

THE ORIENTAL COLUBRINE GENUS *Coelognathus* FITZINGER, 1843 AND CLASSIFICATION OF OLD AND NEW WORLD RACERS AND RATSNAKES (REPTILIA, SQUAMATA, COLUBRIDAE, COLUBRINAE)

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The phylogenetic relationships of the colubrine genus *Coelognathus* is examined on the basis of two partially sequenced mitochondrial genes, COI and 12S rRNA. Maximum parsimony reconstructions show that *C. erythrus*, *C. flavolineatus*, *C. helena*, *C. radiatus*, and *C. subradiatus* share a common ancestor. *Coelognathus* spp. represent an evolutionary lineage among Oriental racers. Based on molecular data, external morphology, and pulmonary features, *Coluber prasinus* Blyth and *Herpetodryas frenatus* Gray are referred to *Gonyosoma* Wagler (four species). *Hemerophis* from Sokotra (monotypic) is the sister taxon of Palaearctic and Saharo-Sindian racers. Their phylogenetic relationships with Oriental racers are not clear. Old and New World racers belong to genetically independent lineages. The latter includes *Salvadora* spp. *Masticophis* Baird is considered to be a junior synonym of *Coluber* Linnaeus. A new generic name, *Oreocryptophis*, is proposed for the East Asian ratsnake taxon *Coluber porphyraceus* Cantor. Coronellini Jan is proposed for Old and New World ratsnakes. The tribe is monophyletic and made up of at least eight Old World (*Coronella*, *Elaphe* [sensu stricto], *Euprepiphis*, *Oocatochus*, *Oreocryptophis*, *Orthriophis*, *Rhinechis*, and *Zamenis*) and ten New World (mostly Nearctic) genera (*Arizona*, *Bogertophis*, *Cemophora*, *Lampropeltis*, *Pantherophis*, *Pituophis*, *Pseudelaphe*, *Rhinocheilus*, *Senticolis*, and *Stilosoma*).

Keywords: *Coelognathus*, *Gonyosoma*, *Oreocryptophis* (nomen novum), Oriental racers, phylogeny, Colubriini, Coronellini, morphology, mtDNA, COI, 12S rDNA.

INTRODUCTION

At the end of the 20th century, roughly 75 species of Old and New World racers and ratsnakes paraded under *Coluber* and *Elaphe* auct. (e.g., Schätti and Wilson, 1986; Schulz, 1996). Generally speaking, the systematic concepts of these highly polyphyletic genera were based on Boulenger (1894) who assigned them to *Zamenis* and *Coluber*, respectively.

Within the last 15 years or so, the systematics of racers underwent drastic changes. Morphological and molecular data demonstrate that Old and New World racers belong to phylogenetically different lineages (e.g., Schätti, 1986, 1987; López and Maxson, 1995; Nagy et al., 2004). The former include, among others, the Palaearctic and Saharo-Sindian genera *Hemerophis* Schätti

and Utiger, 2001 (Sokotra, monotypic), *Hemorrhoids* Boie, 1826, *Hierophis* Fitzinger in Bonaparte, 1834 and the closely related dwarf snakes (*Eirenis* auct.), *Platyceps* Blyth, 1860, and *Spalerosophis* Jan, 1865 (e.g., Schätti, 1988; Schätti and Utiger, 2001).

Morphological, biochemical, and molecular investigations also improved our knowledge regarding the phylogenetic relationships of ratsnakes, i.e., *Elaphe* auct. and related genera. In what concerns Old World genera, the eastern Palaearctic *Oocatochus* Helfenberger, 2001 (*O. rufodorsatus*), the Oriental *Oreophis* Utiger, Helfenberger and Schätti in Utiger et al., 2002 (*O. porphyraceus*), and *Orthriophis* Utiger, Helfenberger and Schätti in Utiger et al., 2002 (four species) were described as new. Helfenberger (2001b) resurrected the Western Mediterranean monotypic genus *Rhinechis* Michahelles, 1833 (*R. scalaris*). Utiger et al. (2002) redefined the Palaearctic genera *Elaphe* Fitzinger, 1833 [sensu stricto] comprising ten nominal species, and *Zamenis* Wagler, 1830 (five spp.). The radiation of Old World ratsnakes also comprises the western Palaearctic *Coronella* Lau-

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renti, 1768 (two spp.). The East Asian *Coluber conspiciellatus* Boie and *C. mandarinus* Cantor were placed in the revalidated genus *Euprepiophis* Fitzinger, 1843 (Utiger et al., 2002). So far, no molecular data of the Oriental species *Coluber prasinus* Blyth and *Herpetodryas frenatus* Gray [*Elaphe (sensu lato)*] were available and their phylogenetic relationships remained a matter of debate.

New World (mostly Nearctic) ratsnakes include *Bogertophis* Dowling and Price, 1988 (two species) and the monotypic genus *Senticolis* Dowling and Fries, 1987 (*S. triaspis*), the recently revalidated *Pantherophis* Fitzinger, 1843 (at least six species including *P. emoryi* and *P. slowinskii*), and *Pseudelaphe* Mertens and Rosenberg, 1943 (*P. flavirufa*) from Central America and Mexico, as well as the genera *Arizona* Kennicott in Baird, 1859, *Cemophora* Cope, 1860, *Lampropeltis* Fitzinger, 1843, *Pituophis* Holbrook, 1842, *Rhinocheilus* Baird in Baird and Girard, 1853, and *Stilosoma* Brown, 1890 (e.g., López and Maxson, 1995; Rodríguez-Robles and De Jesús-Escobar, 1999; Helfenberger, 2001b; Utiger et al., 2002).

Using anatomical and osteological features as well as 19 electrophoretic loci, Helfenberger (2001b) revalidated *Coelognathus* Fitzinger for six Oriental species formerly grouped with *Elaphe* auct., i.e., *C. erythrurus* (Duméril, Bibron et Duméril), *C. flavolineatus* (Schlegel), *C. helena* (Daudin), *C. philippinus* (Griffin), *C. radiatus* (Boie), and *C. subradiatus* (Schlegel). Hemipenis features of these taxa were studied by Schmidt (2000). *Coelognathus* spp. are similar to the Oriental ratsnake genus *Orthriophis* in, for instance, high ventral scale and precaudal vertebra counts and a long slender head.

Based on a portion of the 16S rRNA gene, López and Maxson (1995) concluded “that *Gonyosoma [G. oxycephalum]* is genetically a racer that is morphologically convergent with ratsnakes.” In two brief notes on pulmonary features, Wallach (1997, 1998) referred *Orthriophis cantoris*, *O. hodgsonii*, and *Elaphe (sensu lato) frenata* to *Gonyosoma* Wagler, 1828.

Using molecular techniques (mtDNA sequence data), external morphology as well as vertebra, hemipenis, and pulmonary features, this study examines the validity and systematic content of *Coelognathus* Fitzinger. The objective is to investigate the phylogenetic relationships of this Oriental genus and two hitherto unassigned colubrine species, *Elaphe (sensu lato) frenata* and *E. (sensu lato) prasina*, and to clarify the evolutionary history of Old and New World racers and ratsnakes.

MATERIAL AND METHODS

Scutellation and anatomical data (including limited corroborative evidence from lung morphology) were ascertained in the Oriental colubrine genera *Coelognathus*, *Gonyosoma*, *Orthriophis*, and *Ptyas* as well as in *Elaphe (sensu lato) frenata* and *E. (sensu lato) prasina* (**Appendix A** and **B**). External morphological features include head scales (supralabials, anterior subocular), number of ventral scales, number and reduction pattern of dorsal scale rows (dsr), the condition of the anal plate (single vs. divided) and anatomical (vertebra, hemipenial, pulmonary) characters.

Specimens used for the morphological part of this study were borrowed from the following institutions: The Natural History Museum (formerly British Museum [Natural History]), London (BMNH), Institute of Biology [Department of Zoology], Chengdu (CIB), Muséum d’Histoire naturelle, Geneva (MHNG), Muséum d’Histoire naturelle, Paris (MNHN), Naturhistorisches Museum Basel (NHMB), Naturhistorisches Museum Wien (NMW), Swedish Museum of Natural History, Stockholm (SMNH), and the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). Additional specimens originate from the private collection of N. Helfenberger (SH).

The position of additions or reductions (i.e., a change in the number of dsr) along the body axis is expressed as a percentage of the total number of ventrals (%ve, average of the right and left count). The relative transverse level of the dsr involved (rtl) was calculated by dividing the sum of the right and left counts by the number of dsr immediately in front of a reduction or following an addition. A change in the number of dsr is either lateral (<66%rtl) or ‘high,’ i.e., paravertebral (≥66%rtl) or vertebral. Raw data for scutellation features of 80 specimens of Oriental racers and ratsnakes are listed in **Appendix B**. Lung measurements are given as a percentage of the snout-vent length (svl).

Three characters (number of ventrals, condition of the anal scale, relative transverse level of dsr) were subjected to a multivariate analysis to calculate a discriminant function for *Coelognathus* (six species, 31 specimens) and *Orthriophis* (four, 22) as well as *Gonyosoma janseni* (one specimen) and *G. oxycephalum* (seven) before the allocation of *Elaphe (sensu lato) frenata* and *E. (sensu lato) prasina*. The resulting function was used to assign the latter two taxa to the genus which they fit best morphologically. After this procedure, a second analysis was performed to determine the discriminant factors and for cross validation of the three genera (Fig. 5, Table 3). The analyses were performed with R

(version 1.7.1) for MacOS and MacOS X as well as with SPSS 10 for Macintosh.

109 skeletons of 27 species of Old World ratsnakes were examined to ascertain the number of precaudal and caudal vertebrae: *Coelognathus erythrurus* (4 specimens), *C. flavolineatus* (5), *C. helena* (1), *C. radiatus* (5), *C. subradiatus* (2), *Elaphe bimaculata* (10), *E. carinata* (3), *E. climacophora* (3), *E. davidi* (1), *E. dione* (4), *E. quadrivirgata* (3), *E. quatuorlineata* (7), *E. schrenckii* (5); *Euprepriophis conspicillatus* (2), *E. mandarinus* (5); *Gonyosoma frenatum* (3), *G. janseni* (1), *G. oxycephalum* (2), *G. prasinum* (1); *Oreocryptophis* cf. *porphyraeus* (3, see **Corrigenda**), *Orthriophis cantoris* (1), *O. hodgsonii* (1), *O. moellendorffi* (8), *O. taeniurus* (9, see footnote 7); *Z. hohenackeri* (5), *Z. longissimus* (10), and *Z. situla* (5). As there is no significant difference between the sexes, male and female skeletons were analyzed together (Table 1).

Usually, the author and year of the genera under consideration are cited upon their first mention in the text. Complete specific names are only used where appropriate, for instance in **Appendix A**.

The Oriental genus *Ptyas* Fitzinger, 1843 includes *P. dipsas* (Schlegel), *P. korros* (Schlegel), and *P. mucosus* (L., type species) as well as taxa formerly assigned to *Zaocys* Cope, 1861 (*carinatus*, *dhumnades* [type species], *fuscus*, *luzonensis*, and *nigromarginatus*) with an even, instead of odd, number of dsr (Boulenger, 1893, 1894). As a matter of fact, these nominal genera are very similar in dorsal scale reduction pattern (Clark and Inger, 1942; see Table 2 and **Appendix B**), as well as dentition (Wall, 1914; Smith, 1943: Fig. 48A), and *Zaocys* Cope is considered a junior synonym of *Ptyas* Fitzinger (e.g., Wallach, 1998).

Although referred to as “New World” racers and ratsnakes, the overwhelming number are purely Nearctic taxa including Mexico (e.g., *Salvadora* spp.). At least four species definitely encroach the Neotropical Region, i.e., *Coluber constrictor* Linnaeus (southern Canada to Belize and northern Guatemala), *C.* [“*Masticophis*”] *mentovarius* (Duméril, Bibron et Duméril) from central Mexico to Brazil and southern Bolivia, and the ratsnakes *Lampropeltis triangulum* (Lacépède) and *Pseudelaphe flavirufa* (Cope) which extend as far south as Ecuador and Costa Rica, respectively.

mtDNA was extracted from fresh liver tissue and purified by phenol/chloroform treatment following the procedures of Spolsky and Uzzell (1986) and Sambrook et al. (1989). PCR, sequencing, and alignment, as well as statistics and phylogenetic analyses were performed as described in Utiger et al. (2002).

