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PHYLOGENETIC RELATIONSHIPS OF THE GENUS *SIBYNOPHIS* (SERPENTES: COLUBROIDEA)

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ABSTRACT

We present the results of the first molecular analysis of the phylogenetic affinities of the Asian colubroid genus *Sibynophis*. We recovered a sister-group relationship between *Sibynophis* and the New World *Scaphiodontophis*. Although *Liophidium* sometimes is associated with these genera, the relationship is distant. Morphological characters that *Liophidium* shares with *Sibynophis* and *Scaphiodontophis* are resolved as homoplasies that probably reflect the similarities of their specialized feeding habits. The traditional subfamily *Sibynophiinae* is elevated to the family-level, and *Scaphiodontophiinae* is placed in its synonymy.

KEY-WORDS: *Sibynophiidae*; *Sibynophis*; *Scaphiodontophis*; Phylogeny.

INTRODUCTION

The genera *Liophidium*, *Sibynophis*, and *Scaphiodontophis* occur on three distinct landmasses—Madagascar, Asia, and Central America, respectively. Despite their isolation, these snakes long have been thought to be closely related to each other. In each genus, the dentary bears a peculiar posterior dentigerous

process that is completely detached from the compound bone and teeth are numerous and closely set (Duméril *et al.*, 1854; Boulenger, 1890, 1896).

Duméril *et al.* (1854) were the first authors to place the four species that share these morphological characteristics in the subgenus *Enicognathus* of their genus *Ablabes*. Later, Boulenger (1890) substituted *Enicognathus*, preoccupied, with *Polyodontophis*

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that he recognized as a genus. He added four additional species from India and southeastern Asia to *Polyodontophis*, as well as *P. comorensis* (= *Liophidium mayottensis*) and *P. sumichrasti* from the Comoros Islands and Central America, respectively. Boulenger (1896) further expanded *Polyodontophis* with three additional species, and described the genus *Liophidium*, to accommodate *L. trilineatum* from Madagascar. *Polyodontophis* was posteriorly synonymized with Fitzinger's (1843) *Sibynophis* when Stejneger (1910) noted the latter genus has priority over the former, an arrangement followed by all subsequent authors (e.g., Dunn, 1928; Smith, 1943; Taylor & Smith, 1943).

Dunn (1928) partially formalized Duméril's and Boulenger's perspectives by erecting the subfamily Sibynophiinae to accommodate the Asian and Central American species of the genus *Sibynophis*, but he did not include the Malagasy taxa. Although Dunn did not explicitly refer to the Malagasy species of *Sibynophis*, he implicitly considered them to be unrelated to the Asian and Central American species. According to Dunn (1928), both Asian and Central American *Sibynophis* retain a single-lobed hemipenis with a single sulcus spermaticus—a condition strikingly distinct from the bilobed hemipenis with a forked sulcus that occurs in the Malagasy species of *Sibynophis*. Taken together, both dental and hemipenial similarities between the Asiatic and New World species were so compelling that Dunn decided to consider them congeneric (Dunn, 1928: 20). It was only after Taylor & Smith (1943) that the New World species of *Sibynophis* were allocated in a distinct genus *Scaphiodontophis*.

After Dunn (1928), Bogert (1940) briefly discussed the hemipenial differences between the Malagasy *Sibynophis torquatus* and its Asiatic and Central American congeners, but he did not remove the taxon from Sibynophiinae. Following Bogert (1940), Leviton & Munsterman (1956) erected the genus *Parasibynophis* to accommodate the Malagasy and Comoran species *Sib. torquatus*, *Sib. rhodogaster*, and *Sib. mayottensis*, distinguishing them from the Asian and New World taxa on the basis of 11 osteological and hemipenial characters. Like Bogert (1940), these authors considered the mandibular characters to be of greater phylogenetic importance than the hemipenial features, reinforcing the allocation of all three genera *Scaphiodontophis*, *Sibynophis*, and *Parasibynophis* into the subfamily Sibynophiinae. Later, Guibé (1958) synonymized *Parasibynophis* with *Liophidium*, an arrangement followed by subsequent authors (e.g., Underwood, 1967; Williams & Wallach, 1989; Cadle, 1999).

