

Systematics and phylogenetic relationships of Whip snakes (*Hierophis* Fitzinger) and *Zamenis andreana* Werner, 1917 (Reptilia: Squamata: Colubrinae)

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Systematics and phylogenetic relationships of Whip snakes (*Hierophis* Fitzinger) and *Zamenis andreana* Werner, 1917. - Morphological and molecular data of *Coluber* (sensu lato) *andreas* and all recognised species of the Palaearctic whip snake genus *Hierophis* Fitzinger are presented. Morphologically, Andreas' racer shows remarkable similarities to dwarf snakes (*Eirenis* spp., *Pseudocyclophis persicus*). Derived conditions of head and body pholidosis including dorsal scale reduction pattern and the number of apical pits separate *Eirenis* Jan and *C. (s.l.) andreas* from *Hierophis* spp. Character states strongly support sister group relationship of dwarf snakes to Andreas' racer. Molecular analyses confirm monophyly of *Hierophis* spp., *C. (s.l.) andreas*, and dwarf snakes of the genus *Eirenis*, and paraphyly of *Hierophis* auct. MtDNA sequences indicate a basal position of the eastern Palaearctic *H. spinalis* vis-à-vis the western species group (*H. cypriensis*, *H. gemonensis*, *H. viridiflavus*). These taxa belong to an early radiation within whip and dwarf snakes. The eastern Mediterranean *H. caspius*, *H. jugularis*, and *H. schmidtii* appear to represent a paraphyletic grouping including *C. (s.l.) andreas* (12S rDNA sequence data). Conflicting molecular and morphological results are discussed and the character phylogeny of external morphological features is re-assessed.

Key-words: *Coluber* (s.l.) *andreas* - *Eirenis* - *Hierophis* - morphology - osteology - hemipenis - transformation series - phylogeny - mtDNA.

INTRODUCTION

Without taking account of Oriental taxa (Utiger, 2002), Old World racers and their allies belong to at least eight different genera, i.e., *Eirenis* Jan, 1863, *Hemerophis* Schätti & Utiger, 2001, *Hemorrhois* Boie, 1826, *Hierophis* Fitzinger in Bonaparte, 1834, *Lytorhynchus* Peters, 1862, *Platycephalus* Blyth, 1860, *Pseudocyclophis* Boettger, 1888, and *Spalerosophis* Jan, 1865 (Schätti 1986, 1987; Schätti & Utiger, 2001). The latter genus is the sister taxon of *Hemorrhois* Boie. Together with *Platycephalus* Blyth, they make up a monophyletic group among Old World racers.

The Palaearctic whip snake (or racer) genus *Hierophis* Fitzinger belongs to a distinct evolutionary lineage within Afrotropical, Palaearctic, and Saharo-Sindian racers. It is considered to include *H. caspius* (Gmelin, 1789), *H. cypriensis* (Schätti, 1985), *H. gemonensis* (Laurenti, 1768), *H. jugularis* (Linnaeus, 1758), *H. schmidtii* (Nikolskij, 1909), *H. spinalis* (Peters, 1866), and *H. viridiflavus* (Lacépède, 1789), the type species (Schätti, 1987, 1988, 1993; Schätti & Utiger, 2001; Utiger & Schätti, 2004).

Zamenis andreana Werner, 1917 from the southern Zagros Mountains in Iran is a poorly known and enigmatic species characterised by a number of distinctive external morphological features typically encountered in dwarf snakes of the genus *Eirenis* Jan. Schätti (2001) thought that Andreas' racer is a representative of an early evolutionary lineage among Palaearctic racers. Schätti & Utiger (2001) placed the taxon in their *incertae sedis* section, i.e., *Coluber* sensu lato, stressing the necessity of comparison with *Eirenis* spp.

A preliminary molecular analysis (Schätti & Utiger, 2001) generated low bootstrap values for the European (*Hierophis gemonensis*, *H. viridiflavus*) and eastern Mediterranean (*H. caspius*, *H. jugularis*, *H. schmidtii*) whip snakes. On the basis of mtDNA sequence data, *Eirenis modestus* (Martin, 1838) turned out to be the sister taxon of the latter species group, thus rendering *Hierophis* auct. paraphyletic. The reality of two whip snake groups was also confirmed with cytochrome b sequences (Nagy *et al.*, 2000).

Using external morphological characters, vertebra (only *Hierophis* spp.) and hemipenis features, as well as molecular methods, this study investigates the phylogenetic relationships of *Zamenis andreana* Werner, the systematic composition of *Hierophis*, and the morphological demarcation of whip snakes vis-à-vis dwarf snakes, i.e., *Eirenis* spp. and *Pseudocyclophis persicus* (Anderson, 1872).

MATERIAL AND METHODS

Methods and definitions of terms used in the text are explained in Schätti (1987, 1988). For the purpose of this study, the number of anterior suboculars may include an additional (supplementary) scale. The anterior temporals are made up of the first and second row of scales. Bilateral reductions of the number of longitudinal dorsal scale rows (dsr, at midbody: msr) are either low (lateral) or high (i.e., paravertebral or vertebral). Their position on the posterior portion of the trunk is expressed as a percentage of the total number of ventrals (%ven) and calculated on the basis of the average of the right and left side counts. Vertebra measurements, and in particular the length of the centrum (lc) and neural crest (nc), the least width of the neural arch (wn), and the width across the prezygapophyses (wp), are figured in Helfenberger (2001).

Scientific names of *Hierophis* spp. are cited with the author and year of publication upon their first mention in the text. In the case of *Eirenis* spp. except those used for molecular analyses (see below), as well as Oriental racer genera cited in the Discussion, only the author's name is given.

Acronyms used in the text are CAS (California Academy of Sciences, San Francisco), MHNG (Muséum d'histoire naturelle, Genève), MVZ (Museum of Vertebrate Zoology, Berkeley), and ZMUC (Zoologisk Museum, København).