A total of 53 sequences of COI and 12S rRNA from 43 Old and New World racers and ratsnakes including five *Coelognathus* spp. as well as three potential outgroup species (see below) were examined. Molecular sequences for most taxa are from previous studies (Schätti and Utiger, 2001; Utiger et al., 2002; **Appendix D**). Fourteen sequences from ten species are new (**Appendix C**). They were deposited in the GenBank under the accession numbers AY122647–122664 (COI) and AY122665–122682 (12S rRNA); the series includes four sequences of *Coelognathus erythrurus*, *Coluber constrictor*, *Masticophis* [auct.] *flagellum*, and *Salvadora grahamiae* used for outgroup comparison in Utiger et al. (2002).

The amplified fragments correspond to the positions 303–980 (12S rRNA) and 6509–7151 (COI, using primer COI(+)) of the eastern Palearctic colubrid *Dinodon semicarinatus* (GenBank accession No. NC 001945). A total of 624 positions including insertions or deletions (indels) of the 12S rDNA and 513 base pairs (bp) of COI sequences were aligned as described in Utiger et al. (2002). The final alignment of the 12S rDNA includes a total of 50 indels at 25 different regions. Twelve of them consist of one position, four of two, six of three, and three indels of four positions.

In an initial step, the taxon-variance ratio, a tree-independent phylogenetic signal, of three different outgroup species, *Lamprophis fuliginosus* (Boie, 1827), *Natrix natrix* (Linnaeus, 1758), and *Salvadora grahamiae* Baird and Girard, 1853 as well as the ingroup taxa was measured with RASA (Lyons-Weiler et al., 1996), version 3.0 (Lyons-Weiler, 2001). This procedure allows to check for variance outliers (Fig. 1), i.e., taxa causing parsimony inconsistent estimation conditions (Lyons-Weiler and Hoelzer, 1997). The Afrotropical and Palearctic outgroup species (*L. fuliginosus* and *N. natrix*) were found to be taxon-variance outliers and have been removed from further analyses. The Nearctic *S. grahamiae* has a similar taxon-variance value as the ingroup species and was used as phylogenetically closely related outgroup taxon (see **New World Racers**).

Including the outgroup species *Salvadora grahamiae*, 232 (225 without gaps) of 302 (279) variable characters were parsimoniously informative for the 12S rDNA. The values for COI are 192 and 201, respectively. Combining COI and 12S rDNA resulted in 424 parsimoniously informative out of 503 variable characters. In the combined analysis, the rescaled consistency index (RC; Farris, 1989) of the MP analysis increased from 0.118 to 0.124 when gaps were included as fifth character state. An increase from 41.41 to 44.68 was also observed in the phylogenetic signal RASA. There-

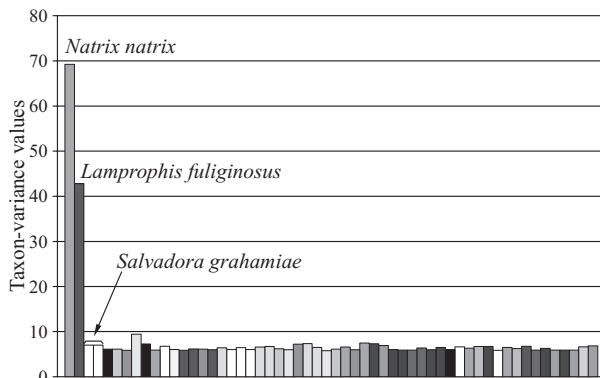


Fig. 1. Taxon-variance ratio of the outgroup species *Natrix natrix*, *Lamprophis fuliginosus*, and *Salvadora grahamiae* calculated with RASA 3.0. *N. natrix* and *L. fuliginosus* are outliers and were excluded from all phylogenetic analyses.

fore, tree reconstruction based on MP method was judged to be the most useful one for an rDNA sequence comparison because of the possibility of including gaps, which obviously bear phylogenetic signals.

Mutational saturation was studied by plotting the non-corrected pairwise sequence divergence (p) of COI against 12S rDNA (Fig. 2). The plot shows a high saturation tendency for COI that begins at an approximate value of 10% sequence divergence of 12S rDNA. Therefore, most distance measures of COI must be affected by a considerable amount of homoplasy.

An incongruence length difference (ILD) test (Farris et al., 1995) implemented as partition homogeneity test in PAUP* was performed with ten random stepwise additions using TBR branch swapping and 1000 randomizations. Defining the COI and 12S rDNA fragments as partitions, the result was highly significant ($P = 0.001$). This value suggests that the two partitions are most probably incongruent. Nevertheless, significance of the ILD test may be interpreted as a consequence of the saturation in one of two hitherto congruent partitions (Dolphin et al., 2000) as shown with the same gene partitions in an earlier study (Schätti and Utiger, 2001). Using an appropriate procedure to downweight the saturated sites the partitions can be analyzed with a total evidence approach (Dolphin et al., 2000). Consequently, the ILD test performed after character weighting resulted in a less significant value ($P = 0.02$).

Heuristic maximum parsimony (MP) searches were performed weighting each character according to the tree dependent RC (Nei, 1996). Gaps were coded as a fifth character in order to include all parsimony-informative sites for the phylogenetic analyses. Heuristic minimum evolution (ME, Rzhetsky and Nei, 1992) and

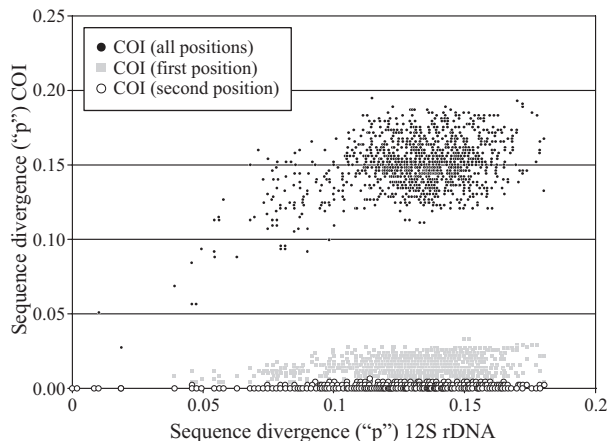


Fig. 2. Correlation of non-corrected pairwise sequence divergence (p) between COI and 12S rDNA.

neighbor joining (NJ, Saitou and Nei, 1987) analyses were performed using a model of evolution estimated with MODELTEST (Posada and Crandall, 1998). Non-parametric bootstrap values (Felsenstein, 1985) from NJ and weighted MP analyses were calculated from 1000 replicates. To check the resolution efficiency of ME and MP algorithms and the influence of character weighting and gap handling, corresponding bootstrap consensus trees were compared. A MP consensus tree that included gaps as fifth character state supports nine additional nodes and loses two compared to the ME and the MP trees handling gaps as missing characters. Obviously, including gaps improves the resolution capability of the MP optimality criterion. In accordance with increasing tree-dependent (RC) and tree-independent statistical values (RASA), Maximum Parsimony apparently gives the best results with the underlying data set. Consequently, the resulting branching pattern will be discussed based on the MP phylogeny, accepting bootstrap values over 50% from the total evidence approach as relevant (Fig. 3).

RESULTS

Character weighting including gaps as a fifth character state produced a single most parsimonious molecular tree with a length of 461.303 and an RC of 0.336 (Fig. 3). Twenty-two out of 40 bootstrap values of our phylogenetic reconstruction considerably increased when COI was added to 12S rDNA for a combined analysis whereas seven decreased.

The resulting overall pattern shows three clearly distinct groups. In particular, it confirms the monophyly of

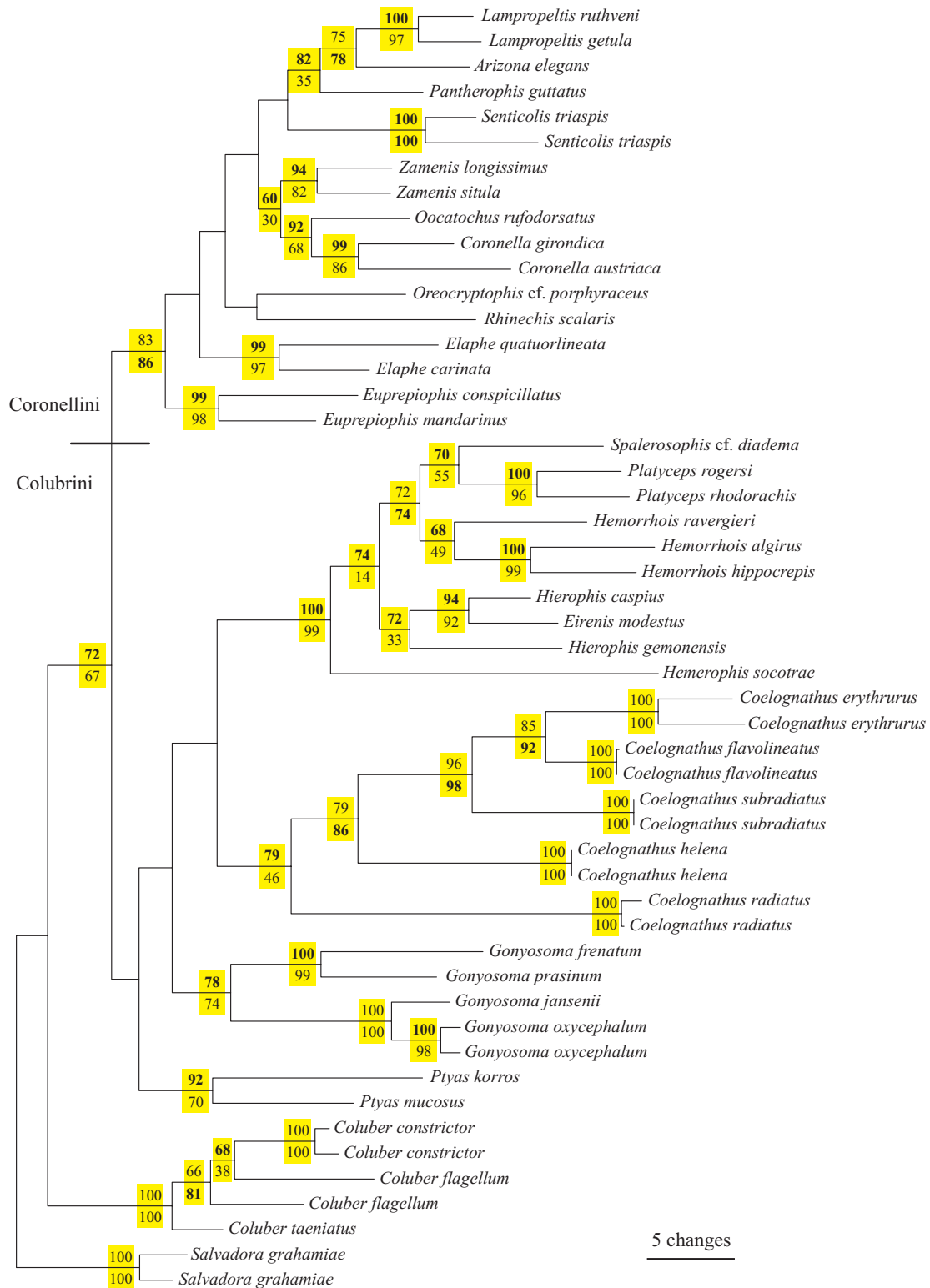


Fig. 3. Tree reconstruction from the combined sequences obtained with weighted MP method including gaps. Bootstrap values from 1000 replicates based on the 12S rDNA sequence (numbers below the branches) and on the combined sequences (above) are indicated as percentage values. Higher value bold-faced; those lower than 50% in both cases are omitted.

