatives of *Lycodon* were found in four separate clades, some sharing a most recent common ancestor with *Dinodon*. Here, the position of *L. futsingensis* renders *Dinodon* paraphyletic and, if we recognized the validity of the genus *Dinodon* (including *L. futsingensis*), then *Lycodon* would be polyphyletic with respect to *Dinodon*. And the rest of the genus *Lycodon* could be placed in at least two genera (*L. zawi* + *L. aulicus*), (*L. subcinctus* + *L. synaptor* + *L. ruhstrati* + *L. fasciatus*). However, this arrangement seems to be unacceptable based on similar external morphology and skull characteristics. Particularly, molecular phylogenetic analyses strongly suggest that both genera were not monophyletic with respect to one another. Thus, on the basis of a combination of molecular phyloygenetic relationships and morphological characters (skull characters and external morphology), we suggest synonymizing *Dinodon* with *Lycodon*. Similar results have recently been obtained by other authors (e.g., Siler et al., 2013), with other studies suggesting that a third genus, the morphologically similar *Dryocalamus* of south and east Asia (which has also previously been classified in *Lycodon*) might also be nested within this group (Pyron et al., 2013).

4.2. The validity of Lycodon futsingensis

Based on the specimens from Fuqing, Fujian, China, Pope (1928) described *Dinodon futsingensis*. However the species was subsequently synonymized with *Lycodon ruhstrati* (Pope, 1929), to which it is morphologically similar (Pope, 1935; Vogel et al., 2009). This arrangement has been followed for a long time by some authors (Zhao et al., 1998; Lanza, 1999). Recently, on the basis of morphological comparison, Vogel et al. (2009) revalidated *Dinodon futsingensis* and recognized it as *Lycodon futsingensis*. In recent years, *L. futsingensis* has been found in additional localities (Zhang et al., 2011a,b). However, the results presented here indicated that this species was more closely related to species of *L. flavozonatum*, *L. rufozonatum* and *L. rufozonatum*, and is only distantly related to *L. ruhstrati* (Fig. 1). Similar cases can also be found in other systematic revisions of snakes (e.g. Herrmann et al., 2004; Guo et al., 2009b). Thus, based on our molecular analysis, we confirm that this species is valid and should be regarded as *L. futsingensis*.

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References

Arèvalo, E., Davis, S.K., Sites, J.W., 1994. Mitochondrial DNA sequence divergence and phylogenetic relationships among eight chromosome races of the *Sceloporus grammicus* complex (Phrynosomatidae) in central Mexico. Syst. Biol. 43, 387–418.

Boulenger, G.A., 1893. Catalogue of the Snakes in the British Museum (Natural History), vol. I. British Museum (Natural History), London.

Boulenger, G.A., 1894. Catalogue of the Snakes in the British Museum (Natural History), vol. II. British Museum (Natural History), London.

Burbrink, F.T., Lawson, R., 2007. How and when did Old World ratsnakes disperse into the New World? Mol. Phylogenet. Evol. 43, 173–189.

Burbrink, F.T., Lawson, R., Slowinski, J.B., 2000. Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. Evolution 54, 2107–2118.

Colborn, J., Crabtree, R.E., Shaklee, J.B., Pfeiler, E., Bowen, B.W., 2001. The evolutionary enigma of bonefishes *Albula* spp. cryptic species and ancient separations in a globally distributed shorefish. Evolution 55, 807–820.

Cundall, D., 1981. Cranial osteology of the colubrid snake genus *Opheodrys*. Copeia 2, 353–371.

Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7, 214.

Flot, J.F., 2010. SEQPHASE: a web tool for interconverting PHASE input/output files and FASTA sequence alignments. Mol. Ecol. Resources 10, 162–166.

Groth, J.G., Barrowclough, G.F., 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. Mol. Phylogenet. Evol. 12, 115–123.

Guo, P., Liu, S.Y., Huang, S., He, M., Sun, Z.Y., Feng, J.C., Zhao, E.M., 2009a. Morphological variation in *Thermophis* Malnate (Serpentes: Colubridae), with an expanded description of the type species *T. zhaoermii*. Zootaxa 1973, 51–60.

Guo, P., Malhotra, A., Li, C., Creer, S., Pook, C.E., Wen, T., 2009b. Systematics of the *Protobothrops jerdonii* complex (Serpentes, Viperidae, Crotalinae) inferred from morphometric data and molecular phylogeny. Herpetol. J., 85–96.

Guo, P., Liu, Q., Xu, Y., Jiang, K., Hou, M., Ding, L., Pyron, R.A., Burbrink, F.T., 2012. Out of Asia: natricine snakes support the Cenozoic Beringian Dispersal Hypothesis. Mol. Phylogenet. Evol. 63, 825–833.

Herrmann, H.W., Ziegler, T., Malhotra, A., Thorpe, R.S., Parkinson, C.L., 2004. Redescription and systematics of *Trimeresurus cornutus* (Serpentes: Viperidae) based on morphology and molecular data. Herpetologica 60, 211–221.

Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics 17, 754–755.

Lanza, B., 1999. A new species of *Lycodon* from the Philippines, with a key to the genus (Reptilia: Serpentes: Colubridae). Trop. Zool. 12, 89–104.

Lawson, R., Slowinski, J.B., Crother, B.I., Burbrink, F.T., 2005. Phylogeny of the Colubroidea (Serpentes): new evidence from mitochondrial and nuclear genes. Mol. Phylogenet. Evol. 37, 581–601.

Nylander, J.A.A., 2004. Mrmodeltest v.2. program distributed by the author. Evolutionary Biology Centre, Uppsala University.

Pope, C.H., 1928. Seven new reptiles from Fukien Province, China. Am. Mus. Novitates 320, 1–6.

Pope, C.H., 1929. A list of reptiles known to occur in Fukien Province, China. Proc. Nat. Hist. Soc., 20–22.

Pope, C.H., 1935. The Reptiles of China. Turtles, Crocodilians, Snakes, Lizards. Natural History of Central Asia, X. American Museum of Natural History, New York.

Pyron, R.A., Burbrink, F.T., 2009. Systematics of the Common Kingsnake (*Lampropeltis getula*; Serpentes: Colubridae) and the burden of heritage in taxonomy. Zootaxa 2241, 22–32.

Pyron, R.A., Burbrink, F.T., Colli, G.R., de Oca, A.N.M., Vitt, L.J., Kuczynski, C.A., Wiens, J.J., 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. Mol. Phylogenet. Evol. 58, 329–342.

Pyron, R.A., Kandambi, H.K.D., Hendry, C.R., Pushpamal, V., Burbrink, F.T., Somaweera, R., 2013. Genus-level molecular phylogeny of snakes reveals the origins of species richness in Sri Lanka. Mol. Phylogenet. Evol. 66, 969–975.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Sambrook, J., Russell, D.W., 2002. Molecular Cloning, A Laboratory Manual. Cold Spring Harbor Laboratory Press, New York.

Siler, C.D., Oliveros, C.H., Santanen, A., Brown, R.M., Multilocus phylogeny reveals unexpected diversification patterns in Asian wolf snakes (genus *Lycodon*). *Zool. Scr.* 2013, http://dx.doi.org/10.1111/zsc.12007

Smith, M.A., 1943. The Fauna of British India, Ceylon and Burma, Reptilia and Amphibia. III, Serpentes. Taylor and Francis, London.

Stamatakis, A., Hoover, P., Rougemont, J., 2008. A rapid bootstrap algorithm for the RAxML web-servers. Sys. Biol. 75, 758–771.

Stephens, M., Smith, N.J., Donnelly, P., 2001. A new statistical method for haplotype reconstruction from population data. Am. J. Hum. Genet. 68, 978–989.

Vogel, G., David, P., 2010. A new species of the genus *Lycodon*(Boie, 1826) from Yunnan Province, China (Serpentes: Colubridae). Bonn zool. Bull. 57, 289–296.

Vogel, G., Luo, J., 2011. A new species of the genus *Lycodon* (Boie, 1826) from the southwestern mountains of China (Squamata: Colubridae). Zootaxa 2807, 29–40.

Vogel, G., David, P., Pauwels, O.S.G., Sumontha, M., Norval, G., Hendrix, R., Vu, N.T., Ziegler, T., 2009. A revision of *Lycodon ruhstrati* (Fischer 1886) *auctorum* (Squamata Colubridae), with the description of a new species from Thailand and a new subspecies from the Asian mainland. Trop. Zool. 22, 131–182.

Wake, D.B., 1991. Homoplasy: the result of natural selection, or evidence of design limitations? Am. Nat. 138, 543–567.

Wall, F., 1911. A popular treatise on the common Indian snakes. J. Bombay Nat. Hist. Soc. XX.

Zhang, F.J., 1988. Studies on the cranial morphology of *Zaocys* (serpents: Colubridae) V. a comparative study on the cranial morphology of Chinese *Zaocys*, *Ptyas*, *Elaphe* and *Entechinus*, with preliminary discussions on the function and phylogeny. Acta Herpetol. Sin. 1, 47–55.

Zhang, J., Jiang, K., Vogel, G., Rao, D.Q., 2011a. A new species of the genus *Lycodon* (Squamata, Colubridae) from Sichuan Province, China. Zootaxa 2982, 59–68.
Zhang, L., Jiang, K., Hu, P., Yu, B.C., Peng, B.Y., Tang, X.P., Hu, H.J., 2011b. *Lycodon futsingensis*: a new snake record in Guangdong Province, China. Chin. J. Zool. 46 (1), 128–130.
Zhao, E.M., Huang, M.H., Zong, Y., (Eds.) 1998. Fauna Sinica: Reptilia, Squamata, Serpentes, vol. 3. Science Press, Beijing.