Several more recent authors recognized either the subfamily Sibynophiinae or tribe Sibynophiini (e.g., Kuhn, 1967; Underwood, 1967; Smith *et al.*, 1977; Ferrarezzi, 1994; Zaher, 1999). Further, Taylor & Smith (1943), Leviton & Munsterman (1956), Underwood (1967), Ferrarezzi (1994), and Zaher (1999) explicitly recognized either the Sibynophiinae or Sibynophiini as a natural assemblage of hinged-teeth snakes that includes *Scaphiodontophis* and *Sibynophis* but excludes *Liophidium*.

Underwood (1967: 91) stated the issue with clarity: "this subfamily [Sibynophiinae] as proposed by Dunn included the Madagascar species now put into *Liophidium*; the relationships of these latter snakes lie elsewhere but the remaining two genera *Sibynophis* and *Scaphiodontophis* are certainly related and systematically rather isolated." Ferrarezzi (1994: 90) provided a diagnosis for the tribe Sibynophiini that, according to the author, includes two putative synapomorphies: "posterior process of the dentary free and elongate; maxillary teeth small, robust and flattened laterally." Although shared by *Scaphiodontophis* and *Sibynophis*, these two characters also are present in *Liophidium*, in which they have evolved homoplastically. Zaher (1999: 28) further documented that *Sibynophis* and *Scaphiodontophis* share an additional putative hemipenial synapomorphy—viz., a sharply curved, U-shaped convolution of the sulcus spermaticus in the proximal region of the hemipenial body.

More recently, Pyron *et al.* (2011) erected a new subfamily of colubroid snakes, the Scaphiodontophiinae, to accommodate the New World genus *Scaphiodontophis*. Their analysis also successfully tested the phylogenetic position of *Liophidium*, which appears as a member of their subfamily Pseudoxypophiinae, and not as the sister-group of *Scaphiodontophis*. However, monophyly of the traditional subfamily Sibynophiinae, including the genera *Sibynophis* and *Scaphiodontophis* (*sensu* Zaher, 1999), requires testing because *Sibynophis* has not been sampled in any of the recent molecular phylogenetic analyses. Here, we test this hypothesis by adding *Sibynophis collaris* to Pyron *et al.*'s (2011) data matrix, and discuss the derived osteological and hemipenial characters shared by these genera.

MATERIAL AND METHODS

DNA from *Sibynophis collaris* was extracted from liver following the protocol of Hillis *et al.* (1996). Sequences for two nuclear protein-coding genes were amplified via polymerase chain reaction (PCR):

oocyte maturation factor (*c-mos*) and recombination-activating gene 1 (*rag1*). To amplify *c-mos* we used the primers described in Zaher *et al.* (2009); and for *rag1* we used the primers Mart.FL1 (5' AGC TGC AGY CAR TAY CAY AAR ATG TA 3') and Amp.R1 (5' AAC TCA GCT GCA TTK CCA ATR TCA 3') as described by Chiari *et al.* (2004). PCRs were performed using standard protocols with the addition of 0.4% of Triton X-100 (Sigma-Aldrich, Saint Louis, MO, USA) and annealing temperature of 54°C.

PCRs were purified with shrimp alkaline phosphatase and exonuclease I (GE Healthcare, Piscataway, NJ). Sequences were processed using a BigDye Terminator cycle sequencing kit in an ABI 3700 sequencer (Applied Biosystems, Foster City, CA, USA). Both strands were sequenced and checked. The consensus of the two strands was constructed using Geneious version 5.4.6 (Drummond *et al.*, 2011).

The voucher of *Sibynophis collaris* used in this study was deposited at the Royal Ontario Museum (ROM 25618). Sequences of *rag1* and *c-mos* were submitted to GenBank, receiving accession numbers JQ994296 and JQ994297, respectively. One sequence of *Sibynophis chinensis* for cytochrome b (*cytb*) was downloaded from GenBank (accession JN571580). We assumed monophyly of the genus *Sibynophis* and this allowed the creation of a combined terminal (*c-mos* and *rag* of *S. collaris* and *cytb* of *S. chinensis*).