Old and New World ratsnakes (bootstrap support 83%) and of Afrotropical, Palaearctic, and Saharo-Sindian racers (100%). The latter are genetically distinct from New World (mostly Nearctic) racers and their allies (*Coluber* L., *Salvadora* Baird). *Coelognathus* Fitzinger, *Gonyosoma* Wagler, and *Ptyas* Fitzinger are Oriental racer genera but not necessarily closely related. The monophyletic relationship of *Elaphe* (*sensu lato*) *frenata* and *E. (sensu lato) prasina* is clearly demonstrated (100%). These taxa show a sister group position to *G. janseni* and *G. oxycephalum*, a correlation that is supported by 78% of all bootstrap trees.

The discriminant function (Fig. 5) placed ten out of 13 specimens of *Elaphe (sensu lato) frenata* and *E. (sensu lato) prasina* to *Gonyosoma* and three (BMNH 72.4.14.350, 1946.1.10.22, and CIB 74 II 5387, see Table 2) to *Orthriophis* (see **Ratsnakes and Suprageneric Classification**). No specimen was grouped with *Coelognathus*. Based on this procedure and the topology of the molecular phylogeny, *Coluber prasinus* Blyth and *Herpetodryas frenatus* Gray are referred to *Gonyosoma* Wagler. The subsequent cross validation procedure (Table 3) predicts the group membership of all 31 specimens of *Coelognathus* correctly. A single out of 21 specimens of *Gonyosoma* examined for the purpose of this study (*G. frenatum*, CIB 74 II 5387) was assigned to *Orthriophis* due to the lack of a paravertebral dsr reduction.

Coelognathus spp. (*erythrurus*, *flavolineatus*, *helena*, *philippinus*, *radiatus* [type species], and *subradiatus*) normally have 3 supralabials in contact with the eye (except *helena*), lack an anterior subocular (sometimes present in *subradiatus*) and paravertebral reductions of dsr, the anal plate is usually single (see **Oriental Racers**), the hemipenis bears basal spines, the tracheal lung is absent or rudimentary and barely vascularized, and the left lung absent or small except in *C. flavolineatus* (0.8 – 1.4%svl) and *C. radiatus* (1.0 – 1.6%svl) which is the only species among Oriental racers examined in this study having a short intrapulmonary bronchus (Plate 1A – D, Fig. 4, Tables 1 – 2).

The genus *Gonyosoma* is composed of *G. frenatum*, *G. janseni*, *G. oxycephalum* (type species), and *G. prasinum*. These racers usually have 3 (2 in *oxycephalum*) supralabials touching the orbit and, as in *Coelognathus* spp., lack an anterior subocular, and have a divided anal plate (occasionally single in *prasinum*). The hemipenis is subcylindrical; in *G. oxycephalum*, it is spinose at the base and bears a few distinct lateral hooks followed by a series of spines, several serrated annuli, and an apical disk (Fig. 4) whereas the hemipenis of *G. frenatum* is “naked” (no ornamentation) at the base, several rows of distinct spines encircle the central portion, and the apex is provided with denticulate calyces (Plate 1E).

Gonyosoma spp. are remarkable for the presence of ‘high’ posterior reductions (except *G. frenatum* CIB

TABLE 1. Morphological Characters of *Coelognathus*, *Gonyosoma*, and *Orthriophis* spp.

Taxon	Character								
	a.sub.	supr.	s.e.	msr	anal	p.v.	tr.l.	l.l.	i.br.
<i>C. erythrurus</i>	0	8 – 10	3	21 (19)	a	216 – 232 (226)	b	b	a
<i>C. flavolineatus</i>	0	8 – 9	3 (2)	21 (19)	a	209 – 226 (217)	b	d	a
<i>C. helena</i>	0	8 – 11	2 (3)	25 – 27*	a (b)	240 (–)	b	a	a
<i>C. philippinus</i>	0	9	3	21 (19)	a	—	b	b	a
<i>C. radiatus</i>	0	8 – 9	3 (2)	19	a	226 – 238 (233)	b	d	b
<i>C. subradiatus</i>	0 (1 – 2)	8 – 9	3 (2)	23 – 25*	a	227 – 233 (230)	b	b	a
<i>G. frenatum</i>	0	8 – 9	3 (2)	17 – 19	b	220 – 224 (222)	c	d	a
<i>G. janseni</i>	0	9 – 10	3	23 – 25	b	252 (–)	d	e	a
<i>G. oxycephalum</i>	0	8 – 11	2 (3)	23 – 27	b	240 – 249 (245)	d	e	a
<i>G. prasinum</i>	0	9 (8)	3 (2)	17 – 19	b (a)	196 (–)	c	d	a
<i>O. cantoris</i>	1 (0 – 2)	8 – 9	2 (3)	19 – 21	a – b	222 (–)	b	b	a
<i>O. hodgsonii</i>	0 (1)	8 (9)	2 (3)	21 – 25	b	239 (–)	a	b	a
<i>O. moellendorffi</i>	1 (2)	9 – 10	2	25 – 27	b	268 – 275 (272)	a	c	b
<i>O. taeniurus</i>	1 (0)	7 – 10	2	23 – 27	b (a)	230 – 299 (260)	a	d	a

Note. Number of anterior subocular(s) (a.sub.), supralabials (supr.), supralabials entering eye (s.e.), midbody dorsal scale rows (msr; *rarely 23 or 29 in *C. helena*, and exceptionally 21 in *C. subradiatus*), condition of anal (a: single, b: divided), precaudal vertebrae (p.v., mean in parenthesis; no data for *C. philippinus* and only one specimen in the case of *C. helena*, *G. janseni*, *G. prasinum*, *O. cantoris*, and *O. hodgsonii*), tracheal lung (tr.l.; a: absent, b: absent or rudimentary, c: present, unchambered, d: distinct and chambered), left lung (l.l.; a: absent or reduced, b: present but small, c: distinct, d: distinct and large, e: strongly developed), and intrapulmonary bronchus (i.br.; a: absent, b: present but short). Uncommon conditions of head scales in parenthesis.

TABLE 2. Reduction Pattern of Dorsal Scale Rows

Species and Access. No.	Sex	1 st anterior reduction (5–15%ve)		2 nd anterior reduction (28%ve)		Anterior addition (13–25%ve)		Midbody reduction (45–70%ve)		1 st posterior reduction (52–83%ve)		2 nd posterior reduction (57–92%ve)		3 rd posterior reduction (63–92%ve)		Precaudal reduction (81–95%ve)		Characters used for discriminant analysis		
		%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	htl	an	ve
<i>C. erythrus</i>																				
NMW 23399	♀	7.6	0.48			61	0.52					88	0.42					0.52	1	225
NHMB 5051	♀	9.7	0.43			64	0.48											0.48	1	228
NHMB 1292	♀	9.4	0.43			61	0.48											0.48	1	223
ZFMK 31689	♀	7.9	0.52			58	0.52					92	0.53					0.53	1	229
NHMB 19703	♀	6.7	0.43			60	0.48					84	0.47					0.48	1	225
NHMB 8510	♀	5.8	0.43			70	0.48											0.48	1	224
<i>C. flavolineatus</i>																				
MHNG 1377.80	♀	8.4	0.48			61	0.53											0.53	1	215
MHNG 1464.64	♂	7.3	0.52			62	0.53											0.53	1	220
ZFMK 16528	♀	8.4	0.48			60	0.53											0.53	1	226
ZFMK 16661	♀	6.7	0.48			61	0.53											0.53	1	223
ZFMK 31686	♀	9.6	0.48			62	0.42											0.48	1	218
ZFMK 33467	♀	7.2	0.43			64	0.53											0.53	1	221
ZFMK 36323	♂	6.0	0.48			61	0.58											0.58	1	217
<i>C. helena</i>																				
MHNG 845.10A	♂	5.6	0.40			19	0.52					56	0.52					0.56	1	251
MHNG 1377.98	♀	5.1	0.44			54	0.48					60	0.43					0.48	1	236
NHMB 1230	♀	7.3	0.48			16	0.56					58	0.26					0.56	1	248
SH 683	♀	6.4	0.48									64	0.43					0.48	1	236
ZFMK 31697	♂					22	0.44					66	0.40					0.44	1	210
ZFMK 33373	♂					18	0.52					60	0.43					0.52	1	220
ZFMK 38755	♀					47	0.40					52	0.43					0.43	1	235
ZFMK 39549	♀					21	0.37					54	0.44			83	0.38	0.44	1	239
<i>C. philippinus</i>																				
MHNG 2096.20	♀	?	?			62	0.57											0.57	1	226
MHNG 2102.62	♂	7.8	0.43			?	?											0.43	1	217
<i>C. radiatus</i>																				
BMNH 98.4. 2.26	♂	8.6	0.57			64	0.47											0.57	1	220
BMNH 1903.4.13.73	♂	6.7	0.48			64	0.53											0.53	1	225
BMNH 1956.1.12.82	♂	8.7	0.57			64	0.47											0.57	1	229
BMNH 1956.1. 12.83	♂	8.0	0.57			63	0.42											0.57	1	226

TABLE 2 (continued)

Species and Access. No.	Sex	1 st anterior reduction (5 – 15%ave)		2 nd anterior reduction (28%ave)		Anterior addition (13 – 25%ave)		Midbody reduction (45 – 70%ave)		1 st posterior reduction (52 – 83%ave)		2 nd posterior reduction (57 – 92%ave)		3 rd posterior reduction (63 – 92%ave)		Precaudal reduction (81 – 95%ave)		Characters used for discriminant analysis		
		%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	htl	an	ve
<i>C. subradiatus</i>																				
BMNH 97.6.21.47	♂	8.7	0.32			24	0.60	58	0.60	72	0.35							0.60	1	231
BMNH 97.12.30.19	♀	7.4	0.48					61	0.30									0.48	1	236
BMNH 97.12.30.33	♀	12.4	0.40					61	0.26	83	0.38							0.40	1	241
BMNH 1946.1.6.16	♂	8.2	0.40					60	0.43	69	0.38							0.43	1	231
<i>G. frenatum</i>																				
BMNH 1924.12.9.195	♂							55	0.95	58	0.47	78	0.93					0.95	2	204
CIB 74 II 5379	♀							56	0.42	57	0.94							0.94	2	218
CIB 74 II 5386	♂							57	0.84	61	0.47							0.84	2	219
CIB 74 II 5387	♀							57	0.53	63	0.47							0.53	2	219
CIB 74 II 5388	♀							58	0.95	61	0.47							0.95	2	219
SH 1010	♂							56	0.95	58	0.47							0.95	2	220
SH 1022	♀							57	0.74	58	0.47							0.74	2	222
<i>G. janseni</i>																				
BMNH 1946.1.6.20	♂							54	0.87	57	0.29	64	0.95	83	0.94			0.95	2	250
<i>G. oxycephalum</i>																				
BMNH 1946.1.14.59	juv.	9.8	0.96					54	0.92	58	0.78	55	0.38	68	0.95	95	0.94	0.96	2	234
MHNG 1363.82	♀							54	0.48	58	0.87	57	0.38	72	0.95			0.95	2	253
MHNG 1363.83	♀	9.6	0.96			24	0.96	52	0.96	57	0.96	58	0.35	63	0.95	81	0.95	0.96	2	251
MHNG 1363.84	♀	15.0	0.96			24	0.96	51	0.96	56	0.35	58	0.95	66	0.95	94	1.00	1.00	2	246
MHNG 2439.61	♂							53	0.35	55	0.86	57	0.74	79	0.94			0.94	2	244
MHNG 2439.62	♂							56	0.91	56	0.38	62	0.95	79	0.94			0.95	2	247
MHNG 2439.63	♀	13.1	0.96			25	0.88	56	0.96	58	0.96	58	0.38	70	0.95			0.96	2	244
<i>G. prasinum</i>																				
BMNH 72.4.14.350	♂							54	0.95	58	0.47							0.95	1	196
BMNH 1914.3.2.13	♀							51	0.42	61	1.00							1.00	2	193
BMNH 1926.3.17.3	♀	7.2	0.38					57	0.42	62	1.00							1.00	2	202
BMNH 1938.8.7.44	♂							53	0.95	55	0.47	82	0.93					0.95	2	203
BMNH 1946.1.10.22	♂							54	0.95	59	0.47							0.95	1	195
CIB 625237	♂							60	0.68	59	0.47							0.68	2	180
<i>O. cantoris</i>																				
BMNH 2.5.8.12.28	♀	9.2	0.52			16	0.48	56	0.48	64	0.53							0.53	2	228
BMNH 53.8.12.22	♂	7.4	0.48			17	0.48	55	0.48	61	0.53							0.53	2	222

