

Review of the Malagasy tree snakes of the genus *Stenophis* (Colubridae)

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Abstract

We provide a review of the tree snakes in the Malagasy genus *Stenophis*, based on examination of types, additional voucher specimens, and field observations. We document live colouration for eight species. The validity of several recently described taxa is considered as questionable here, and three of these are treated as junior synonyms: *Stenophis capuroni* as synonym of *S. granuliceps*, *S. jaosoloa* of *S. arctifasciatus*, and *S. tulearensis* of *S. variabilis*. Also the status of *S. carleti* is uncertain; this taxon is similar to *S. gaimardi*. In contrast, some additional species may be recognized in the future. The available material of *S. betsileanus* contains large and small specimens with a distinct size gap (275-315 vs. 920-985 mm snout-vent length). A specimen from Benavony in north-western Madagascar is characterized by a unique combination of meristic and chromatic characters, probably indicating taxonomic distinctness. *Stenophis inopiniae* shares more characters with species classified in the subgenus *Stenophis* (17 dorsal scale rows, relatively short tail, low number of subcaudal scales, iris colouration) than with the subgenus *Phisalixella*, indicating that its current classification should be evaluated.

Some species seem to be closely related species pairs with allopatric distributions: *Stenophis gaimardi* (east) and *S. carleti* (south-east), *S. granuliceps* (north-west) and *S. pseudogranuliceps* (west), *S. arctifasciatus* (east) and *S. variabilis* (west).

Key words: Squamata: Serpentes: Colubridae: *Stenophis*; taxonomy; distribution; Madagascar.

1 Introduction

The colubrid snakes of Madagascar comprise 18 genera (GLAW & VENCES 1994, CADLE 1999). Among the most peculiar and less known of these is the genus *Stenophis*. Together with *Langaha*, these nocturnal species are among the most arboreal-specialized snakes in Madagascar. They are conspicuous in being elongated, often very thin, and usually have large eyes with slit-like vertical pupils (prolate pupils sensu CADLE 1996b).

Until recently, *Stenophis* was considered as junior synonym of the genus *Lycodryas*. DOMERGUE (1995) argued that the name *Lycodryas* should be restricted to the Comoran species, whereas he resurrected the genus *Stenophis* for the Malagasy taxa. Some authors, however (e. g., NUSSBAUM et al. 1999, RASELIMANANA et al. 2000), continue to consider the Madagascan species as belonging to *Lycodryas*.

In fact, whereas some colubrid snake genera from Madagascar were revised or reviewed in the last 20 years by DOMERGUE (1986, 1987), RAXWORTHY & NUSSBAUM (1994), CADLE (1996a, b, 1999), ZIEGLER et al. (1997), ANDREONE & RAXWORTHY (1998) and NUSSBAUM & RAXWORTHY (2000a), no recent comprehensive account exists on the genus *Stenophis*. Over ten years ago, C.A. DOMERGUE had written a manuscript with detailed descriptions of eight new *Stenophis* species, but unfortunately this paper was never published (C.A. DOMERGUE in litt.). Feeling urge for making the new names available, this author then published a preliminary diagnosis (DOMERGUE 1995) which very briefly described the new species, resurrected the genus *Stenophis*, and divided it into three subgenera, without any illustration or detailed morphological account.

Because many *Stenophis* are restricted to forest habitats, and some may indeed be local endemics deserving special attention in conservation efforts, we feel that a better knowledge on this genus is badly needed. We therefore revised most of the type

material of the genus and all additional material available to us. In the present paper we summarize the information we gathered during our field surveys, and also update the species' diagnoses by morphology and general colouration. The aim of this paper, therefore, is not to be an exhaustive genus revision: rather, we would like to provide some crucial information and to stress some key problems. We are aware that we did not examine several important characters, such as hemipenial morphology and gular scale arrangement, and emphasize that a more in depth revisionary work, extended also to genetic methods and species inhabiting the Comoro Islands (genus *Lycodryas*), is needed.