Hierophis Fitzinger (sensu Utiger & Schätti, 2004) is understood to contain two European taxa, the endemic Cyprus whip snake, three eastern Mediterranean species, as well as the eastern Palaearctic *H. spinalis*. Lacépède's whip snake (*H. viridiflavus*) from NE Spain to Dalmatia, Malta, and Gyaros Island (Cyclades) in the Aegean Sea, the Balkans whip snake (*H. gemonensis*) from Dalmatia to the Aegean region, and *H. cypriensis* make up the western species group. Eastern Mediterranean species include *H. caspius* from the Balkans eastward and two Anatolia-Caucaso-Iranian species, *H. jugularis* and *H. schmidtii*. As to the systematic make-up of dwarf snakes, the reader is referred to the appropriate section in the text.

External morphological data for *Coluber* (s.l.) *andreae* are from five specimens reported earlier (Schätti, 2001) and MHNG 2626.59. Scale features of *Eirenis* and *Hierophis* spp. are from Boulenger (1894, 1914), Eiselt (1976), Schmidtler & Schmidtler (1978), Docenko (1985), Schätti (1985, 1987, 1988), Docenko (1989), Franzen & Sigg (1989), Schmidtler & Eiselt (1991), Böhme (1993), Schätti (1993), Schmidtler (1993), Schmidtler & Baran (1993b), Schmidtler (1997), Sivan & Werner (2003), and Utiger & Schätti (2004).

A partial sequence of the mitochondrial small ribosomal subunit (12S rRNA) of six racer or dwarf snake taxa and presumably related colubrids was obtained from frozen muscle or a dry skin (*Eirenis* sp.). Voucher specimens are *Coluber* (s.l.) *andreae* (Werner, 1917) MHNG 2626.59 (Iran: Gavilah, Khuzestan), *Eirenis medus* (Chernov in Terentjev & Chernov, 1940) MHNG 2627.4 (Iran: vicinity of Mahniyah, Hamadan/Zanjan border), *E. punctatolineatus* (Boettger, 1892) MHNG 2626.99 (Iran: vicinity of Hashtijan, Fars), *Eirenis* sp. MHNG 2626.71 (Iran: Mehkuyeh, Fars; sloughed skin, see Dwarf Snakes), *Lytorhynchus diadema* (Duméril, Bibron & Duméril, 1854) MHNG 2427.32 (Yemen: Jabal Mafluq), and *Spalerosophis microlepis* Jan, 1865 MHNG 2626.70 (Iran: Mehkuyeh, Fars).

The technique of DNA isolation as well as PCR and sequencing procedures are described in Utiger *et al.* (2002). The obtained data were added to a selection of 16 Palaearctic, Saharo-Sindian, and an Oriental racer species from an existing sequence file consisting of two partially analysed mitochondrial genes, cytochrome oxidase subunit I (COI) and 12S rRNA (Utiger & Schätti, 2004). Due to constraints in laboratory facilities, only one gene region (12S rRNA) was investigated for the new taxa presented in this study. The lacking COI characters were coded as missing.

Phylogenetic analyses were performed with PAUP* version 4.0b10 for Mac (Swofford, 1998). Weighted maximum parsimony (MP) procedures are described in Utiger *et al.* (2002) and Utiger & Schätti (2004). Gaps in the 12S rDNA sequence were treated as fifth character state. After a first run with heuristic search and tree-bisection reconnection (TBR) branch swapping, characters were weighted with the rescaled consistency index (RC, Farris, 1989) and a second heuristic search was performed. The procedure was repeated once; further weighting did not alter the parameters of the resulting tree. Nonparametric bootstrap values (Felsenstein, 1985) with 1000 replicates were calculated for unweighted and weighted characters.

TABLE 1. Sequence properties and tree reconstruction parameters

	gaps: missing unweighted MP	gaps: 5 th character state unweighted MP	weighted MP
Length of sequence alignment (COI/12S)	1017 (407/610)	1017 (407/610)	1017 (407/610)
Total of variable characters (COI/12S)	339 (142/197)	350 (142/208)	350 (142/208)
- parsimony-informative ((COI/12S)	249 (116/133)	256 (116/140)	256 (116/140)
Number of most parsimonious trees	4	2	1
Tree length	1067	1121	266.72
Rescaled consistency index (RC)	0.195	0.199	0.478

RESULTS

Hierophis Fitzinger, 1834

Loreal and preocular single (the latter rarely divided). Usually eight supralabials (seven to nine), fourth and fifth entering eye. Anterior subocular situated between third and fourth supralabial; sometimes very small or, rarely, lacking in *Hierophis jugularis*; occasionally absent or with an additional small scale in *H. spinalis*. Two postoculars, normally only upper in contact with parietal. Usually two (one to, sometimes, three) scales in first row of temporals, and two or three (rarely one) in second. Nine or ten (eight to twelve) sublabials (Tb. 3).

Ventrals in ♂♂ 163-174 (*gemonensis*) and 178-211, ♀♀ 168-182 and 194-227, respectively; subcaudals 86-125 (♂♂) and 84-117 (♀♀). Maximum total length ca. 100 cm (*cypriensis*, *gemonensis*, *spinalis*) to over 200 cm (*caspius*, *jugularis*).

TABLE 2. Selected morphological data for *Hierophis* spp. Dorsal scale rows (dsr) on the neck, at midbody, and prior to the vent, posterior reduction pattern (prp: low (l) or high (h), see Material and Methods), number of maxillary (max), palatine (pal), pterygoid (pter), and dentary (den) teeth as well as vertebrae ratios (length of the centrum: lc, length of neural crest: nc, least width of neural arch: wn, width across prezygapophyses: wp).