TABLE 2 (continued)

Species and Access. No.	Sex	1 st anterior reduction (5 – 15%ve)		2 nd anterior reduction (28%ve)		Anterior addition (13 – 25%ve)		Midbody reduction (45 – 70%ve)		1 st posterior reduction (52 – 83%ve)		2 nd posterior reduction (57 – 92%ve)		3 rd posterior reduction (63 – 92%ve)		Precaudal reduction (81 – 95%ve)		Characters used for discriminant analysis		
		%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	%ve	rtl	htl	an	ve
BMNH 1940.6.4.96	♂	10.0	0.38			19	0.48	56	0.38	64	0.42							0.48	2	235
NMW 26920.1	♂	7.6	0.48			19	0.57	57	0.57	66	0.47							0.57	2	224
SH 2462	♂					22	0.48	54	0.48	58	0.53							0.53	1	223
SH 2516	♂	6.3	0.35					55	0.48	59	0.53							0.53	1	222
<i>O. hodgsonii</i>																				
BMNH 1940.3.7.16	♂	5.9	0.48					56	0.52	61	0.52							0.52	2	236
BMNH 1946.1.6.12	♀	8.5	0.52			17	0.52	57	0.61	64	0.48	83	0.63					0.63	2	234
BMNH 1946.1.6.15	♀	6.3	0.44					57	0.57	64	0.48	87	0.53					0.57	2	247
BMNH 1946.1.6.23	♂	9.6	0.52			16	0.52	52	0.57	60	0.52	72	0.58					0.58	2	223
SH 681	♀	6.3	0.52			19	0.52	54	0.61	61	0.48	74	0.53					0.61	2	238
SH 812	♀	8.0	0.52			15	0.52	55	0.61	60	0.48	81	0.58					0.61	2	237
<i>O. moellendorffi</i>																				
MHNG 1377.82	♀					23	0.52	51	0.56	57	0.48	68	0.52	91	0.48			0.56	2	275
SH 525	♂					20	0.52	56	0.59	60	0.48	68	0.52	92	0.48			0.59	2	267
ZFMK 29879	♀	7.3	0.52			13	0.52	56	0.48	60	0.52	75	0.52					0.52	2	268
ZFMK 29880	♂	7.1	0.44			19	0.52	56	0.52	60	0.48	74	0.52					0.52	2	268
<i>O. taeniturus</i>																				
BMNH 1946.1.7.34	♂	8.2	0.44					56	0.56	62	0.39	86	0.48					0.56	2	281
BMNH 1946.1.7.36	♂	9.4	0.37					56	0.56	61	0.43	85	0.48					0.56	2	277
BMNH 1946.6.2.1	♂	5.0	0.44					54	0.57	64	0.52							0.57	2	249
SNHM 23013	?	8.0	0.44					53	0.48	58	0.35	78	0.43					0.48	2	292
BMNH 1988.233	♀	12.6	0.35			23	0.52	57	0.43	65	0.48	91	0.32					0.52	2	239
BMNH 1988.234	♂	7.1	0.48			22	0.52	53	0.60	58	0.43	67	0.48					0.60	2	240
<i>P. korros</i>																				
MHNG 1375.33	♀							59	0.47	78	0.54							0.54	2	167
MHNG 1375.34	♀							52	0.53	58	0.54							0.54	2	167
MHNG 1375.35	♀							56	0.47	58	0.46							0.47	2	166
<i>P. mucosus</i>																				
MHNG 1375.26	♂							50	1.00	57	0.38							1.00	2	200
MHNG 1375.27	♀	14.1	0.53	28	1.00					59	0.38							1.00	2	199
SH 2461	♂	8.7	0.42					56	1.00	56	0.38							1.00	2	195

Note. Position along the body axis (%ve), relative transverse level (rtl) of dsr (highest: htl), condition of anal plate (1: single, 2: divided), and number of ventrals for *Coelognathus*, *Gonyosoma*, and *Orthriophis* spp. (see **Material and Methods**, footnote 7, and **Appendix B**). Bold-faced htl values indicate paravertebral or vertebral reductions ($\geq 0.66\%$ artl).

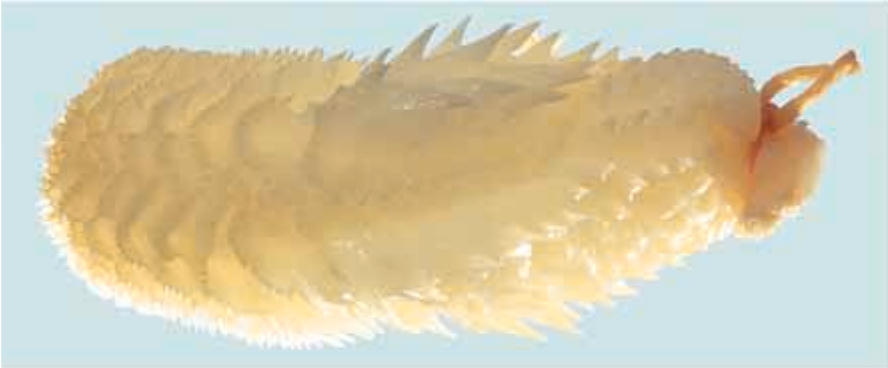
E*D**C**B**A*

Plate 1. Sulcate view of right hemipenis of *Coelognathus erythrus* (A), *C. flavolineatus* (B), *C. radiatus* (C), *C. subradiatus* (D), and *Gonyosoma frenatum* (E) from Schmidt (2000). Line equals 1 cm.

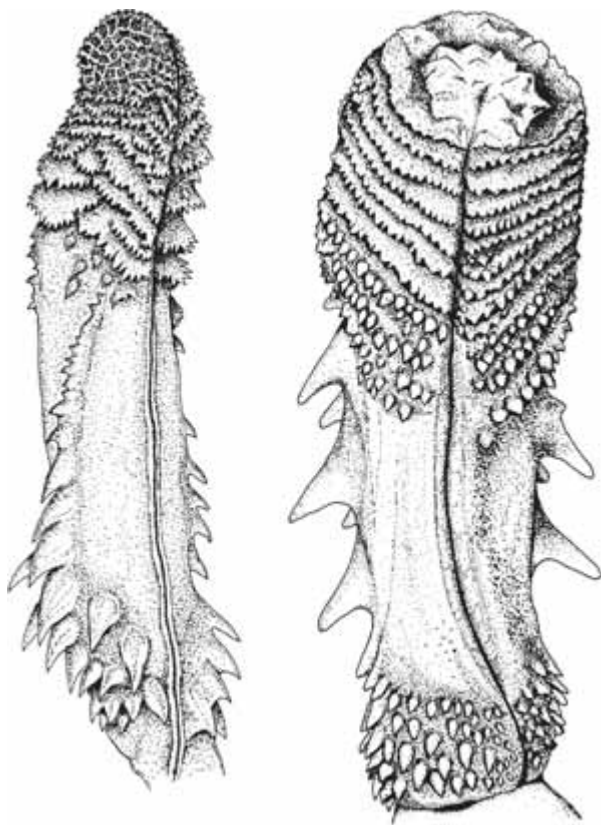


Fig. 4. Sulcate view of hemipenis of *Coelognathus philippinus* (left) and *Gonyosoma oxycephalum* (right) from Schulz (1996). Scale unknown.

74 II 5387), a strongly developed tracheal lung (moderately so in *frenatum* and *prasinum*), and a comparatively large left lung (Tables 1 – 2) attaining ca. 2%svl in *janseni* and *oxycephalum* and 1%svl in *prasinum* (0.7%svl in *frenatum*). The tracheal lung is multicameral in *janseni* and *oxycephalum* and unicameral, not reach that far cranially, in *frenatum* (“sparsely vascularized along the cranial half and saccular along the caudal half,” Wallyach, 1998) and *prasinum*. Furthermore, *Gonyosoma* spp. are outstanding for a high number of subcaudals and caudal vertebrae (see **Discussion**).

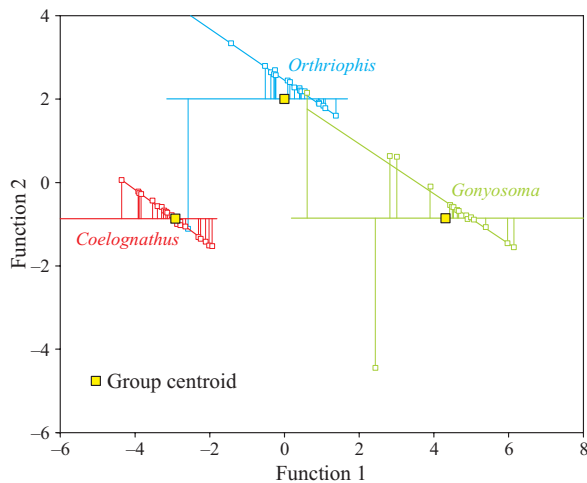


Fig. 5. Distribution of the discriminant function scores of the genera *Coelognathus*, *Gonyosoma*, and *Orthriophis* after the allocation of *G. frenatum* and *G. prasinum*.

DISCUSSION

Oriental Racers

Although the ME phylogeny prefers a sister group relationship of *Coelognathus radiatus*, *Gonyosoma frenatum*, and *G. prasinum* vis-à-vis the remaining *Coelognathus* spp. (no bootstrap support, tree not shown), a combined MP analysis (Fig. 3) confirms the monophyly of this genus (bootstrap support 79%) with *C. radiatus* (type species) as the most basal taxon.

Several morphological features including dsr reduction, dorsal color pattern, and pulmonary characters support the systematic concept of *Gonyosoma* as discussed in this paper (see below). It largely agrees with the generic grouping proposed by Günther (1864a) who considered three “British India” species, i.e., *frenatum*, *oxycephalum*, and *prasinum* (as *G. gramineum* Günther), to belong to this genus. Schmidt (1925), for instance, respected *Gonyosoma* when describing *G. caldwelli*, a junior synonym of *G. frenatum* from “Fukien” Province, China. Pope (1935) noted that “There is certainly no ob-

TABLE 3. Cross validation procedure after the generic allocation of *Gonyosoma frenatum* and *G. prasinum*

Genus	Predicted group membership			Total
	<i>Coelognathus</i>	<i>Gonyosoma</i>	<i>Orthriophis</i>	
<i>Coelognathus</i>	31 (100%)	0	0	31 (100%)
<i>Gonyosoma</i>	0	20 (95.2%)	1 (4.8%)	21 (100%)
<i>Orthriophis</i>	2 (9.1%)	0	20 (90.9%)	22 (100%)

jection to recognizing the genus *Gonyosoma* Wagler (type, *G. viride*, i.e., *Coluber oxycephalus* Boie) and placing *frenata* and *prasina* in it. I have not done so simply because of the generally conservative treatment of genera followed in this work. In the case of a genus as large as *Elaphe* [auct.], it may be just as well, or even best, to have the splitting off of small groups of species to a future reviser who, one hopes, will clear the matter up once and for all.” His anticipation took a good while to be brought to fruition⁴.

Gonyosoma spp. except *G. prasinum* (91–111) have a high number of subcaudals, i.e., 118–157 (Schulz, 1996). This is reflected in the number of caudal vertebrae expressed as a percentage of precaudal vertebrae, which is 0.49–0.67 (including *G. prasinum*), significantly higher than in *Coelognathus* spp. (0.34–0.47) and Old World ratsnakes (see **Material and Methods**) except *Elaphe climacophora* which attains 0.51% (0.42–0.51%, 0.25–0.46% in remaining taxa).

Vertebra features (i.e., the shape of the accessory processes, haemal keels, articulation surface of the prezygapophyses, and zygosphenes) of *Gonyosoma frenatum* and *G. prasinum* show remarkable similarities to *Coelognathus* spp. The haemal keel is flat in *G. jansanii* and *G. oxycephalum* but bears a distinct ridge in *G. frenatum*, *G. prasinum*, and all *Coelognathus* spp. (Helfenberger, 2001b)⁵.