2 Materials and Methods

Preserved specimens were examined for standard morphometric and meristic characters as given in table 1. Museum acronyms used are: BMNH, The Natural History Museum, London; MNHN, Museum national d'Histoire naturelle, Paris; MRSN, Museo Regionale di Scienze Naturali, Torino; MZUT, Museo di Zoologia dell'Universita di Torino (collection now housed at the MRSN); SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt; UADBA, Université d'Antananarivo, Département de Biologie Animale; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; ZSM, Zoologische Staatssammlung München. For abbreviations of variables, see captions to tables 1 and 2. Information on distribution is taken from the specimens examined by us; considering the unsolved taxonomy and different schemes used by various authors, we used published locality data only when we considered the identification of the species reported as sufficiently reliable.

3 Results

Genus *Stenophis* BOULENGER, 1896

The genus *Stenophis* was erected by BOULENGER (1896) to accommodate a number of arboreal snake species from Madagascar. Subsequently, the same author (BOULENGER 1915) accepted *Stenophis* as a valid genus besides *Lycodryas*, which contained a snake species from the Comoro islands. GUIBÉ (1958) synonymised *Stenophis* with *Lycodryas*. DOMERGUE (1995) considered the two genera as different without providing any formal justification, but in an unpublished manuscript (C.A. DOMERGUE, in litt.) he emphasized the existence of strong hemipenial divergence of *Lycodryas* as compared to species of *Stenophis*. These presumed hemipenial differences need further study and documentation; anyhow, we here tentatively follow the arrangement of *Stenophis* as separate genus which is also in agreement with taxonomic databases (e. g., Reptiliaweb and Genbank, as of June 2003).

Subgenus *Stenophis* BOULENGER, 1896

According to DOMERGUE (1995), this subgenus is characterized by having 17 rows of dorsal scales, with the vertebral row not being conspicuously enlarged, all or part of the subcaudal scales divided, and a deeply bifurcated hemipenis (only ascertained in one species). At least the character of subcaudal scales, however, is not fully diagnostic, because in several species (*S. gaimardi*, *S. carleti*, *S. citrinus*) specimens with completely undivided subcaudals do occur.

The tail is relatively short (24-41 % of SVL, see Tab. 1). DOMERGUE (1995) designated his new *Stenophis pseudogranuliceps* as type species of this subgenus,

although this species was clearly not one of the “originally included nominal species” as required by Article 67.2 of the International Code of Zoological Nomenclature (fourth edition).

Stenophis gaimardi (SCHLEGEL, 1837)

This species is characterized by a light brown colouration with dark brown, very distinct crossbands that are not or very faintly bordered by white (Fig. 1a). It is among the *Stenophis* with highest ventral counts (266-284: Tab. 1-2). This species is known from low-altitude localities along the central and northern east coast of Madagascar.

Stenophis carleti DOMERGUE, 1995

This taxon is similar to *S. gaimardi*, and only appears to differ by its lower counts of ventrals (252-258) and subcaudals (97). It seems an allopatric relative or variant of *S. gaimardi*, occurring in south-eastern Madagascar only (Tolagnaro and Manakara regions).

Stenophis sp.

One specimen from Benavony (Fig. 1b), next to Ambanja in the north-west (ZSM 404/2000), agrees with *S. gaimardi* and *S. carleti* in the number of the crossbands, but differs by its lower ventral count (238) and by the shape of the crossbands. In its undivided subcaudals and colouration, this specimen also differs clearly from *S. granuliceps* and *S. pseudogranuliceps* which likely occur in the same area. *Stenophis inopiniae* (see below) is similar by meristic values (see Tab. 2), but has a much less distinct colouration without dark crossbands. Unfortunately, the tail of ZSM 404/2000 is incomplete so that the character states in subcaudals, relative tail length, and crossband number cannot be ascertained with full reliability. This specimen may represent a new species, but further material is needed to ascertain its status.

Stenophis pseudogranuliceps DOMERGUE, 1995

This species includes the *Stenophis* with distinct brown crossbands from western Madagascar (Fig. 1e) and is poorly differentiated from *S. granuliceps* (see below). By general pattern it is also similar to *S. gaimardi* and *S. carleti*, but it differs by having all subcaudal scales divided (vs. not or partly divided), and by its lower number of ventral scales (220-239). It is known from a wide array of localities between Ankara-fantsika and Tolagnaro. The dark crossbands are sometimes bordered by white, especially in larger specimens, but they are usually regularly arranged.