We included the sequences of *Sibynophis* in the matrix of Pyron *et al.* (2011), while preserving the

existing alignment, by using the command "--add" available in MAFFT version 6.864 (Katoh *et al.*, 2002). We conducted a maximum likelihood analysis using RAxML 7.2.8 (Stamatakis, 2006). As performed by Pyron *et al.* (2011), the concatenated data were partitioned by codon position and the GTRGAMMA model was used for all partitions. The rapid bootstrap algorithm was employed, and 500 non-parametric bootstrap replicates were performed using the cluster hosted at the Laboratório de Alto Desempenho – Pontifícia Universidade Católica do Rio Grande do Sul (LAD-PUCRS). This approach allowed 100 complete searches because it used the tree generated at every fifth bootstrap replicate as the starting tree for an independent LSR (Lazy Subtree Rearrangement) swapping. Nodal support was assessed through bootstrapping (BS).

We compared the hemipenial, palato-maxillary, and dentary complexes of *Sibynophis chinensis* with those of *Scaphiodontophis annulatus*, *Liophidium rhodogaster*, and *L. torquatus*. Taylor & Smith (1943), Leviton & Munsterman (1956) and Zaher (1999) previously described these complexes.

Cleared-and-stained skulls were prepared following the technique of Dingerkus & Uhler (1977) in which cartilage is stained with Alcian blue, bone with Alizarin red, and tissue is macerated with Trypsin. Skeletal nomenclature follows that of Cundall & Irish (2008). Methods for hemipenial preparation and terminology followed those of Zaher (1999) and Zaher & Prudente (2003).

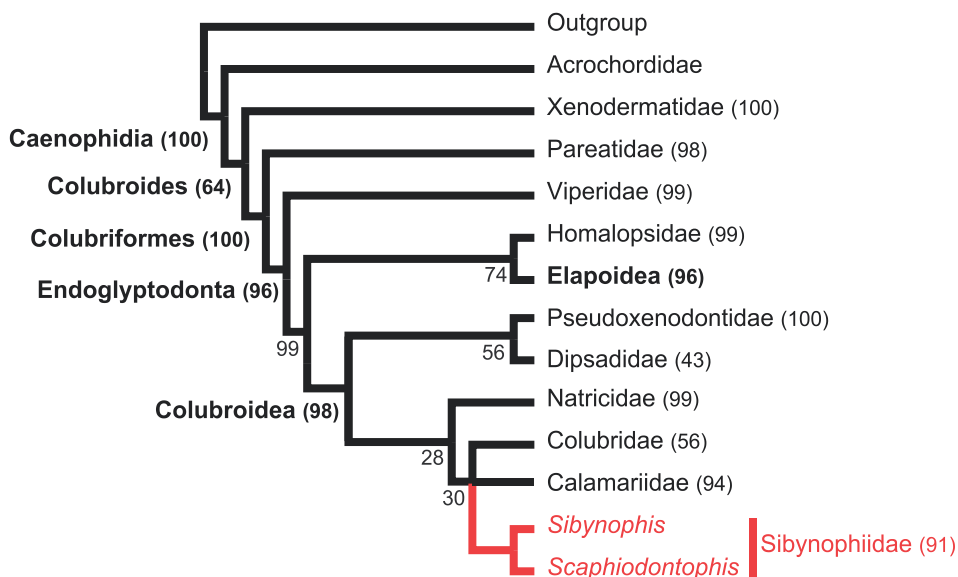


FIGURE 1: Summary tree showing the major clades of Caenophidia as recovered in the maximum likelihood analysis of Pyron *et al.*'s (2011) data set with *Sibynophis* sequences added (full topology in Appendix S1). Taxon names in bold indicate high-level taxa (higher than family). Numbers near nodes indicate bootstrap values for unnamed clades. Numbers in parenthesis after a taxon name indicate bootstrap values for that clade.