Morphologically, *Coelognathus* and *Gonyosoma* spp. agree in a number of features including the absence of an anterior subocular and usually 3 supralabials entering the eye (see **Results** for exceptions) as well as a long slender head. However, these genera differ in, for instance, the condition of the anal plate (single vs. divided) and their posterior dsr reduction pattern, i.e., laterally ($\leq 60\%$ rtl) in *Coelognathus* spp. vs. at least one fusion involving paravertebral or vertebral rows ($\geq 74\%$ rtl) in twenty out of 21 *Gonyosoma* specimens examined for

this study (Table 2, **Appendix B**). The single (undivided) anal plate of *Coelognathus* spp. (rarely divided in *C. helena*) is an outstanding character state among Old World genera discussed in this paper; it is occasionally observed in *G. prasinum*.

The hemipenes of *Coelognathus* and *Gonyosoma* spp. (everted organs unknown for *C. helena*, *G. jansanii*, and *G. prasinum*) are surprisingly variable regarding ornamentation and shape (Plate 1, Fig. 4; Schulz, 1996: Figs. 33–36). In *G. frenatum*, several rows of enlarged spines encircle the central part similar to the comparatively short and stout hemipenis of *C. radiatus*. However, the basal portion is distinctly spinose in the latter and congeneric taxa whose hemipenis, in turn, differs from the one of the type species (*C. radiatus*) in being long and slender, and subcylindrical throughout (*subradiatus*) or tapering distally (*erythrurus*, *flavolineatus*, and *philippinus*). *C. erythrurus* and *C. philippinus* are very similar as to hemipenis shape and ornamentation. It is noteworthy that the hemipenis of *G. frenatum* is much shorter (19% of the total length) than in *Coelognathus* spp. (29–42%) according to Schmidt (2000).

Coelognathus is in need of further systematic studies. *C. subradiatus sensu* Schulz (1996, as *Elaphe* auct.) is likely to involve at least two species; in particular, specimens from Timor (type locality) differ from more western populations in dimensions and shape (populations from the Sunda islands are much larger and stouter), head pattern, as well as ventral and subcaudal counts. Schulz (1996) downgraded *Coluber enganensis* Vinciguerra from Engano Island, off Sumatra, to a subspecies of *C. subradiatus* (see Wallach, 1997). The former taxon, only known from three specimens, may deserve specific status within the *C. erythrurus-philippinus* complex.

Apart from the green dorsal color pattern (black tail in *G. jansanii*) often found in arboreal reptiles in general, *Gonyosoma* spp. are outstanding among Old and New World colubrid genera discussed in this study except *Ptyas korros* (see below) for their well developed left lung, and a distinct tracheal lung in *G. jansanii* and *G. oxycephalum* (see **Results**).

Wallach (1997: 110) stated that “*Gonyosoma* differs from *Elaphe sensu stricto* [sic] in having a chambered avascular tracheal lung. Besides *G. oxycephalum*, this lung structure is present in at least *G. [sic] cantoris* and *G. hodgsonii*.” Wallach (1998: Appendix C.4) noted a multicameral avascular tracheal lung, as well as a left lung, in “*Elaphe hodgsonii*, *Gonyosoma*” (see footnote 4), *Ptyas korros*, and “*Xenelaphis*” (see below). However, our observations (Table 1) do not confirm its presence in *Orthriophis hodgsonii* and only a very weakly developed (or missing) tracheal lung in *O. cantoris* (barely vascularized if present).

Probably as a consequence of a large tracheal lung, *Gonyosoma jansanii* and *G. oxycephalum* are able to inflate their neck. This conspicuous defensive behavior,

⁴ The taxonomy of Wallach (1998) with regard to, for instance, *Gonyosoma* is inconsistent. Appendix B (“Systematic list of specimens and illustrations”) lists *G. frenatum* under *Elaphe* auct. but the species is referred to as *G. frenata* [sic] in the text (p. 162). *G. jansanii* (p. 127, Table 4) is listed as “*E. jansanii*” in Appendix B. *G. prasinum* and certain Oriental ratsnakes, in particular *Orthriophis cantoris* and *O. hodgsonii* (as *Gonyosoma* spp. in Wallach, 1997), are also referred to *Elaphe* auct. Without further evidence, Mattison (1999) considered *Gonyosoma* to include *G. frenata* and *G. prasina* [sic]. The reasons for this action are not specified.

⁵ It is noteworthy that the genera *Coelognathus* (except *C. helena*) and *Ptyas* spp. (*korros*, *mucosus*) are very similar regarding the caudal extension of the hypapophyses (reaching far posteriorly, Helfenberger, 1989) as well as a caudally shifted heart (Twerenbold, 1987; Helfenberger, 2001a: Table 1). We consider these adaptations as associated with arboreal habits and have no explanation for their occurrence in these basically terrestrial genera.

unknown for *G. frenatum* and *G. prasinum*, is also displayed by *Ptyas korros*, *P. mucosus*, and Oriental taxa which are virtually devoid of a tracheal lung (Table 1) as, for instance, *Coelognathus helena*, *C. radiatus*, *C. subradiatus*, and the ratsnake *Orthriophis taeniurus*, which inflate their neck (and body) by means of the right lung.

Wallach (1998) emphasized that “what appears to be a secondarily enlarged [avascular or saccular] left lung” is associated with arboreal habits. As a matter of fact, *Gonyosoma* spp. including *G. frenatum* from dry habitats in southern China and India and *G. prasinum*, inhabiting humid mountain rain forests from Thailand to Vietnam, are arboreal whereas most other Old World racer (and ratsnake) genera discussed in this paper, and in particular *Coelognathus* and *Ptyas* spp., are terrestrial (see footnote 5). However, we observed a comparatively large left lung in, for instance, *C. radiatus* (with a distinct bronchus) and the ratsnake *Orthriophis taeniurus* (Table 1).

Ptyas korros and *P. mucosus* have 15–17 dsr at midbody and a comparatively simple reduction pattern involving a vertebral fusion in the case of *P. mucosus* (Clark and Inger, 1942; Table 2). The hemipenis of the latter species is slightly bilobed (Schleich and Kästle, 2002: Figs. 1–2; bulbous according to Pinou and Dowling, 2000: Fig. 3) and surprisingly similar to the organ of the Neotropical colubrid *Spilotes pullatus* (e.g., Dowling and Duellman, 1978: Fig. 112c.3). *Ptyas* spp. including *P. carinatus* have a distinct to large left lung of 0.6–2.3%svl (Brongersma, 1957; Twerenbold, 1987; Wallach, 1998: 231 and 236). Wallach (1998: Appendix C.4), for instance, reported a multicameral avascular tracheal lung of 10–12%svl *P. korros*; according to Twerenbold (1987), it is partially vascularized in this species.

Apart from zoogeographical considerations, Boulenger (1893–94) grouped *Coelognathus* and *Gonyosoma* spp., after all, with ratsnakes (as *Coluber sensu* Boulenger) for the length of their maxillary teeth, i.e., “nearly equal” vs. the “posterior increasing in size or the last strongly enlarged” as in Old and New World racers (Boulenger, 1894: 1, 5). In the latter (*Zamenis sensu* Boulenger, including *Ptyas dipsas*, *P. korros*, and *P. mucosus*) the maxillary teeth are “forming a continuous series or the two last separated from the others by a very narrow interspace” (Boulenger, 1893: 379).

Coelognathus, *Gonyosoma*, and *Ptyas* spp. differ from Afrotropical, Palaearctic, and Saharo-Sindian racer genera in the dentition of the maxillary, i.e., teeth of similar size throughout and arranged in a continuous subiso-

dont series instead of the last two enlarged and separated by a diastema.

Our morphological and molecular data (Figs. 3 and 5) show that *Coelognathus* and *Gonyosoma* are clearly defined evolutionary lineages within Oriental colubrids. These genera and *Ptyas* spp. are not necessarily close relatives and more detailed investigations on many potentially related taxa are necessary to elucidate the evolution of Oriental racers. *Xenelaphis* Günther from Thailand and Vietnam to Indonesia may belong to the same radiation group. *X. ellipsifer* Boulenger and *X. hexagonatus* (Cantor) have a continuous series of maxillary teeth “gradually increasing in size” (Boulenger, 1894: Fig. 1) and differ from *Ptyas* spp. in, for instance, the size and shape of the vertebral row of dorsal scales, i.e., “slightly enlarged and six-sided” instead of subequal.

To judge from our molecular data (Fig. 3), a close relationship of the Oriental genera *Coelognathus*, *Gonyosoma*, and *Ptyas* with Palaearctic, Saharo-Sindian, and Afrotropical racers is not compelling. This radiation group includes the monotypic *Hemerothis* from the Sokotra archipelago, the sister taxon of the monophyletic genera *Hemorrhhis*, *Hierophis* including dwarf snakes (*Eirenis* auct. and *Pseudocyclophis* Boettger, 1888; see Nagy et al., 2004; Schätti and Monsch, 2004), *Platyceps*, and *Spalerosophis* (Schätti and Utiger, 2001) as well as probably further genera as, for instance, *Argyrogena* Werner, 1924 and *Lytorhynchus* Peters, 1862⁶.

New World Racers

Considering the position of *Masticophis* spp. in the molecular phylogeny (Fig. 3), this nominal genus is paraphyletic with regard to the Black racer *Coluber constrictor* (type species of *Coluber* Linnaeus, 1758). The non-corrected pairwise distances from the combined analysis between the nominal genera *Coluber* L. and *Masticophis* Baird in Baird and Girard, 1853 (i.e., *M. flagellum* and *M. taeniatus*) are similar (7.4–10.2%) to those within *Masticophis* auct. (8.2–9.2%) and the bootstrap support for the whole group is 100%. Based on these facts and morphological evidence including hemipenis features, *Masticophis* Baird (type species *M. ornatus* Baird and Girard, 1853, i.e., *Leptophis taeniata* Halliwell, 1852) is considered to be a junior synonym of *Coluber* Linnaeus as suggested by Schätti (1986, 1987).

⁶ Wallach (1998) assigned the Palaearctic colubrid genus *Rhynchocalamus* Günther, 1864 to the Oligodontini. According to Dowling et al. (1996: Table VII), this tribe (“Oriental Eggeaters”), basically made up of *Oligodon* Boie in Fitzinger, 1826 with its numerous species, also includes the Nearctic leaf-nosed snake genus *Phyllorhynchus* Stejneger, 1890 (*P. browni*, *P. decurtatus*).

“*Coluber*, with a single species, might appear to be a very recent entrant into Nearctica, but this is more a figment of taxonomic arrangement than of reality. When the generic limits of *Coluber* [auct.] are ultimately drawn on a world-wide base, it will almost surely include the nominal genus *Masticophis*” (Dowling, 1975b). Dowling et al. (1983) stated that “The morphologically similar genera *Masticophis* and *Coluber* (Ortenburger, 1928), are also similar biochemically (ID = 10).” As a matter of fact, the immunological distance between *Coluber constrictor* and *Masticophis flagellum* found by Dowling et al. (1983: Table III) is roughly equal (ID = 11) to, for instance, the Nearctic kingsnakes *Lampropeltis getulus* vis-à-vis *L. calligaster* and *L. mexicanus*.

Ortenburger (1928) separated *Masticophis* from *Coluber* L. on the basis of “structural” criteria “involving differences in dentition, in labials, in proportionate head width, in scale row formulae, in methods of reduction of number of scale rows, in numbers of ventrals and caudals, and in the penes.” However, virtually all alleged differences between these taxa were rendered null and void with Auffenberg’s (1955) exhaustive study on *C. constrictor*. This author states that “The high incidence of a vertebral reduction in *Coluber* and the fact that the race *ruthveni* of *Masticophis taeniatus* is more or less characterized by having no vertebral reduction (58% of the specimens have a scale formula of 15 – 13 *vide* Ortenburger, 1928: 87) lends support to the proposition that perhaps the two genera should be united, and not given generic distinction as indicated by Inger and Clark (1943: 492).” Nevertheless, later authors continued to consider *Masticophis* spp. as generically distinct from *C. constrictor*.