Species	dsr	prp	max	pal	pter	den	lc/wn	lc/wp	nc/wn
<i>caspius</i>	17-19-15	l - l(-h)	12-15	9	14-18	14-17	1.25-1.44	0.70-0.77	0.88-1.05
<i>cypriensis</i>	17-17-13	l - h	16-18	10-11	17-20	19-20	1.38-1.58	0.74-0.80	1.11-1.28
<i>gemonensis</i>	17-19-15	l - l	16-19	9-12	20-23	16-23	1.23-1.35	0.70-0.74	0.95-1.03
<i>jugularis</i>	17-19-15	l - l	12-14	11	18-20	16-20	1.16-1.36	0.71-0.73	0.94-1.04
<i>schmidtii</i>	17-19-15	l - l	12-15	9	17-19	14-17	1.36-1.39	0.72-0.75	1.00-1.08
<i>spinalis</i>	17-17-15	l	13-15	8-10	10-12	16-18	1.45-1.53	0.74-0.81	1.05-1.21
<i>viridiflavus</i>	17-19-15	l - l	14-16	9-11	15-20	15-18	1.28-1.44	0.68-0.82	0.88-1.05

Dorsal scales with paired apical pits, in 17 longitudinal rows at neck (15th ventral), 17-19 msr, and 13-15 in front of vent. A lateral increase of the number of dsr on anterior portion of trunk except in *Hierophis cypriensis* and *H. spinalis*. One (*spinalis*) or two lateral reductions involving rows 2-5 on both sides of posterior portion of body; a third fusion (rows 6-8), in most cases unilateral (i.e., 14 dsr prior to vent), sometimes occurs in *H. caspius*. *H. cypriensis* has 17 dsr throughout the

TABLE 3. Selected morphological characters in *Hierophis* spp. (*caspius*, *gemonensis*, *jugularis*, *schmidtii*, *viridiflavus*), *H. cypriensis*, *H. spinalis*, *Coluber* (s.l.) *andreaus*, *Eirenis* spp. (*africanus*, *aurolineatus*, *barani*, *collaris*, *coronella*, *coronelloides*, *decentilineatus*, *eiselti*, *hakkariensis*, *levantinus*, *medus*, *modestus*, *rechargingeri*, *rothi*, *thospitis*), *E. lineomaculatus*, *E. p. punctatolineatus*, and *Pseudocyclophis* (*P. persicus*). Number of loreal, preocular (preoc), anterior subocular (suboc), see Material and Methods), supralabial (supral), sublabial (sublab, *: see Results), postocular (postoc, *: sometimes single in *E. medus*), and anterior (first and second) temporal (temp) scales, apical pits (a.p.), longitudinal scale rows at midbody (msr), and posterior reduction pattern (prp: low (l), high (h), or no fusion (0), see Material and Methods). Unusual conditions in parenthesis.

Taxa	loreal	preoc	suboc	supral	sublab	postoc	1st temp	2nd temp	a.p.	msr	prp
<i>Hierophis</i> spp.											
<i>H. cypriensis</i>	1	1 (2)	1 (0)	8 (7,9)	9-10 (*)	2	2 (1,3)	2-3	2	19	1-l(-h)
<i>H. spinalis</i>	1	1	1	8 (9)	10	2	2 (1)	2-3	2	17	1-h
<i>C. (s.l.) andreaus</i>	1	1	1 (0,2)	8 (9)	9 (8,10)	2	2 (1,3)	2-3	2	17	1
<i>Eirenis</i> spp.	1	1	0-2	7	8	2	1	2 (1)	1	17	1 or 0
<i>E. lineomaculatus</i>	1	1 (2)	0	7	7-8 (9)	2 (1*)	1	2 (1)	1	15-17	1 or 0
<i>E. punctatolineatus</i>	0 (1)	1	0	7	8 (7)	1 (2)	1	2 (1)	1	17	1
<i>Pseudocyclophis</i>	1	1	0	7	9 (8,10)	2	1	2	1	17	1
	0 (1)	1	0	7	8	1 (2)	1	1	1	15	1 or 0

forebody, a first reduction involving the third and fourth row at 61-68%ven, and a paravertebral or vertebral reduction (rows 6+7 or 7+8) to 13 dsr situated between 66-79%ven (Tbs 2-3).

Maxillary with 12-19 teeth, palatinum 8-12, pterygoid 10-12 (*spinalis*) and 14-23, and dentary 14-23. Vertebra ratios are: lc/wn 1.16-1.58, lc/wp 0.68-0.82, nc/wn 0.88-1.28 (Tb. 2).

Hemipenis with 3-6 distinct rows of spines; enlarged basal hook present in *Hierophis cypriensis*, *H. gemonensis*, and *H. spinalis*. Apex calyculate and bulbous in everted state (two longitudinal grooves *in situ*); borders of calyces denticulate proximally, usually smooth towards apex.

Coluber (sensu lato) *andreas* (Werner, 1917)

Pl. 1

Loreal and preocular single. Seven supralabials, third and fourth in contact with eye. Anterior subocular single, paired, very small, or absent (Schätti, 2001: Tb. 1; one



PLATE 1

Coluber (sensu lato) *andreas* (♀) MHNG 2626.59 from Khuzestan (Gavilah), Iran.

distinct subocular in MHNG 2626.59). Two postoculars, both (lower only partially) in contact with laterally extended parietal. First temporal single, coalesced with sixth supralabial in ZMUC R6044 (Schätti, 2001: Fig. 1)¹, usually two (one) scales in second temporal row. Eight sublabials (Tb. 3).

¹ Erroneously stated to be fused with the parietal (Schätti, 2001).

Ventrals show a pronounced sexual dimorphism, i.e., 217-218 (two ♂♂) and 247-269 (four ♀♀); subcaudals 92-96 and 84-94, respectively. Maximum total length 445+155 mm (♂) and 586+164 mm (♀) in syntypes (Werner, 1917).

Dorsal scales with single apical pits (best visible on flanks), in 17 longitudinal rows on anterior portion of trunk and at midbody, and 17 (no reduction) or 15 dsr in front of vent (Schätti, 2001). CAS 100474 (♂) with a lateral reduction involving row 2+3 at 87%ven; MHNG 2626.59 (♀) has 17-15-17 (etc.) dsr between ventrals 221-246 (89-99%ven), fluctuation between rows 2-4, and row 1+2 in the case of the last reduction to 15 dsr.

Maxillary with 9-13 teeth (10 in MHNG 2626.59). Proximal portion of hemipenis spinose (no further data available, vertebra ratios unknown).