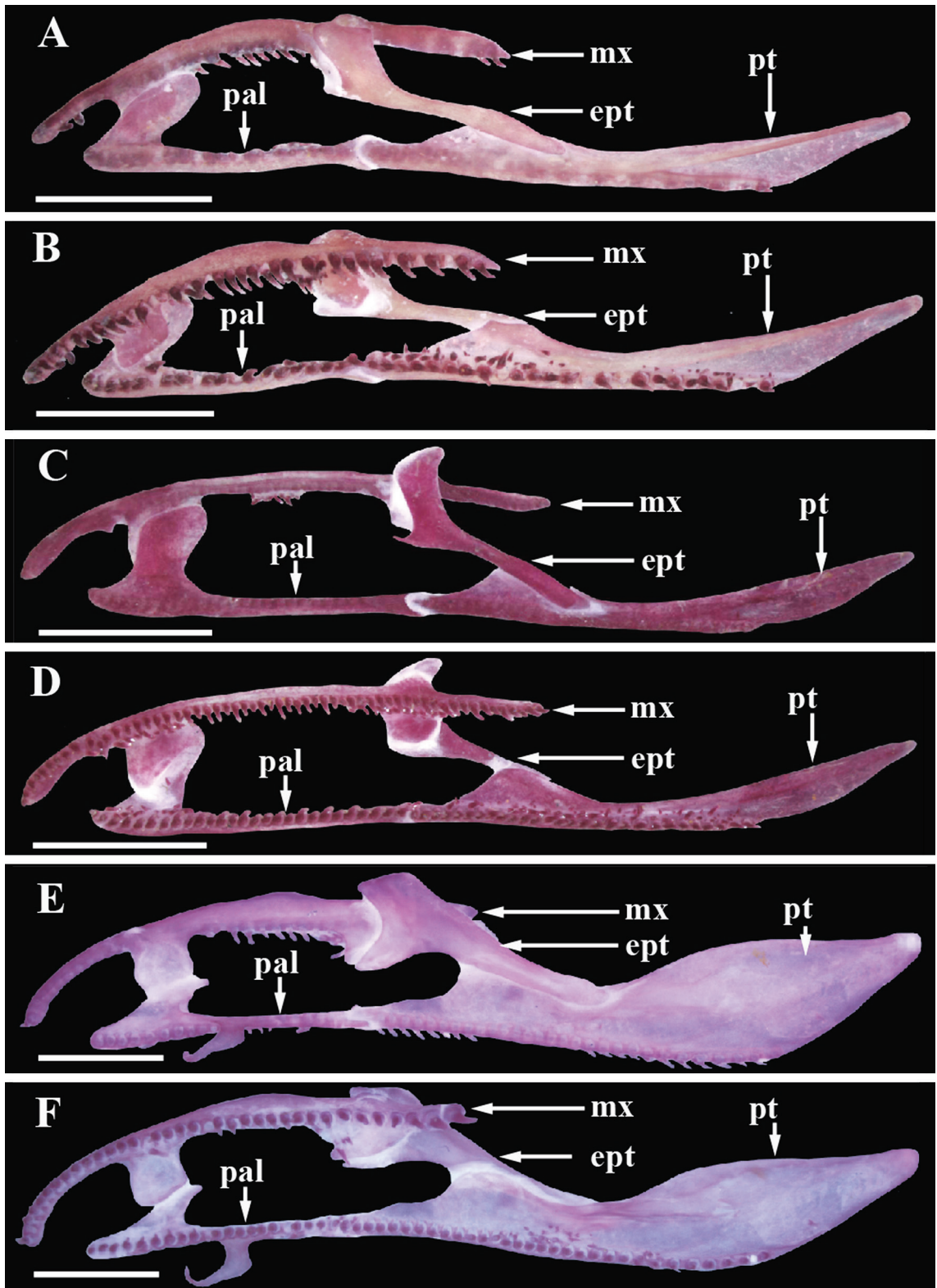


FIGURE 2: Palatomaxillary arch. **A:** Dorsal view of *Sibynophis chinensis* AMNH 34534; **B:** Ventral view of *Sibynophis chinensis* AMNH 34534; **C:** Dorsal view of *Scaphiodontophis annulatus* KU 191073; **D:** Ventral view of *Scaphiodontophis annulatus* KU 191073; **E:** Dorsal view of *Liophidium rhodogaster* UMMZ 209427; **F:** Ventral view of *Liophidium rhodogaster* UMMZ 209427. Abbreviations: ept = ectopterygoid; mx = maxilla; pal = palatine; pt = pterygoid. Scale bar = 2 mm.