A molecular investigation of a wide array of Afro-tropical, Asiatic, Palaearctic, and Nearctic racer taxa by Nagy et al. (2004) also revealed a close relationship between *Coluber constrictor* and *Masticophis flagellum*. Furthermore, the authors conclude from their data that “*Salvadora* is sister taxon to a *C. constrictor*/*Masticophis* clade.”

The genus *Salvadora* Baird *in* Baird and Girard, 1853 was initially considered to be the outgroup taxon for our analysis. However, non-corrected pairwise distances between *Coluber* spp. and *S. grahamiae* (12.7 – 13.7%) are similar to those between *Hemerophis socotrae* and Palaearctic and Saharo-Sindian racers (12.9 – 14.4%). Comparatively small genetic distances and the branching pattern (Fig. 3) suggest that patch-nosed snakes (*Salvadora* spp.) belong to the same radiation group as *Coluber* L.

New World (mostly Nearctic) racers are made up of the name bearing genus (including *Masticophis* auct.), *Salvadora* and, probably, *Phyllorhynchus* Stejneger, 1890 (see footnote 6), the monotypic genera *Liochlorophis* Oldham and Smith, 1991 (*L. vernalis*) and *Ophedryas* Fitzinger, 1843 (*O. aestivus*) as well as *Drymar-*

chon Fitzinger, 1843 and further Central and South American genera as, for instance, *Drymoluber* Amaral, 1930 and *Mastigodryas* Amaral, 1934 (Dowling and Duellman, 1978; Dowling et al., 1983; López and Maxson, 1995).

Corrigenda

In a brief note, Helfenberger and Tillack (*in* Whitaker and Captain, 2004) notified that *Oreophis* Utiger, Helfenberger and Schätti *in* Utiger et al., 2002 is preoccupied by *O. boulengeri* Dugès, 1897 (see Williams and Wallach, 1989), a junior synonym of *Lampropeltis mexicana* (Garman) according to Smith and Taylor (1945). We herewith propose the substitute name *Oreocryptophis* for the East Asian ratsnake taxon *Coluber porphyraceus* Cantor, 1839.

The new generic name alludes to the secretive way of live of *Oreocryptophis porphyraceus* in mountainous areas, and stems from the Greek words **ορος** (oros), meaning mountain, **κρυπτος** (kryptos), meaning hidden or secret, and **οφις** (ophis), i.e., snake; the gender is masculine. This genus includes at least one species different from *O. porphyraceus* as averred by Utiger et al. (2002) and evidenced by unpublished mtDNA data.

Ratsnakes and Suprageneric Classification

The present study reveals a monophyletic origin of all ratsnakes. Furthermore, it confirms a common origin for New World ratsnakes as well as the isolated position of *Oreocryptophis porphyraceus* (see **Corrigenda**) and *Rhinechis scalaris* (Schinz), a monotypic Western Mediterranean genus, as recently elaborated by Utiger et al. (2002). It also supports the phylogenetic affinities of *Zamenis* Wagler with *Coronella* Laurenti and *Oocatochus* Helfenberger (bootstrap support 60%).

Based on molecular and morphological data, the Oriental genus *Orthriophis* Utiger, Helfenberger and Schätti makes up one of several monophyletic groups within ratsnakes (Utiger et al., 2002: Fig. 3). *Orthriophis* spp. have 2 or 3 supralabials in contact with the eye, normally one subocular (usually absent in *hodgsonii*), and lack ‘high’ reductions of *dsr* (Tables 1 – 2). Utiger, Helfenberger and Schätti (*in* Utiger et al., 2002) stated that this genus has “19 – 27 dorsal rows at mid-body (50% ventrals), at least one reduction involving sixth row or situated more paravertebral.” Actually, the posterior fusions involve the fifth (*cantoris*), sixth, or seventh row (**Appendix B**).

The anal plate of *Orthriophis* ssp. is usually divided; it is often entire in *O. cantor* as exemplified by two specimens (SH 2462, 2516) grouped with *Coelognathus*

in the discriminant analysis (Fig. 5, Table 3). The hemipenis is bilobed and similar to *Elaphe* [*sensu stricto*] spp. (e.g., Schulz, 1996: Figs. 23 – 25; Utiger et al., 2002: Fig. 5). The tracheal lung is absent (rudimentary and barely vascularized in *O. cantoris*), the left lung absent or small (largest in *O. taeniurus*: 0.7 – 1.0%svl), and there is a short intrapulmonary bronchus in *O. moellendorffi* (Tables 1 – 2).

Orthriophis taeniurus auct. from the Himalayan region to Taiwan and the Greater Sunda Islands is probably a composite taxon; *Coluber friesi* Werner (Taiwan) and *Coluber taeniurus ridleyi* Butler (Thailand to Malaysia) are likely to be valid species. *O. taeniurus* auct. is highly variable with regard to, for instance, ventral (Table 2) and subcaudal counts⁷. Based on literature data, Pope (1935: Table 38) listed 225 – 264 ventrals for Chinese specimens including Hainan.

This Southeast Asia ratsnake genus resembles *Coelognathus* spp. in, for instance, high ventral scale and precaudal vertebra counts (up to 240 and 299 in *C. helena* and *Orthriophis taeniurus*, respectively; Tables 1 – 2, see footnote 7) and a long slender head. However, this represents convergence; molecular data (Fig. 3; Utiger et al., 2002) clearly demonstrate that *Coelognathus* and *Orthriophis* belong to different evolutionary lineages of Oriental colubrids.

Ratsnakes are a highly diverse tribe consisting at the time of this writing of 18 different Old and New World genera that evolved within the last 20 mybp or so. Therefore, it is not surprising that there are no obvious diagnostic characters for this group. Nevertheless, one typical feature is the complete absence of ‘high’ dsr reductions (unpublished data). Fusions of this type often occur in colubrid groups such as Saharo-Sindian racers and *Gonyosoma* and are probably a plesiomorphic character state.

Without further comment, Dowling (1975a) “separated the American kingsnake group as the Lampropeltiini.” This tribe was originally made up of the genera *Cemophora*, *Lampropeltis*, *Rhinocheilus*, and *Stilosoma*, and diagnosed as having “the few maxillary teeth enlarged posteriorly” and “a mainly spinose” hemipenis “with a few rows of calyces apically” (Dowling, 1975b).

Some authors (e.g., Dowling and Duellman, 1978; Dowling and Fries, 1987; Dowling and Maxson, 1990) used a slightly different way of spelling, i.e., Lampropeltiini. As a whole, the terminology for, and hierarchy of, New World (mostly Nearctic) ratsnake groups is confusing. Dowling (1975a) employed two vernacular names, i.e., “the American kingsnake group” or “Kingsnakes & Allies,” for the Lampropeltiini. Dowling and Maxson (1990), for instance, distinguished “ratsnakes, s.s. (Elaphini)”

from “kingsnakes, s.s. (Lampropeltiini).” In the same paper (Tables 1 and 3), these authors referred to these assemblages either as “Elaphini” and “Lampropeltiini” or the “Ratsnake group (s.s., elaphini)” which includes *Senticolis*, and “Kingsnake group (lampropeltiini),” respectively. The term Elaphini (for *Arizona elegans*, *Pantherophis obsoletus*, and *Pituophis melanoleucus*) infers tribal status although, strangely, the name bearing genus (*Elaphe* Fitzinger) is not included. To make the confusion complete, Dowling and Fries (1987) denoted Old and New World taxa under consideration as “lampropeltiini genera,” Dowling and Maxson (1990: 83 – 84) referred to them as the “lampropeltiini group” or “lampropeltiini (s.s.),” and Rodríguez-Robles and De Jesús-Escobar (1999) used “lampropeltinines” as a collective term for these genera.

Dowling and Fries (1987: Table 1 and p. 206) considered the “Lampropeltiini” to be composed of the “Kingsnake group” including New World (mostly Nearctic), Palaearctic (*Coronella*), and two Afrotropical genera (*Aeluroglena* Boulenger, 1898 and *Meizodon* Fischer, 1856), a Holarctic “Ratsnake group” (i.e., *Arizona*, *Bogertophis* [as “*Elaphe*”], *Pituophis*, *Senticolis*, and Old and New World *Elaphe* auct.), as well as an unallocated “genus being resurrected for six Oriental species,” i.e., *Orthriophis moellendorffi* (as *Elaphe* auct.) and five unspecified taxa (see below).

As far as New World ratsnakes (*Elaphe* auct.) are concerned, Wallach (1997) briefly noted that “...it is just a matter of time before they are separated (as they represent a monophyletic clade) under the name *Pantherophis*...” To judge from later specifications (Wallach, 1998: 145, 204), this action was intended to include the Central American *Pseudelaphe flavirufa* (Cope), a monotypic genus different from *Pantherophis* and not examined, for instance, in the study of Rodríguez-Robles and De Jesús-Escobar (1999). These authors and other students (e.g., Wallach, 1998) considered the “Lampropeltini” to be a purely New World colubrid tribe.

Utiger et al. (2002) showed that Nearctic taxa are only one of several evolutionary lineages among ratsnakes. They comprise the Palaearctic genera *Coronella*, *Elaphe*, *Euprepiophis*, *Oocatochus*, *Rhinechis*, and *Zamenis*, the Oriental *Orthriophis* spp., *Oreocryptophis porphyraceus* (see **Corrigenda**), and the mainly Nearctic ratsnakes, i.e., *Bogertophis*, *Lampropeltis*, *Pantherophis*, *Pituophis* as well as the monotypic genera *Arizona*, *Cemophora*, *Pseudelaphe*, *Rhinocheilus*, *Senticolis*, and *Stilosoma* (bootstrap support 83%).

The correct name for this tribe is Coronellini Jan, 1863, based on the family Coronellidae composed of three subfamilies and 29 distinct genera, with *Coronella Laurenti*, 1768 (including *C. austriaca*, the type species) as the typical group.

To judge from biochemical and molecular data as well as geological and palaeontological evidence (see,

⁷ Ventral data for *Orthriophis taeniurus* (Table 2) do not include a damaged specimen (SH 1099) from “Hong Kong” (pet trade) with 299 precaudal vertebrae (see Table 1).

e.g., Dowling et al., 1983; Holman, 2000; Utiger et al., 2002), ratsnakes, Old World racers, and New World (mostly Nearctic) racers have been genetically isolated for at least 18 – 20 mybp. Although we are not in a position to determine the migration route of Old and New World racers (from the eastern Palearctic to the Nearctic region or vice versa), there can be no doubt that New World ratsnakes derive from an Old World coronelline stock.

The Colubrini as understood by students of higher snake classification (e.g., Underwood, 1967; Dowling and Duellman, 1978; Dowling et al., 1983; Dowling et al., 1996) represent a large and morphologically poorly defined group including a plethora of Afrotropical, Oriental, Palearctic, and New World genera. Based on allele comparison of four slow-evolving proteins, Dowling et al. (1996) considered the Colubrini Opperl, 1811, i.e., “the racers and ratsnakes and their allies” to include two main clades. These are the “Holarctic ratsnakes and Nearctic racers and their relatives (*Coluber constrictor* through *Senticolis triaspis*)” and the “Neotropical and Old World racers and their relatives (*Chironius carinatus* through *Spalerosophis cliffordi*)” including, for instance, *Gonyosoma* and *Ptyas* (*carinatus*, *korros*), suggesting “a recent Oriental-derived radiation of racers in Central and South America similar to the pattern seen in elapids.”

Wallach (1998) placed Old and New World racers including Oriental taxa discussed in this study (i.e., *Argyrogena*, *Coluber* auct., *Drymarchon*, *Drymoluber*, *Eirenis* auct., *Gonyosoma*, *Liochlorophis*, *Lytorhynchus*, *Masticophis* auct., *Mastigodryas*, *Opheodrys*, *Phyllorhynchus* [see footnote 6], *Ptyas*, *Salvadora*, *Spalerosophis*), the Afrotropical genera *Meizodon* (five species) and *Aeluroglena* (*A. cucullata*, see Schätti, 1985), Old World ratsnakes (as *Elaphe* auct., see footnote 4) including *Coronella*, as well as the Nearctic *Senticolis triaspis* in the Colubrini auct. The remaining New World rat-snake genera are “Lampropeltini” (i.e., Coronellini) as proposed by Keogh (1996) who stated that this tribe is defined by a single synapomorphy, i.e., the presence of an intrapulmonary bronchus (absent in *S. triaspis*, Underwood, 1967). The latter is also found in, for instance, *Orthriophis moellendorffi* and the Oriental racer *Coelognathus radiatus*.