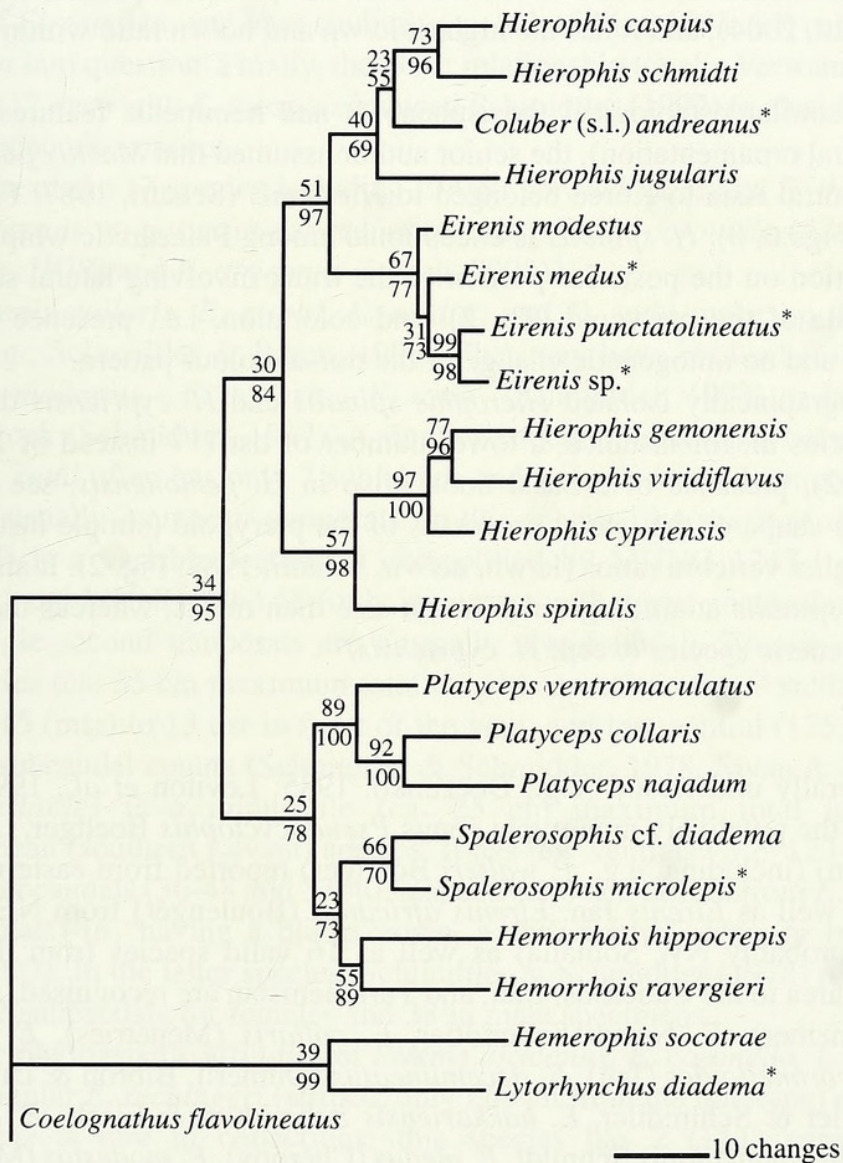


FIG. 1

Weighted maximum parsimony (MP) tree of two partially sequenced gene regions (COI and 12S RNA) with the Oriental racer *Coelognathus flavolineatus* (Schlegel) as outgroup. In the case of taxa with an asterisk reconstruction is based on 12S rDNA sequence data only. Bootstrap values (1000 replicates) from unweighted (upper) and weighted (lower values) MP analysis.

COMPARATIVE MORPHOLOGY

Coluber (s.l.) *andreas* differs from *Hierophis* spp. in lower supralabial and sublabial counts (7 instead of 8 and 8 vs. usually 9-10, respectively), parietal shape, i.e., laterally extended and in contact with lower postocular, and a single first temporal scale (parietal usually not reaching beyond upper postocular, 2 first temporals)², 247 or more ventrals in females (227 or less), single apical pits (paired), only one lateral dsr reduction that is sometimes absent (invariably present, Tb. 3), and a maximum total length of ca. 75 cm vs. 100-200 cm or more. Andreas' racer possesses a surprising number of external morphological character states in common with *Eirenis* spp. (see Tbs 3-4 and Discussion).

Hierophis cypriensis differs from congeneric species in, for instance, the occurrence of a paravertebral or vertebral reduction on the posterior portion of the trunk (Utiger & Schätti, 2004), and it has the highest lc/wn and nc/wn ratio within the genus (Tbs 2-3).

Due to similar osteological (basisphenoid) and hemipenis features (bulbous shape and general ornamentation), the senior author assumed that *Masticophis spinalis* Peters from Central Asia to Korea belonged to *Hierophis* (Schätti, 1987: Figs 1, 3.e; Schätti, 1988: Figs 6, 8). *H. spinalis* is exceptional among Palaearctic whip snakes in only one reduction on the posterior portion of the trunk involving lateral scale rows, low tooth counts of the pterygoid (Tb. 2), and coloration, i.e., presence of a light vertebral stripe and no ontogenetic change of the dorsal colour pattern.

The geographically isolated *Hierophis spinalis* and *H. cypriensis* differ from congeneric species in, for instance, a lower number of dsr (17 instead of 19) on the forebody (Tb. 2), presence of a basal hook (also in *H. gemonensis*, see Character Phylogeny), the shape of the lateral process of the pterygoid (simple instead of bicuspid), and higher vertebra ratios (lc/wn, nc/wn, Schätti, 1987: Fig. 2). It also appears that female *H. spinalis* attain larger maximum size than males, whereas the contrary applies to congeneric species except *H. cypriensis*.