Institutional codes are, as follow: **AMNH**, American Museum of Natural History; **KU**, Museum of Natural History, University of Kansas; and **UMMZ**, University of Michigan, Museum of Zoology. The following specimens were examined: *Sibynophis chinensis* (skull: AMNH 34534; hemipenis: AMNH 34102); *Scaphiodontophis annulatus* (skull and hemipenis: KU 191073); *Liophidium rhodogaster* (skull: UMMZ 209427; hemipenis: UMMZ 209424); and *L. torquatus* (skull: UMMZ 209450).

RESULTS

Our tree-search procedure in RAxML produced a topology with a score of $\ln L = -376071.295841$. A summary of the tree topology is given in Figure 1, and the full tree is provided as supplementary material (Appendix S1). Although we retrieved the same well-supported clades (BS > 70%) as did Pyron *et al.* (2011), the relationships at poorly supported nodes frequently differed (*e.g.*, affinities between elapoid families *sensu* Zaher *et al.*, 2009).

Our analysis clustered *Sibynophis* with *Scaphiodontophis* in a robustly supported clade within Colubroidea (*sensu* Zaher *et al.*, 2009), with a bootstrap value of 91 (Fig. 1; Appendix S1). In contrast, *Liophidium* maintained its elapoid affinities (Zaher, 1999; Nagy *et al.*, 2003; Pyron *et al.*, 2011), clustering with the other Malagasy snakes as the sister-group of a clade formed by *Heteroliodon*, *Pseudoxyrhopus*, and *Liopholidophis* (Nagy *et al.*, 2003). This result corroborated the monophyly of the sibynophiines, as previously recognized by Underwood (1967), Ferrarezzi (1994), and Zaher (1999). Sibynophiines, calamariids, and colubrids (including Grayiinae and Colubrinae of Pyron *et al.*, 2011) appeared rooted in an unresolved polytomy, forming a weakly supported clade (BS = 30; Fig. 1) that also was retrieved by Pyron *et al.* (2011) with a slightly higher bootstrap value (BS = 52).

DISCUSSION

According to the phylogenetic affinities recovered in our molecular analysis (Fig. 1), *Scaphiodontophis* and *Sibynophis* share four putative morphological synapomorphies that are absent in *Liophidium* and all remaining pseudoxyrhophiines. These are, as follow: (1) distally broadened, plate-like maxillary process of the palatine with an anterior edge projecting from the level of the anterior tip of the palatine and covering completely the palatine process of the maxilla (Fig. 2);



FIGURE 3: Hemipenis. **A:** asulcate view of *Sibynophis chinensis* AMNH 34102; **B:** sulcate view of *Sibynophis chinensis* AMNH 34102; **C:** asulcate view of *Scaphiodontophis annulatus* KU 191073; **D:** sulcate view of *Scaphiodontophis annulatus* KU 191073; **E:** asulcate view of *Liophidium rhodogaster* UMMZ 209424; **F:** sulcate view of *Liophidium rhodogaster* UMMZ 209424. Scale bar = 2 mm.

(2) maxilla projects posteriorly to the maxillary-ectopterygoid contact, forming a significantly long “dentigerous process” posterior to the ectopterygoid process of the maxilla (Fig. 2); (3) choanal process of the palatine absent (Fig. 2); and (4) sharply curved U-shaped convolution of the sulcus spermaticus in the proximal region of the hemipenial body (Fig. 3).