Our molecular (mtDNA) data (Fig. 3) argue for three radiation groups among racers and ratsnakes as conceived by us, i.e., Old and New World ratsnakes (Coronellini), Old World racers, and New World racers. For the time being, it cannot be ruled out that the Coronellini and Old World racers are sister groups.

Accepting ratsnakes as well as New World racers and their allies as two different tribes, Afrotropical, Palearctic, and Saharo-Sindian racers may belong to a yet unnamed colubrine radiation. Without taking into account Oriental genera, and assuming that Old World racers, Coronellini, and New Worlds racers belong to three taxonomically equivalent groups, the Old World racers might deserve tribal status within the Colubrinae. In any case, this grouping remains undefined. Hopefully, the higher systematics of Old and New World racers, ratsnakes, and related groups will be on the herpetologists’ agenda in the years to come.

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APPENDIX A

Material examined with regard to scutellation features (see **Appendix B** for dorsal scale rows), pulmonary characters (*), and the number of precaudal vertebrae (°). *Coelognathus erythrurus* (Duméril, Bibron et Duméril, 1854): *NHMB 1292 – 93, 8510, 19703; °SH 969 – 70, 1319 – 20; *ZFMK 31689; *C. flavolineatus* (Schlegel, 1837): *MHNG 1377.80 – 81, 1464.64; °SH 697, 1055 – 58; *ZFMK 16528, 16661, 31685 – 86, 33467, 36323; *C. helena* (Daudin, 1803): °SH

684; *ZFMK 31697 – 98, 33373, 38755 – 58, 39549; *C. phillipinus* (Griffin, 1909): *MHNG 2096.20, 2102.62; *C. radiatus* (Boie, 1827): *BMNH 98.4.2.26, 1903.4.13.73, 1956.1.12.82 – 83; °SH 864, 971, 1324, 1333, 1338; *C. subradiatus* (Schlegel, 1837): *BMNH 97.12.30.19 – 21; °SH 870, 872. *Gonyosoma frenatum* (Gray, 1853): *BMNH 1924.12.9.195; °SH 585, 1010, 1022; *G. janseni* (Bleeker, 1858): °SH 1147; *G. oxycephalum* (Boie, 1827): °SH 1097, 1198; *G. prasinum* (Blyth,

1854): *BMNH 72.4.17.350, 1914.3.2.13, 1926.3.17.3, 1938.8.7.44; °SH 2189. *Orthriophis cantoris* (Boulenger, 1894): *BMNH 52.8.12.33, 60.3.19.1428; °SH 2616; *O. hodgsonii* (Günther, 1860): *BMNH 1940.3.7.16; *MHNG 1377.100, 1378.1; °SH 681; *O. moellendorffi* (Boettger, 1886): *MHNG 1330.90, 1377.82; °SH 479, 490, 550, 598 – 600, 990; *ZFMK 29879 – 80; *O. taeniurus* (Cope, 1861): *BMNH 1974.3885, 1988.233 – 34; °SH 542, 581 – 82, 962 – 63, 1015, 1019, 1329, 1335.

APPENDIX B

Dorsal scale row (dsr) formula (number of longitudinal dsr, left/right position of dsr reductions in terms of ventrals [one value if identical], and row[s] involved in the fluctuations; see **Material and Methods**), number of ventral, anal (1: single, 2: divided), and subcaudal scales, supralabials (higher value of both sides), and subocular(s) (higher value) of Oriental racers (*Coelognathus*, *Gonyosoma*, and *Ptyas* spp.) and the ratsnake genus *Orthriophis*. A question mark denotes missing data. *Coelognathus erythrurus* NHMB 1292 (♀, Mindanao, Philippines): 23 (20/21: 5) 21 (133/136: 5) 19; 223; 1; 104; 9; 0. NHMB 5051 (♀, Celebes): 23 (21/22: 5) 21 (145/147: 5) 19; 228; 1; 97; 9; 0. NHMB 8510 (♀, Cabalian, Leyte, Philippines): 23 (13: 5) 21 (153/161: 5) 19; 224; 1; 105; 9; 0. NHMB 19703 (♀, Manila, Philippines): 23 (14/15: 5) 21 (137/135: 5) 19 (192: 5/188: 4) 17; 225; 1; 94; 9; 0. NMW 23399 (♀, India? [“vermutlich Indien”]): 23 (16: 6/18: 5) 21 (136: 5/140: 6) 19 (202/195: 4) 17; 225; 1; ?; 9; 0. ZFMK 31689 (♀, Celebes): 23 (18: 6) 21 (130: 6/136: 5) 19 (201/215: 5) 17; 229; 1; 98; 9; 0. *C. flavolineatus* MHNG 1377.80 (♀, “Sumatra or Malaysia”): 21 (18: 5) 19 (131/133: 5) 17; 215; 1; ?; 9; 0. MHNG 1464.64 (♂, Kuala Lumpur, Malaysia): 21 (15: 5/16: 6) 19 (136/135: 5) 17; 220; 1; 98; 9; 0. ZFMK 16528 (♀, Subang, Malaysia): 21 (17/20: 5) 19 (136/133: 5) 17; 226; 1; 101; 9; 0. ZFMK 16661 (♀, Tapoh, Malaysia): 21 (16/14: 5) 19 (139/135: 5) 17; 223; 1; ?; 9; 0. ZFMK 31686 (♀, Java): 21 (21: 5) 19 (137/133: 4) 17; 218; 1; 88; 9; 0. ZFMK 33467 (♀, Buitenzorg, Java): 21 (15: 5/17: 4) 19 (145/139: 5) 17; 221; 1; ?; 9; 0. ZFMK 36323 (♂, Simpang Rengam, Malaysia): 21 (14/11: 5) 19 (132: 6/134: 5) 17; 217; 1; ?; 9; 0. *C. helena* MHNG 845.10A (♂, “Indes méridionales”): 25 (12/15: 5) 23 (47: 7/48: 6) 25 (114/111: 7) 23 (140/139: 6) 21 (144/142: 3) 19; 251; 1; 80; 9; 0. MHNG 1377.98 (♀, Hyangcha, Kanbe Nangla, Nepal): 27 (11/12: 6) 25 (127/128: 6) 23 (142/140: 5) 21 (177/178: 4) 19; 236; 1; 75; 9; 0. NHMB 1230 (♀, Mangalore, India): 25 (17/18: 6) 23 (38/42: 7) 25 (123: 7/130: 6) 23 (145: 3) 21 (147/146: 5) 19; 248; 1; 76; 9; 0. SH 683 (♀, Pokhara Campus, Nepal): 25 (14/15: 6) 23 (133: 5/130: 6) 21 (145: 4/158: 5) 19; 236; 1; 78; 9; 0. ZFMK 31697 (♂, “Ceylon” [Sri Lanka]): 25 (48/44: 6) 27 (129/131: 6) 25 (140/137: 5) 23 (158/152: 5) 21; 210; 1; 82; 10; 0. ZFMK 33373 (♂, “Ceylon” [Sri Lanka]): 23 (44: 6/36: 7) 25 (121/117: 5) 23 (131/132: 5) 21 (194/196: 4) 19; 220; 1; 95; 10; 0. ZFMK

38755 (♀, Sri Lanka [born in captivity; “Nachzucht, Elterntiere Ceylon”]): 25 (103/118: 5) 23 (126/120: 5) 21 (162/165: 4) 19; 235; 1; 85; 10; 0. ZFMK 39549 (♀, “Ceylon” [Sri Lanka]): 25 (48/50: 5) 27 (121/125: 6) 25 (130: 6/127: 5) 23 (141/138: 5) 21 (194/203: 4) 19; 239; 1; 84; 10; 0. *C. philippinus* MHNG 2096.20 (♀, Dipaculao, Aurora Province, Philippines): 23 (? : ?) 21 (140: 6) 19; 226; 1; ?; 9; 0. MHNG 2102.62 (♂, Baler, Aurora, Philippines): 23 (16/17: 5) 21 (? : ?) 19; 217; 1; 92; 9; 0. *C. radiatus* BMNH 98.4.2.26 (♂, Bangkok, Thailand): 21 (19/18: 6) 19 (143: 5/138: 4) 17; 220; 1; 90; 9; 0. BMNH 1903.4.13.73 (♂, Jalor, Malaysia): 21 (13/16: 5) 19 (144/142: 5) 17; 225; 1; 93; 8; 0. BMNH 1956.1.12.82 (♂, Hong Kong): 21 (20: 6) 19 (147: 5/145: 4) 17; 229; 1; 100; 9; 0. BMNH 1956.1.12.83 (♂, Hong Kong): 21 (17/18: 6) 19 (142: 3/144: 5) 17; 226; 1; 96; 8; 0. *C. subradiatus* BMNH 97.6.21.47 (♂, Sumba Island, Indonesia): 25 (20: 4) 23 (52: 7/57: 8) 25 (134: 8/132: 7) 23 (163/168: 4) 21; 231; 1; 101; 9; 1. BMNH 97.12.30.19 (♀, Alor Island, Ombasi [Omkasi], Indonesia): 25 (18/17: 6) 23 (145: 4/144: 3) 21; 236; 1; 90; 9; 0. BMNH 97.12.30.33 (♀, Atapupu, West Timor): 25 (27/33: 5) 23 (147/149: 3) 21 (197/202: 4) 19; 241; 1; 92; 9; 2. BMNH 1946.1.6.16 (♂, “one of the types,” Timor): 25 (19: 5) 23 (138/140: 5) 21 (162/158: 4) 19; 231; 1; 93; 9; 1. *Gonyosoma frenatum* BMNH 1924.12.9.195 (♂, Ngoi-Tio, Tonkin, Vietnam): 19 (112/111: 9) 17 (118: 4) 15 (157/160: 7) 13; 204; 2; 144; 9; 0. CIB 74 II 5379 (♀, Huoshan, Anhui Province, China): 19 (123: 4) 17 (124: 8) 15; 218; 2; 128; 8; 0. CIB 74 II 5386 (♂, Huoshan, Anhui): 19 (125/126: 8) 17 (132/133: 4) 15; 219; 2; 142; 8; 0. CIB 74 II 5387 (♀, Huoshan, Anhui): 19 (125: 5) 17 (139/137: 4) 15; 219; 2; 132; 7; 0. CIB 74 II 5388 (♀, Huoshan, Anhui): 19 (127/126: 9) 17 (134/133: 4) 15; 219; 2; 137; 8; 0. SH 1010 (♂, pet trade): 19 (125/123: 9) 17 (127/126: 4) 15; 220; 2; 143; 8; 0. SH 1022 (♀, pet trade): 19 (125/126: 7) 17 (128/128: 4) 15; 222; 2; 138; 8; 0. *G. janseni* BMNH 1946.1.6.20 (♂, Manado, Celebes): 23 (136: 10) 21 (142/141: 3) 19 (161/158: 9) 17 (207: 8) 15; 250; 2; 140; 10; 0. *G. oxycephalum* BMNH 1946.1.14.59 (juv. holotype of *Alopecophis chalybeus* Gray, “Mauritius” [most probably in error]): 27 (23: 13) 25 (126: 12/11) 23 (136: 9) 21 (127/131: 4) 19 (159: 9) 17 (223: 8) 15; 234; 2; 134; 11; 0. MHNG 1363.82 (♀, Penang, Malaysia): 25 (137/135: 6) 23 (148/145: 10) 21 (146/143: 4) 19 (183/181: 9) 17; 253; 2; ?; 9; 0. MHNG 1363.83 (♀, Penang, Malaysia): 27 (25/24: 13) 25 (60: 13) 27 (133/129: 13) 25 (143/144: 12) 23 (144/146: 4) 21 (160/158: 10) 19 (202/205: 9) 17; 251; 2; 131; 10; 0. MHNG 1363.84 (♀, Penang, Malaysia): 25 (37: 12) 23 (59: 12) 25 (128/125: 12) 23 (138/136: 4) 21 (144/143: 10) 19 (165/161: 9) 17 (222: 8/239: 9) 15; 246; 2; ?; 10; 0. MHNG 2439.61 (♂, “Malaysia”): 23 (130/129: 4) 21 (134: 9) 19 (138: 7) 17 (189/196: 8) 15; 244; 2; 144; 10; 0. MHNG 2439.62 (♂, “Malaysia”): 23 (137: 11/138: 10) 21 (139/138: 4) 19 (155/153: 9) 17 (195: 8) 15; 247; 2; 145; 10; 0. MHNG 2439.63 (♀, “Malaysia”): 25 (32: 12) 23 (60: 11) 25 (135/136: 12) 23 (141: 11) 21 (140/143: 4) 19 (171/173: 9) 17; 244; 2; 132; 10; 0. *G. prasinum* BMNH 72.4.14.350 (♂, Khasi Hills, Assam [Meghalaya], India): 19 (105/105: 9) 17 (113/115: 4) 15; 196; 1; 105;