DWARF SNAKES

As generally understood (e.g., Docenko, 1985; Leviton *et al.*, 1992), dwarf snakes contain the putatively monotypic genus *Pseudocyclophis* Boettger, i.e., *P. persicus* (Anderson) (including, e.g., *P. walteri* Boettger) reported from eastern Anatolia to Pakistan, as well as *Eirenis* Jan. *Eirenis africanus* (Boulenger) from NE Sudan to Djibouti (and probably NW Somalia) as well as 16 valid species from the eastern Mediterranean area to the Caucasus, Iran, and Turkmenistan are recognised, i.e., *E. aurolineatus* (Venzmer), *E. barani* Schmidtler, *E. collaris* (Ménétriés), *E. coronella* (Schlegel), *E. coronelloides* (Jan), *E. decemlineatus* (Duméril, Bibron & Duméril), *E. eiselti* Schmidtler & Schmidtler, *E. hakkariensis* Schmidtler & Eiselt, *E. levantinus* Schmidtler, *E. lineomaculatus* Schmidt, *E. medus* (Chernov), *E. modestus* (Martin), the type species (Schmidtler & Schmidtler, 1978), *E. punctatolineatus* (Boettger), *E.*

² The antero-lateral extension of the parietal, and its contact with the lower postocular, is correlated with the condition of the first temporal scale (single).

rechingeri Eiselt, *E. rothi* (Jan), and *E. thospitis* Schmidtler & Lanza. Nine *Eirenis* spp. (53%) were described or revalidated (*E. coronelloides*) over the last 33 years.

Pseudocyclophis persicus attains a total maximum length of ca. 50 cm and is characterised by the usual absence of a loreal (small if present) and a single postocular (Tbs 3-4). *P. persicus* has 15 msr and sometimes a posterior dsr reduction, 2 (1+1) anterior temporals, a slender habitus as well as high ventral (up to 224 in ♂♂, 238 in ♀♀) and subcaudal counts (95 and 85, respectively, Doczenko, 1985).

Doczenko (1989) assigned *Eirenis collaris*, *E. coronella*, *E. eiselti*, *E. medus*, *E. rechingeri*, and *E. rothi*, i.e., species with 15 msr except *E. africanus* (not examined), to a new subgenus, *Collaria*. Schmidtler & Eiselt (1991) noted that, for instance, the closely related *E. hakkariensis* and *E. thospitis* with 17 and 15 msr, respectively (see below), caused considerable doubt ("erhebliche Bedenken") as to the taxonomic division of *Eirenis* Jan, and later studies (e.g., Schmidtler, 1993: 94) called the validity of *Collaria* into question. Finally, the close relationship ("nahe Verwandtschaft") of *E. modestus* (17 msr) with *E. thospitis* induced Schmidtler (1997) to abandon Doczenko's (1989) subgeneric concept.

Nine of the 17 species including *Eirenis coronelloides* and *E. thospitis* have 15 msr and there is no posterior dsr reduction except in *E. coronella* (fide Schmidtler & Schmidtler, 1978) and *E. africanus* (Ineich, 2003)³.

Eirenis collaris, *E. eiselti*, *E. medus*, and *E. rothi* make up the "*E. collaris* group" (e.g., Schmidtler & Baran, 1993a) that may have evolved from *E. modestus* ("Linie *E. modestus* - *E. collaris* - *E. rothi*", Schmidtler, 1993) or from a common ancestor stock (Schmidtler, 1997). A single postocular sometimes occurs in *E. medus* (Tb. 3). *E. rothi* often has only 7 sublabials and a single second temporal, i.e., only 2 instead of usually 3 anterior temporals. In this species, the shape of the parietal (see footnote 2) is a variable feature as exemplified by MHNG 1247.1 (borders lower postocular) and MHNG 1363.58 (only in contact with upper postocular).

Single second temporals are normally also found in *Eirenis coronella*. This small species (ca. 35 cm maximum total length) sometimes has 9 sublabials, a reduction from 15 (msr) to 13 dsr in front of the vent, and low ventral (125 in ♂♂, 143 in ♀♀) and subcaudal counts (Schmidtler & Schmidtler, 1978; Sivan & Werner, 2003). *E. coronelloides* is a minuscule (ca. 25 cm maximum total length) eastern Mediterranean (southern Levant) species. It has few ventrals (♂♂ 123-134, ♀♀ 140-155) and subcaudals (36-48 and 33-40, respectively) and differs from *E. coronella* (40-67 subcaudals) in "having a black crown, a dark ventral stripe or both" (Sivan & Werner, 2003). In the latter species, Schmidtler & Schmidtler (1978) recorded a minimum of 32 subcaudals for females and 38 in male specimens.

The phylogenetic affinities of *Eirenis africanus*, *E. coronella*, *E. coronelloides*, and the singular *E. rechingeri* (striped, only known from the holotype) remain unclear. *E. africanus* is rare in collections; this species has 2 (1+1) anterior temporals (Boulenger, 1914) but, according to Scortecci (1930: Fig.), the parietal does not touch the lower postocular (see footnote 2).

³ This character state could not be ascertained for *Eirenis thospitis* and *E. coronelloides*. In the latter species, it is supposed that there is no difference vis-à-vis *E. coronella*, i.e., that *coronelloides* has a reduction to 13 dsr prior to the vent.

The “*Eirenis modestus* complex” (sensu Schmidtler, 1997) includes *E. thospitis* with 15 msr and five species (*aurolineatus*, *barani*, *hakkariensis*, *levantinus*, and *modestus*) with 17 msr and, usually, a reduction to 15 dsr prior to the vent (see footnote 3).

The posterior reduction may be present or absent in *Eirenis aurolineatus* and *E. levantinus*. *E. modestus* has exceptionally (“sehr selten”, Schmidtler & Baran, 1993b) 19 msr; this number is more often found in *E. m. cilicius* Schmidtler from around Burdur, Turkey (Schmidtler, 1997). Specimens of *E. modestus* with 17 dsr at midbody and in front of the vent (i.e., no reduction) are documented (e.g., Schmidtler & Eiselt, 1991; Schmidtler, 1993: Tb. 1).

A considerable number (33%, n=13) of northern Anatolian *Eirenis m. modestus* examined by Schmidtler (1997) have a single postocular and, rarely, there are 2 temporals in the first row (Schmidtler & Baran, 1993b). All taxa of the “*E. modestus* complex” show variation in the number of preoculars (1-2), although two scales are uncommon in *E. levantinus* and *E. hakkariensis* (Schmidtler & Eiselt, 1991: Tb. 1; Schmidtler, 1993: Tb. 1)⁴. The latter species is comparatively large (ca. 50 cm maximum total length) and has 8-9 sublabials. Schmidtler & Eiselt (1991) discuss differences of the Hakkari dwarf snake and *E. punctatolineatus* (see below).