Alternately, five morphological characters found in *Scaphiodontophis* and *Sibynophis* appear to have evolved homoplastically in *Liophidium*. These characters include: (1) numerous, closely set teeth (Figs. 2, 4); (2) compound bone anterior to the mandibular fossa with a long, tubular and dorsally curved shape (Fig. 4); (3) splenial and angular bones reduced (Fig. 4); (4) mandibular fossa reduced and restricted to the posterior one-fifth of the compound bone (Fig. 4); and (5) posterior dentigerous process of the dentary elongated and detached from the compound bone (Fig. 4). These homoplastic characters likely reflect the specialized durophagous diet of these snakes (Savitzky, 1981, 1983).

Cadle (1999), following Savitzky’s (1981) lead, found hinged and peculiarly shaped teeth in *Pseudoxyrhopus*, *Exalloodontophis*, *Heteroliodon*, and *Pararhadinaea*; all of these Malagasy genera are closely related to *Liophidium* and known to feed on durophagous prey. Cadle (1999) also pointed out that hinged teeth occur in some African and Asian snakes that feed on hard prey (e.g., *Lycophidion*, *Mehelya*, *Chamaelycus*, *Tropidonophis*). The apparently widespread geographical distribution of hinged teeth represents additional evidence that this peculiar tooth morphology has arisen independently several times.

Higher level taxonomic ranking of Colubroidea (sensu Zaher et al., 2009)

Pyron et al. (2011) differ from Zaher et al. (2009) in preferring the traditional meaning of the superfamily Colubroidea, including the Xenodermatidae, Preatidae, Viperidae, Homalopsidae, Elapidae,