Stenophis granuliceps BOETTGER, 1877

This species was originally described from Nosy Be. The material that we examined and that we assigned to *S. granuliceps* (Tab. 1) is characterized by a rather low ventral scale count (224-245), and by having all subcaudals divided. A larger size and a higher number of crossbands (99-113) that are usually rather irregularly shaped and bordered by white in large specimens (Fig. 1d), are the major difference to *S. pseudogranuliceps* (although the holotype of this taxon also has 99 crossbands). In juveniles the crossbands are more regular (Fig. 1c). We also consider a number of other specimens from north-western and northern Madagascar as belonging to *S. granuliceps*, and thereby extend its distribution area beyond the offshore island Nosy Be: The individuals from Sahamalaza, Antsiranana, and Montagne des Français agree in number and state of crossbands with Nosy Be specimens (Tab. 1), and we therefore consider them

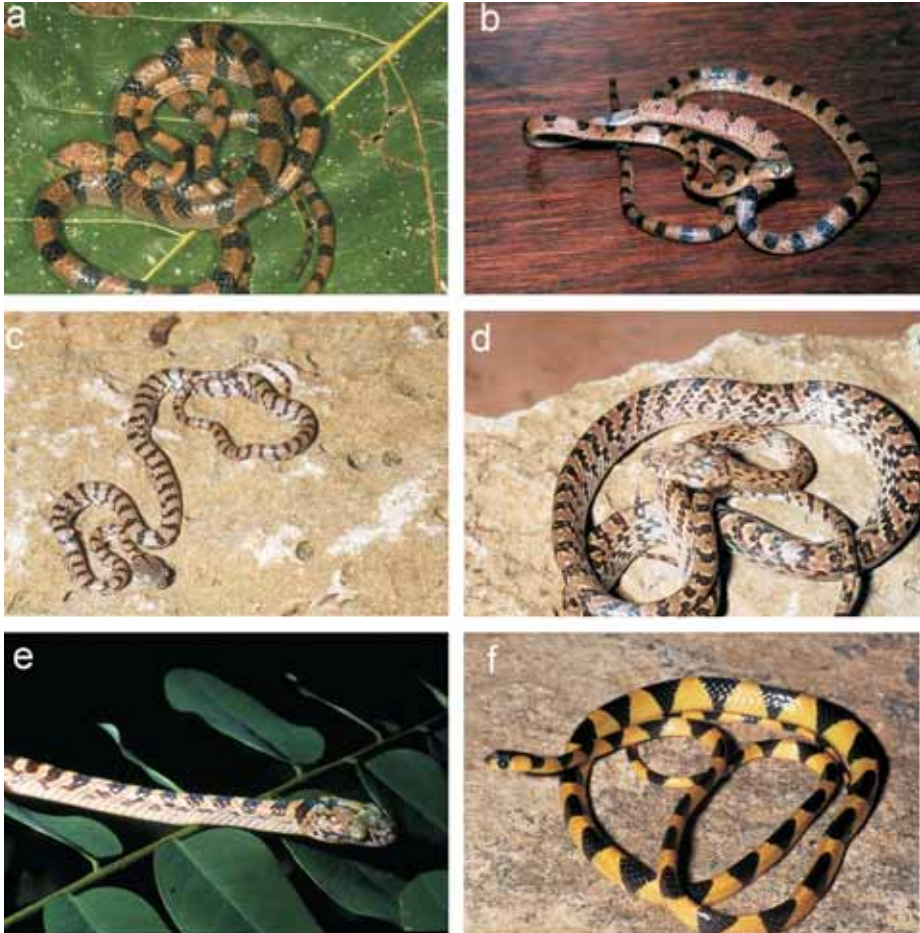


Fig. 1. Colour photos of *Stenophis* specimens assigned to the subgenus *Stenophis* / Farbabbildungen von *Stenophis*-Exemplaren aus der Untergattung *Stenophis* sensu DOMERGUE (1995): (a) *Stenophis gaimardi* (not collected / nicht gesammelt), Marojejy. (b) *Stenophis* sp. (ZSM 404/2000), Benavony. (c) *Stenophis granuliceps*, juvenile, near Antsiranana (UADBA; field number FG/MV 2000.325). (d) *Stenophis granuliceps* (ZSM 550/2000), Montagne des Français. (e) *Stenophis pseudogranuliceps* (not collected; identification not verified / nicht gesammelt, Bestimmung nicht überprüft), Ampijoroa. (f) *Stenophis citrinus*, Kirindy (ZFMK 59794).

as *S. granuliceps* rather than *S. pseudogranuliceps*. However, it must be mentioned that the specimens from the northernmost localities (Antsiranana and Montagne des Français) resemble *S. pseudogranuliceps* in having fewer ventral scales (Tab. 1). Adults of *S. granuliceps* seem to have relatively small eyes (see Fig. 3b).