Eirenis lineomaculatus with a posterior reduction from 17 to 15 dsr involving lateral rows is among the smallest species (ca. 30 cm maximum total length, Schmidtler & Schmidtler, 1978) of the genus (see *E. coronelloides*). *E. lineomaculatus* is outstanding for a usually single postocular and absence of the loreal, or its small size if present (Tbs 3-4), as well as extremely low ventral (103-119 in ♂♂, 117-132 in ♀♀) and subcaudal (28-38 and 21-33, respectively) counts (Schmidtler & Schmidtler, 1978).

Eirenis decemlineatus and *E. punctatolineatus* possess a posterior reduction from 17 to 15 dsr involving lateral rows. The latter is remarkable for an elevated number of sublabials (9, sometimes 10) in the nominate subspecies (Tbs 3-4); *E. p. kumerloevei* Eiselt sometimes has 8 sublabials (Eiselt, 1976: Tb.; Franzen & Sigg, 1989: Tb. 1). *E. decemlineatus*, with a total length of up to 90 cm by far the largest dwarf snake, has 7-9 sublabials and may have 3 second temporals. Schmidtler & Eiselt (1991) noted that these species are probably not closely related (“vermutlich nicht einmal näher miteinander verwandt”), and that the intraspecific (“geographische”) variation of *E. decemlineatus* requires further studies.

A sloughed skin of an *Eirenis* sp. from Fars Province (Iran, see Material and Methods) lacked the anteriormost portion (including head) and tail tip and could not be identified with certainty. Given the length of the fragment (ca. 65 cm), 17 msr, and clear genetic differences vis-à-vis *E. punctatolineatus* (Fig. 1), it cannot be excluded that the exuvia is from *E. decemlineatus*. Eiselt (1971) noted that this species had not yet been recorded from the vicinities of Shiraz.

The dwarf snake fauna of Iran is not yet well explored as exemplified by *Eirenis medus* (see Material and Methods). It appears that Eiselt’s (1971) reference to *E. decemlineatus* and the presence of this species in “Iran” as noted by Leviton *et al.* (1992) rely on Wall’s (1908) “*Contia*

⁴ Most probably, the alleged absence of a preocular in certain specimens of *Eirenis barani* and *E. levantinus* (Schmidtler, 1993: Tb. 1) is in error.

decemlineata” from Maidan Mihaftan (Masjed Soleyman, Khuzestan). The specimens having “In the posterior part [...] spots [that] become rearranged in longitudinal interrupted lines” most probably belong to *E. punctatolineatus*. This pattern is unknown in *E. decemlineatus* (F. J. Schmidtler in litt. August 2003).

CHARACTER PHYLOGENY

Schätti (2001) regarded the outstanding features of *Coluber* (s.l.) *andreas*, i.e., the low number of supralabial, sublabials, and temporal scales, the occasional absence of an anterior subocular, few dsr, and the absence of posterior reductions (or a single fusion involving paraventral rows) as probably ancestral character states (“wahrscheinlich plesiomorphe Merkmalszustände”). Mostly single preoculars, two supralabials entering the orbit, and the absence of high (paravertebral or vertebral) dsr reductions in most species led Schätti & Utiger (2001) consider *Hierophis* a conservative genus vis-à-vis other Palaearctic as well as Saharo-Sindian and Afrotropical racers and allied genera (*Hemorrhois*, *Platyceps*, and *Spalerosophis* spp.). Although molecular (mtDNA) data of the type species of *Eirenis* Jan (*E. modestus*) suggested sister group relationship of dwarf snakes to eastern Mediterranean *Hierophis* spp., the authors put forward putatively ancestral conditions of external morphology in dwarf snakes, in particular the absence of an anterior subocular and few supralabial and temporal scales.

Schmidtler & Eiselt (1991) considered *Eirenis modestus* with 17 msr a very conservative (“sehr ursprüngliche”) species. Taxa with 15 msr and including mostly small-sized (“eher kleinwüchsig”) species were thought to be more advanced (“fortschrittliche”) dwarf snakes (Docenko, 1989; Schmidtler, 1993: 90). New studies using multivariate analyses (Schmidtler, 1993, 1997) suggest that *E. decemlineatus*, the largest dwarf snake, is a very conservative and systematically isolated taxon (“extreme Außengruppe”, Schmidtler, 1993: 93).

According to Schmidtler (1997), a large loreal (“großes Frenale”) and high degree of fragmentation of the temporals (“hoher Zerfallgrad der Temporalia”) are derived character states. This assertion collides with results showing that *Pseudocyclophis persicus* (loreal absent, 1+1 anterior temporals) is a highly advanced species (see Discussion) as evidenced by an extremely low reduction index (19, Schmidtler, 1993: Tb. 3). The third presumably advanced (“wohl synapomorphe”) condition within dwarf snakes, i.e., the contact of the first temporal with the supralabial bordering the orbit (“häufiger Kontakt 1. Temporale und suboculares Supralabiale”, Schmidtler, 1997: 49), is purely quantitative and highly variable. In the “*Eirenis modestus* complex”, for instance, values range from 0% in *E. m. modestus* and certain populations of *E. m. semimaculatus* (Boettger) to 39% in *E. aurolineatus* (Schmidtler, 1997: Tb. 1, character 15).

In dwarf snakes, the loss (“Verschwinden”) of the loreal (in *Eirenis lineomaculatus* and *Pseudocyclophis persicus*), the number of posterior (!) temporals, and in particular the cranial shift of the dsr reduction from 17 to 15 are correlated with the reduction of total length (“reduktionsrelevante Merkmale”). Dwarfism (“Verzwergung”) also affects the diameter of the eye, width of the frontal, dimensions of the anterior and posterior inframaxillary scales, and, in males, the number of subcaudals.

The number of preocular, postocular, and gular scales are not influenced by this phenomenon (Schmidtler, 1997).