9; 0. BMNH 1914.3.2.13 (♀, Wuling Chan, Yunnan, China): 19 (100/98: 4) 17 (118/116: 9/8) 15; 193; 2; 100; 8; 0. BMNH 1926.3.17.3 (♀, Maymyo, Myanmar): 21 (12/17: 4) 19 (115/114: 4) 17 (127/125: 8/9) 15; 202; 2; 103; 9; 0. BMNH 1938.8.7.44 (♂, Ban Na, Yousane, Annam, Vietnam): 19 (110/107: 9) 17 (112/110: 4) 15 (163/168: 7) 13; 203; 2; 104; 9; 0. BMNH 1946.1.10.22 (juv. ♂ holotype of *Gonyosoma gramineum* Günther, Khasi Hills, Assam [Meghalaya], India): 19 (106/104: 9) 17 (115/114: 4) 15; 195; 1; 118; 9; 0. CIB 625237 (♂, Yunnan, China): 19 (103/112: 4/9) 17 (105/109: 4) 15; 180; 2; 98; 9; 0. *Orthriophis cantor* BMNH 25.8.12.28 (♀, Sikkim): 21 (20: 6/22: 5) 19 (37/36: 5) 21 (126/129: 5) 19 (148/142: 5) 17; 228; 2; 72; 8; 1. BMNH 53.8.12.22 (♂, Sikkim): 21 (17/16: 5) 19 (36/38: 5) 21 (120/124: 5) 19 (136/137: 5) 17; 222; 2; 74; 8; 1. BMNH 1940.6.4.96 (♂, “Pangramadin Triangle, Upper Burma” [Myanmar]): 21 (23/24: 4) 19 (45: 5) 21 (131/132: 4) 19 (156/145: 4) 17; 235; 2; 82; 8; 1. NMW 26920.1 (♂, Sikkim): 21 (17: 5) 19 (? /43: 6) 21 (130/127: 6) 19 (150: 5/146: 4) 17; 224; 2; ?; 8; 1. SH 2462 (♂, Rakse, Ilam District, Nepal): 19 (48: 5) 21 (120: 5) 19 (130/128: 5) 17; 223; 1; ?; 7; 0. SH 2516 (♂, Rakse, Ilam): 23 (14: 4) 21 (122/120: 5) 19 (131/130: 5) 17; 222; 1; ?; ?; ?.

O. hodgsonii BMNH 1940.3.7.16 (♂, Simla, Nepal): 25 (13/15: 6) 23 (134/132: 6) 21 (145: 6/5) 19; 236; 2; 88; 8; 1. BMNH 1946.1.6.12 (♀, Darjeeling, India): 23 (20: 6) 21 (40: 6) 23 (136/131: 7) 21 (150/151: 5) 19 (196: 7/194: 5) 17; 234; 2; 83; 9; 1. BMNH 1946.1.6.15 (♀ lectotype [Kramer, 1977], “Ladakh, Tibet”): 25 (18: 6/13: 5) 23 (143: 6/141: 7) 21 (156/158: 5) 19 (210/219: 5) 17; 247; 2; 88; 8; 0. BMNH 1946.1.6.23 (♂ paralectotype [Kramer, 1977], “Nepal”): 23 (20/23: 6) 21 (36/37: 6) 23 (117: 6/116: 7) 21 (132: 5/134: 6) 19 (163: 5/158: 6) 17; 223; 2; 78; 7; 0. SH 681 (♀, Daman, Paluntar, Nepal): 23 (15: 6) 21 (45/44: 6) 23 (129/128: 7) 21 (144/147: 5) 19 (179/173: 5) 17; 238; 2; ?; 8; 0. SH 812 (♀, Katmandu, Nepal): 23 (18/20: 6) 21 (36/34: 6) 23 (130/131: 7) 21 (142/144: 5) 19 (192: 5/191: 6) 17; 237; 2; 77; 8; 0.

O. moellendorffi MHNG 1377.82 (♀, Hong Kong): 25 (58/67: 7) 27 (139: 8/140: 7) 25 (155 /157: 6) 23 (191/184: 6) 21 (251: 5) 19; 275; 2; 99; 9; 1. SH 525 (♂, Hong Kong): 25 (54/52: 7) 27 (150/148: 8) 25 (158/160: 6) 23 (181/184: 6) 21 (249/242: 5) 19; 267; 2; 95; 9; 2. ZFMK 29879 (♀, “China”): 27 (20/19: 7) 25 (36/33: 7) 27 (150: 7/152: 6) 25 (161: 7/160: 6) 23 (203/200: 6) 21; 268; 2; 94; 9; 1. ZFMK 29880 (♂, “China”): 27 (17/21: 6) 25 (48/54: 7) 27 (150: 6/151: 8) 25 (161/162: 6) 23 (200/196: 6) 21; 268; 2; 96; 9; 1. *O. taeniurus* BMNH 1946.1.7.34 (♂, “one of the types” of *Elaphis grabowski* Fischer, “S. E. Borneo,” Indonesia): 27 (23: 6) 25 (157/155: 7) 23 (173: 4/5) 21 (239/243: 5) 19; 281; 2; 92; 9; 1. BMNH 1946.1.7.36 (♂, “one of the types” of *Elaphis grabowski* Fischer, “S. E. Borneo”): 27 (26: 5/? : ?) 25 (153/155: 7) 23 (175/165: 5) 21 (234/237: 5) 19; 277; 2; 99; 9; 1. BMNH 1946.6.2.1 (♂ holotype of *Elaphis yunnanensis* Anderson, Tengzueh, Yunnan, China): 25 (12: 5/13: 6) 23 (135: 6/7) 21 (160: 6/158: 5) 19; 249; 2; 93; 8; 1. BMNH 1988.233 (♀, “China”): 23 (30: 5/3) 21 (54/55: 6) 23 (135/136: 5) 21 (156/155: 5) 19 (217/216: 3) 17; 239; 2; 90; 8; 1.

BMNH 1988.234 (♂, “China”): 25 (17: 6) 23 (52: 6/7) 25 (128: 8/7) 23 (140/138: 5) 21 (162/160: 5) 19; 240; 2; 100; 9; 1. SMNH 23013 (sex unknown, holotype of *Coluber taeniurus pallidus* Rendahl, “Kawkareik, Dawha Hills, Karen State, Burma” [Myanmar]): 27 (23/24: 6) 25 (153/155: 6) 23 (168/170: 4) 21 (231: 5/222: 4) 19; 292; 2; ?; 9; 1. *Ptyas korros* MHNG 1375.33 (♀, Tandjong, Sumatra): 15 (98: 4/3) 13 (131: 4/3) 11; 167; 2; ?; 8; 1. MHNG 1375.34 (♀, Bangkok, Thailand): 15 (88/87: 4) 13 (97/98: 4/3) 11; 167; 2; ?; 8; 1. MHNG 1375.35 (♀, Bangkok, Thailand): 15 (92: 3/93: 4) 13 (95/96: 3) 11; 166; 2; ?; 8; 1. *P. mucosus* MHNG 1375.26 (♂, between Sunauli and Devanandpur; Nepal): 17 (100: 9) 16 (114/115: 3) 14; 200; 2; ?; 8; 1. MHNG 1375.27 (♀, Calcutta, India): 19 (28: 5) 17 (55: 9) 16 (116/118: 3) 14; 199; 2; ?; 8; 1. SH 2461 (♂, Katmandu, Nepal): 19 (16/18: 4) 17 (110: 8) 16 (110: 3) 14; 195; 2; 118; 8; 0.

APPENDIX C

DNA samples prepared for this study (SH, SR: tissue collection of N. Helfenberger and M. Ruf, respectively; GenBank Accession number COI/12S). *Coelognathus flavolineatus* SH 1055 (Java, AY122648/122666); *C. helena* SH 1179 – 1180 (pet trade, AY122656 – 57/122674 – 75); *C. radiatus* SH 533 (pet trade, AY122659/122677) and 971 (N of Suphanburi, Thailand, AY122658/122676); *C. subradiatus* SH 1066 and 1078 (pet trade, AY122654 – 55/122672 – 73). *Coluber taeniatus* SR 493 (Pandale rd, 3 miles N of highway 90, Val Verde Co., Texas, AY122651/122669). *Gonyosoma janseni* SH 1147 (Celebes, AY122653/122671); *G. oxycephalum* SH 1098 and 1102 (Java, AY122660 – 61/122678 – 79). *Lamprophis fuliginosus* SH 1210 (outgroup taxon; AY122663/122681). *Natrix natrix* SH 1296 (outgroup taxon; AY122664/122682). *Ptyas korros* SH 1414 (Hong Kong, AY122652/122670).

APPENDIX D

GenBank numbers of DNA sequences from earlier studies (Schätti and Utiger, 2001; Utiger et al, 2002) used for this study (see **Appendix C**). *Arizona elegans* SR 547 (AY122726/122810). *Coelognathus erythrurus* SH 969 (AY122647/122665), SH 1011 (AY122692/122776); *C. flavolineatus* SH 1077 (AY039200/039162). *Coluber constrictor* MHNG 2415.34 (AY122735/122819), SR 649 (AY122649/122667); *C. flagellum* MHNG 2414.63 (AY122739/122823), SR 492 (AY122650/122668). *Coronella austriaca* SH 1103 (AY122752/122836); *C. girondica* SH 1067 (AY122751/122835). *Eirenis modestus* SH 1115 (AY039181/039143). *Elaphe carinata* SH 575 (AY122755/122839); *E. quatuorlineata* SH 975 (AY122714/122798). *Euprepiophis conspicillatus* SH 572 (AY122690/122774); *E. mandarinus* SH 578 (AY122700/122784). *Gonyosoma frenatum* SH 1010 (AY122693/122777); *G. prasi-*

num SH 2189 (AY122708/122792). *Hemorrhoids algirus* MHNG 2415.6 (AY039187/039149); *H. hippocrepis* MHNG 2415.94 (AY039196/039158); *H. ravergeri* SH 561 (AY039169/039131). *Hemerophis socotrae* MHNG 2610.88 (AY039178/039140). *Hierophis caspius* SH 1148 (AY039164/039126); *H. gemonensis* SH 557 (AY039183/039145). *Lampropeltis getula* SR 315 (AY122738/122822); *L. ruthveni* SR 405 (AY122736/122820). *Oocatochus rufodorsatus* SH 1416 (AY122715/122799). *Oreocryptophis* cf. *porphyraceus* (see **Corrigenda**) SH 1091 (AY122707/122791). *Pantherophis guttatus* SR 448 (AY122758/122842). *Platycephalus rhodorachis* MHNG 2554.13 (AY039189/039151); *P. rogersi* MHNG 2443.24 (AY039165/039127). *Ptyas mucosus* SH 2461 (AY122744/122828). *Rhinechis scalaris* SH 814 (AY122717/122801). *Salvadora grahamiae* SR 349 (AY122662/122680), SR 494 (AY122763/122847). *Senticolis triaspis* SR 314 (AY122732/122816), SR 588 (AY122764/122848). *Spalerosophis* cf. *diadema* MHNG 2547.44 (AY039182/039144). *Zamenis longissimus* SH 1111 (AY122696/122780); *Z. situla* SH 1538 (AY122721/122805).