One recently described species from the same region in north-western Madagascar is *Stenophis capuroni* DOMERGUE, 1995. The holotype and sole specimen however, is similar to *S. granuliceps* in many characters. There are no regular crossbands, but



Fig. 2. Colour photos of *Stenophis* specimens assigned to the subgenera *Phisalixella* (a-d) and *Parastenophis* (e-f) / Farbabbildungen von *Stenophis*-Exemplaren aus den Untergattungen *Phisalixella* (a-d) und *Parastenophis* (e-f) sensu DOMERGUE (1995). (a) *Stenophis arctifasciatus*, Andasibe (ZSM 231/2002). (b) *Stenophis variabilis*, Kirindy (UADBA). (c) *Stenophis inopiniae*, Montagne des Français (ZSM 551/2000 or 552/2000). (d) specimen from Ankarana (not collected / nicht konserviert; photo B. LOVE) that probably represents / wahrscheinlich *Stenophis inopiniae*. (e) *Stenophis betsileanus*, “giant” specimen, Marojejy (ZFMK 60500). (f) *Stenophis betsileanus*, Masoala Corridor (MRSN R1973).

irregular markings, very similar in this to the state in large *S. granuliceps* that also lose the crossband pattern. The main difference is a relatively high number of ventrals (257 vs. 245 in the specimen with highest count from Nosy Be). Two further distinctive features discussed by C. DOMERGUE in an unpublished manuscript available to us, and verified by us in the type, are the postgulars which are separated by two pairs of small scales, and the sixth supralabial which is fused with a scale usually located above it. We do not believe that these characters are sufficient to accept *capuroni* as separate species and therefore consider it as junior synonym of *S. granuliceps*.

Catalogue	Number	Locality	SVL	TaL	V	TaL/ SVL	SC	CB
<i>Stenophis carleti</i>								
MNHN	1988.322 (PT)	Tolagnaro region	605	167	258	0.28	97	90
MNHN	1988.321 (HT)	Haute Mananono, Manakara	550	(70)	252	(0.13)	(46)	(70)
MNHN	1895.233	SE coast, Madagascar	240	59	255	0.25	97	77
<i>Stenophis gaimardi</i>								
MNHN	1978.2916	Maroantsetra	675	162	284	0.24	117	82
MNHN	3869	Madagascar	610	162	266	0.27	106	77
MNHN	3868 (HT)	Madagascar	445	118	269	0.27	105	85
MNHN	1978.2918	probably Maroantsetra	347	82	279	0.24	116	86
MZUT	R3564-2	Moramanga	297	80	271	0.27	111	86
MZUT	R3564-1	Moramanga	594	(145)	283	(0.24)	(98)	(76)
ZFMK	21819	Toamasina	614	157	275	0.26	113	72
<i>Stenophis</i> sp.								
ZSM	404/2000	Benavony	458	(73)	238	(0.16)	(45)	(66)
<i>Stenophis pseudogranuliceps</i>								
MNHN	1978.42 (HT)	Ampijoroa	564	146	234	0.26	117	99
MNHN	1961.647	Ampijoroa	543	150	237	0.28	103	96
MNHN	1977.1061	Ampijoroa	345	118	231	0.34	114	91
MNHN	1988.324	Beroboka	523	153	227	0.29	101	86
MNHN	1978.2917	Marofandilia	500	136	227	0.27	96	84
MNHN	1906.119	Toliara	438	149	225	0.34	115	88
MNHN	1929.177	Fiherenana valley	450	164	226	0.36	118	84
MNHN	1899.401	Toliara environments	365	116	220	0.32	97	76
MNHN	1901.225	Tolagnaro	325	93	221	0.29	95	73
MNHN	1901.392	Befaisitra	468	136	229	0.29	103	79
MNHN	1929.178	Maroamalona	475	153	225	0.32	108	82
MNHN	1992.5331	Marofandilia	181	52	232	0.29	103	69
MNHN	1992.5330	Marofandilia	170	42	234	0.25	75	70
MNHN	1992.5329	Marofandilia	174	49	220	0.28	101	67
MNHN	1420	Madagascar	445	135	239	0.30	110	82
<i>Stenophis granuliceps</i>								
SMF	19612 (HT)	Nosy Be	760	223	238	0.29	108	99
MNHN	1887.260	Nosy Be	545	174	237	0.32	115	103
MNHN	1966.960	Nosy Be	785	(128)	242	(0.16)	?	?
ZFMK	17738	Antsiranana	774	207	231	0.27	99	104
ZSM	550/2000	Montagne des Français	605	180	224	0.30	103	113
ZSM	553/2000	Montagne des Français	400	131	224	0.33	122	105
MRSN	R1974	Nosy Be	400	130	245	0.33	120	102
MRSN	R1832	Sahamalaza	374	125	245	0.33	116	103
MNHN	1988.325 (HT <i>capuroni</i>)	Ankarana	892	(128)	257	(0.14)	(96)	100
<i>Stenophis guentheri</i>								
MNHN	1978.2914	Itremo	420	100	209	0.24	75	103
MNHN	1950.161	Ambovombe	322	106	204	0.33	94	105
MNHN	7825	Madagascar	262	72	188	0.27	81	92
BMNH	1946.1.2.53 (HT)	SW Madagascar	349	91	185	0.26	70	86
<i>Stenophis arctifasciatus</i>								
MNHN	1950.162	Madagascar	622	239	246	0.38	166	115
MNHN	1901.72	Moramanga	590	284	225	0.48	???	116
MNHN	3870 (HT)	Madagascar	296	138	228	0.47	155	116
MNHN	1930.372	Tananarive	198	77	214	0.39	144	100
MRSN	R1971	Tsararano	594	306	240	0.52	179	142
MRSN	R1972	Moramanga-Zahamana	406	194	247	0.48	177	124
ZSM	231/2002	Andasibe	537	235	238	0.44	154	(98)
MNHN	1988.323 (HT <i>jaosoloa</i>)	Andasibe	587	318	234	0.54	158	104