Without anticipating the situation in *Hemerophis socotrae* (Günther), the genera *Hemorrhoids*, *Platycephalus*, and *Spalerosophis*, as well as the unassigned racers *Coluber* (s.l.) *dorri* (Lataste), *C.* (s.l.) *scorteccii* (Lanza), and *C.* (s.l.) *zebrinus* (Broadley & Schätti) from the western Sahel (Sudanese Arid), Somalia, and Namibia, respectively (see Schätti & Utiger, 2001), the morphological and molecular data presented in this study, and in particular the phylogenetic affinities of *C.* (s.l.) *andreanus* and *Eirenis* spp., suggest character polarities for Palaearctic whip and dwarf snakes as listed in Table 4.

TABLE 4. Distribution of character states in dwarf and whip snakes. Taxa and their abbreviations are *Coluber* (s.l.) *andreanus* (A), *Eirenis lineomaculatus* (B), *E. p. punctatolineatus* (C), *Eirenis* spp. (D, see Tb. 3), *Hierophis caspius*, *H. jugularis*, and *H. schmidtii* (E), *H. gemonensis* and *H. viridiflavus* (F), *H. cypriensis* (G), *H. spinalis* (H), and *Pseudocyclophis persicus* (I). Characters (0 for ancestral, 1 for derived condition) are (1) loreal: present (0), absent (1); (2) postocular(s): paired (0), single (1); (3) subocular: present (0), absent (1); (4) sublabials: 9 or more (0), 7 or 8 (1); (5) supralabials: 8 or more (0), 7 (1); (6) first temporal(s): paired (0), single (1); (7) second temporal(s): 2 or 3 (0), single (1); (8) midbody dorsal scale rows: 19 (0), 15-17 (1); (9) posterior reduction(s): 2, rarely 3 (0), 1 or absent (1); (10) apical pits: paired (0), single (1). Conditions found in 95% or more of the individuals per species are shown; not considered are, in particular, the occasional occurrence of a single postocular in *E. medus* (Tb. 3) or rare character states found in other *Eirenis* spp., e.g., a single postocular and two first temporals (*modestus*) or the occasional presence of 9 sublabials (*decemlineatus*, *hakkariensis*, see Dwarf Snakes).

no.	character	A	B	C	D	E	F	G	H	I
1	loreal	0	1	0	0	0	0	0	0	1
2	postocular(s)	0	1	0	0	0	0	0	0	1
3	anterior subocular	0/1	1	1	1	0	0	0	0 (1)	1
4	sublabials	1	1	0 (1)	1	0	0	0	0	1
5	supralabials	1	1	1	1	0	0	0	0	1
6	first temporal(s)	1	1	1	1	0	0	0	0	1
7	second temporal(s)	0 (1)	0 (1)	0	0 (1)	0	0	0	0	1
8	midbody scale rows	1	1	1	1	0	0	1	1	1
9	posterior reduction(s)	1	1	1	1	0	0	0	1	1
10	apical pits	1	1	1	1	0	0	0	0	1

Stickel (1951) and Doczenko (1985: Fig.) studied hemipenis features of *Eirenis modestus* and dentigerous bones (palatinum, pterygoid) of *E. collaris*, *E. modestus* auct., and *Pseudocyclophis persicus*. However, published information about phylogenetically significant osteological (skull, vertebrae) and hemipenis characters are lacking for most dwarf snake species and *Coluber* (s.l.) *andreanus*. According to Sivan & Werner (2003), Shwayat (1998) investigated "hemipenis morphology" of Jordan *Eirenis* spp.

The striking resemblance of *Hierophis jugularis*, *H. viridiflavus*, *Eirenis modestus* (and possibly other dwarf snake species), and Palaearctic ratsnakes as, for instance, *Elaphe schrenckii* Strauch and *Zamenis longissimus* (Laurenti) with respect to hemipenis ornamentation and its bulbous shape (Schätti, 1988: Figs 6-7; Schmidtler & Baran, 1993b: Fig. 55; Utiger *et al.*, 2002: Fig. 5) is most probably based on ancestral

character states. This is also the case with the enlarged basal spine found in *Hierophis* spp. (*cypriensis*, *gemonensis*, *spinalis*), *E. modestus*, and ratsnakes, e.g., *Zamenis lineatus* (Camerano) and species of the genera *Euprepiophis* Fitzinger and *Oreophis* Utiger, Helfenberger & Schätti.

DISCUSSION

Without taking account of the Oriental racer genera *Coelognathus* Fitzinger, *Gonyosoma* Wagler (including, e.g., *Herpetodryas frenatus* Gray and *Coluber prasinus* Blyth), and *Ptyas* Fitzinger (see Utiger, 2002), our molecular approach (Fig. 1) reveals three major evolutionary lineages of Old World colubrids. They are represented by five Palaearctic and Saharo-Sindian genera (*Eirenis*, *Hemorrhois*, *Hierophis*, *Platycephalus*, *Spalerosophis*), Saharo-Sindian leaf-nosed snakes (*Lytorhynchus* spp.), and the Socotra racer (*Hemierophis socotrae*). The uncorrected sequence divergence (p) for 12S rDNA of *H. socotrae* and *Lytorhynchus diadema* is 14%, and, for instance, 10% in the case of *H. socotrae* and *Hierophis viridiflavus*.

The geographically isolated Namibia racer *Coluber* (s.l.) *zebrinus* belongs to a lineage that diverged from the common racer stock prior to the evolution of Afrotropical, Palaearctic, and Saharo-Sindian racers and related genera (Schätti & Charvet, 2003). The sequence divergence (p) vis-à-vis *Hemierophis socotrae* and *Hierophis viridiflavus* is 14.5% and 12%, respectively (unpubl. data).

Whip snakes of the genus *Hierophis* (sensu Utiger & Schätti), *Coluber* (s.l.) *andreas*, and *Eirenis* spp. are monophyletic (Fig. 1). They represent a distinct evolutionary lineage probably including *Pseudocyclophis persicus*.

MtDNA sequences corroborate preliminary molecular data (12S and COI rDNA) for *Eirenis modestus* and the phylogenetic affinities of dwarf snakes, paraphyly of *Hierophis* (sensu Utiger & Schätti), close relationship of *H. cypriensis*, *H. gemonensis*, and *H. viridiflavus*, and sister group status of the western whip snakes to the eastern Palaearctic *H. spinalis* (Schätti & Utiger, 2001; Utiger & Schätti, 2004). Furthermore, the phylogenetic tree (Fig. 1) indicates an early separation of western *Hierophis* spp. from a common ancestor stock giving rise to Palaearctic whip and dwarf snakes and suggests that *Eirenis* spp. are the sister group of *Coluber* (s.l.) *andreas* and the eastern Mediterranean *H. caspius*, *H. jugularis*, and *H. schmidtii*.