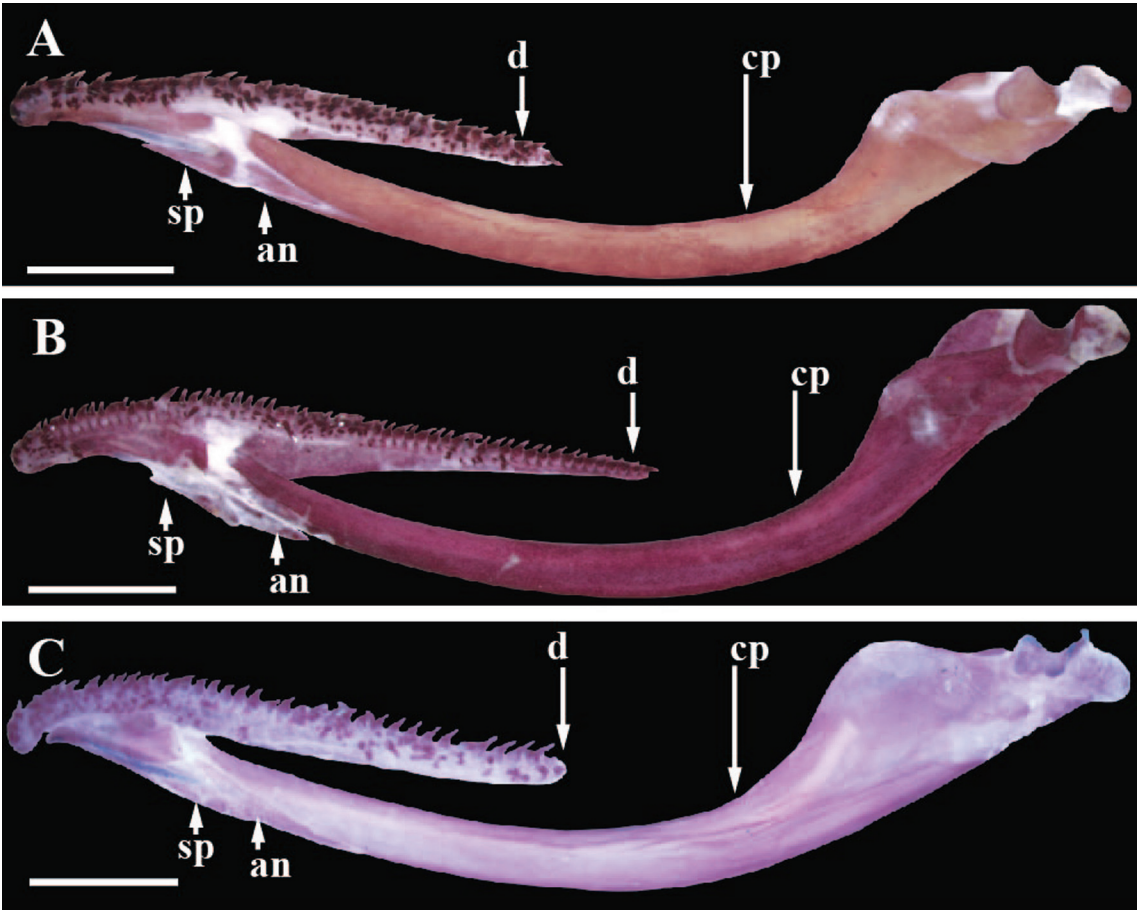


FIGURE 4: Mandible. **A:** Medial view of *Sibynophis chinensis* AMNH 34534; **B:** Medial view of *Scaphiodontophis annulatus* KU 191073; **C:** Medial view of *Liophidium rhodogaster* UMMZ 209427. Abbreviations: an = angular; cp = compound bone; d = dentary; sp = splenial. Scale bar = 2 mm.

an expanded Lamprophiidae, and a highly speciose Colubridae. We acknowledge the fact that this scheme promotes taxonomic stability for the long-standing name Colubroidea. However, such traditional taxonomic hierarchy no longer accommodates new knowledge of phylogenetic affinities within the group appropriately (Vidal *et al.*, 2007; Kelly *et al.*, 2009; Zaher *et al.*, 2009).

As knowledge of the phylogenetic affinities of colubroideans improves, additional taxonomic changes that create a certain amount of instability will be required to accommodate the newly resolved relationships (Lawson *et al.*, 2005; Vidal *et al.*, 2007; Zaher *et al.*, 2009). Such taxonomic adjustments, provided that they are stated explicitly (Zaher *et al.*, 2009), are necessary to incorporate the diversity and newly discovered monophyletic groupings of the colubroidean radiation.

As pointed out by Frost *et al.* (2006: 143) “We expect that regulated nomenclature will increasingly be pushed toward the terminal taxa and that unregulated taxa will increasingly be rankless. The reason for this is that there really is a practical limit to the number of ranks that workers are willing to use ... So, our observation is that sociological pressures will push workers towards ever smaller families ... Regardless, we think that this process will correspond with enormous progress in phylogenetic understanding.” Zaher *et al.*'s (2009) new taxonomic scheme represents a step in that direction for the largest, most speciose group of snakes.

In the present study, *Scaphiodontophis* and *Sibynophis* form a well-supported clade rooted in a polytomy along with families Colubridae and Calamariidae (Fig. 1). Therefore, we recognize Sibynophiidae Dunn, 1928 (ex Sibynophiinae) as a distinct family that includes the genera *Scaphiodontophis* Taylor & Smith, 1943 and *Sibynophis* Fitzinger, 1843 (type genus) within Zaher *et al.*'s (2009) taxonomic scheme. Because Sibynophiidae Dunn, 1928, has priority over Scaphiodontophiinae Pyron *et al.*, 2011, we synonymize the latter into the former.

RESUMO

Os resultados apresentados correspondem à primeira análise molecular feita acerca das afinidades filogenéticas do gênero Sibynophis, um colubróideo de origem asiática. Sibynophis aparece como sendo o grupo-irmão do gênero Neotropical Scaphiodontophis. Embora Liophidium esteja por vezes associado a estes dois gêneros, a sua relação é apenas distante. Os caracteres morfológicos

compartilhados entre Liophidium, Sibynophis e Scaphiodontophis correspondem a homoplasias que refletem provavelmente os hábitos alimentares especializados semelhantes, presentes nos três gêneros em questão. A tradicional subfamília Sibynophiinae é elevada ao nível de família, enquanto que Scaphiodontophiinae passa para sua sinonímia.

PALAVRAS-CHAVE: Sibynophiidae; *Sibynophis*; *Scaphiodontophis*; Filogenia.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Maximum likelihood phylogeny of Caenophidia based on the concatenated dataset used by Pyron *et al.* (2011) with sequences added for *Sibynophis*. Numbers near nodes are bootstrap values.

Appendix S1