With regard to external morphology, European and eastern Mediterranean *Hierophis* spp. show ancestral character states. Most of these species are remarkable for large body size. The smaller *H. cypriensis* and *H. spinalis* are advanced whip snakes on the basis of low msr. The absence of an increase of dsr on the forebody in these taxa (present in congeneric species) is correlated with the number of msr. The single posterior dsr reduction and, rarely, the absence of an anterior subocular in *H. spinalis* are derived conditions.

Apart from Oriental genera (see above), *Hierophis caspius* and *H. jugularis* are the largest Old World racers. The reduction of body size is a remarkable evolutionary trend in Palaearctic whip and dwarf snakes affecting various scale characters as exemplified by the small *Eirenis lineomaculatus*, but not the minuscule *E. coronelloides* (see Dwarf Snakes and Character Phylogeny).

Character state distribution within the ingroup (Tb. 3) suggests that para-vertebral and/or vertebral dsr reductions found in *Hierophis cypriensis* may be derived

conditions. However, the occurrence of high reductions in *H. caspius* (Schätti, 1988) and the criterion of the correlation of transformation series (Hennig, 1979) might favour the opposite view. In the case of the presence of a light vertebral stripe in *H. spinalis*, the outgroup criterion within whip and dwarf snakes supports autapomorphy for this character state. This might also be true for larger female maximum size of *H. spinalis* or the distinct sexual dimorphism of ventral scales in *Coluber* (s.l.) *andreas*. Coloration features including melanism in Mediterranean *Hierophis* spp. are possibly correlated with large body size.

Based on the conditions in *Eirenis collaris*, *E. modestus*, and *Pseudocyclophis persicus* (Docenko, 1985: Fig.), the shape of the lateral processus of the pterygoid in *Hierophis cypriensis* and *H. spinalis* (see Comparative Morphology) may be derived states. The character phylogeny of other osteological conditions found in these species, i.e., high lc/wn and nc/wn ratio, or few pterygoid teeth in *H. spinalis*, are difficult to assess for the lack of comparative material.

On higher systematic levels, the slow evolving 12S rDNA generally provides better results than the protein-coding COI sequence. Although 12S sequence data (Fig. 1) suggest paraphyly of eastern Mediterranean *Hierophis* spp., we consider the generic allocation of *Coluber* (s.l.) *andreas* as debatable. Reservations concerning the association of Andreas' racer with these whip snakes stem from morphological evidence, i.e., a considerable number of derived character states supporting sister group relationship of Andreas' racer to dwarf snakes.

Coluber (s.l.) *andreas*, *Eirenis* spp., and *Pseudocyclophis persicus* have a low number of supralabial (third and fourth bordering eye), sublabial (except *E. p. punctatolineatus*), and anterior temporal scales, the parietal in contact with the lower postocular (see footnote 2), 15-17 msr with single apical pits (Boulenger 1894; Böhme, 1993), and at most one posterior dsr reduction involving lateral or paraventral rows (Tbs 3-4). The occasional absence of an anterior subocular in *C. (s.l.) andreas* is the normal condition encountered in dwarf snakes. Furthermore, the maximum total length of these taxa does not exceed 100 cm.

Assuming the character phylogeny determined for whip and dwarf snakes (Tb. 4), an evolutionary history as indicated by molecular data (Fig. 1) would imply parallelism in *Coluber* (s.l.) *andreas* and *Eirenis* spp., or postulate reversal of the polarity in at least six transformation series (sublabials, supralabials, first temporal, msr, dsr reduction, and apical pits) in both eastern Mediterranean whip snake sections, i.e., *Hierophis jugularis* and *H. caspius - schmidtii*.

Derived conditions of head pholidosis including the occasional absence of an anterior subocular in *Coluber* (s.l.) *andreas* as well as derived dorsal scale features (few msr, at most one posterior dsr reduction, low reduction levels, and single apical pits) advocate monophyly of Andreas' racer, *Eirenis* spp., and *Pseudocyclophis persicus*. The occurrence of few body scale rows (dsr, msr) and lateral (low) reductions in *Hierophis spinalis* are due to parallelism.

Certain derived character states met with in *Coluber* (s.l.) *andreas*, e.g., the absence of a dsr reduction or only 2 (1+1) anterior temporals, are characteristic for *Eirenis africanus*, *E. coronella*, *E. rothi*, and *Pseudocyclophis persicus*. The latter species, morphologically the most strongly advanced dwarf snake, and the minute *E.*

lineomaculatus are distinguished by the absence of a loreal and single postoculars (synapomorphies). Remarkably, *P. persicus* and *C. (s.l.) andreanus* are similar in, for instance, their slender habitus and comparatively high ventral and subcaudal counts.

The dilemma posed by conflicting morphological and molecular data in *Coluber (s.l.) andreanus* calls for field work and further investigation in the laboratory. Certainly, paraphyly of the eastern Mediterranean *Hierophis* spp. and, hence, parallelism in Andreas' racer and *Eirenis* spp. as evidenced by mtDNA sequences cannot be excluded. From the molecular point of view, the systematic position of *C. (s.l.) andreanus* requires confirmation because a non coding sequence (12S rDNA) from a single specimen was analysed, i.e., a nuclear origin cannot be ruled out.

The examination of hemipenis and osteological characters, and more genetic information for *Coluber (s.l.) andreanus* and dwarf snake species such as *Eirenis africanus*, *E. coronella*, *E. lineomaculatus*, and *Pseudocyclophis persicus* are crucial for the understanding of the perplexing results presented in this study and the evolution of morphological characters including body size in Palearctic whip and dwarf snakes.

Taxonomic decisions with regard to Andreas' racer and the paraphyletic whip snake genus *Hierophis* (sensu Utiger and Schätti) are postponed pending further studies.

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