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<i>Stenophis variabilis</i>							
BMNH	1946.1.7.10 (ST)	Madagascar	389	148	253	0.38	151 139
BMNH	1946.1.7.11 (ST)	Madagascar	835 (257)	251 (0.31)	(104)	(118)	
MNHN	1988.337	Toliara, pK32	890	365	266	0.41	165 132
MNHN	1988.318	Andranovory-Tulear	735	314	257	0.43	156 105
MNHN	1994.3138	Ankarafantsika	1060	437	275	0.41	166 128
MNHN	1950.371	Nosy Be	730	345	244	0.47	154 0
MNHN	1988.319 (HT <i>tulearensis</i>)	Ampijoroa	1049 (275)	278 (0.26)	(98)	0	
<i>Stenophis iarakaensis</i>							
MNHN	1988.320 (HT)	Iharaka	199	91	235	0.46	157 129
<i>Stenophis inornatus</i>							
MNHN	1421	Madagascar	380	155	210	0.41	110 0
MNHN	1977.1062	Zampongotra	470	177	229	0.38	114 0
BMNH	1946.1.7.9 (HT)	unknown	405	146	234	0.36	106 0
<i>Stenophis inopiniae</i>							
MNHN	1950.160 (HT)	Antongobato	455	164	238	0.36	113 90
ZFMK	62200	Ankarana	478 (52)	248 (0.11)	(33)	(75)	
ZSM	551/2000	Montagne des Français	344	110	223	0.32	108 104
ZSM	552/2000	Montagne des Français	332	105	235	0.32	111 111
<i>Stenophis citrinus</i>							
MNHN	1978.2790 (HT)	Beroboka	310	95	254	0.31	126 57
ZFMK	59794	Kirindy	535	170	243	0.32	111 50
ZSM	923/2000	unknown	351	107	239	0.30	115 58
<i>S. betsileanus</i> "small"							
MNHN	1903.225	Ambositra	285	80	212	0.28	93 47
MNHN	1978.1423	Nosy Mangabe	315 (84)	211 (0.27)	(90)	(48)	
MRSN	R1145	Andohahela	275	80	229	0.29	100 52
MRSN	R1973	Masoala	290	80	209	0.28	105 44
<i>S. betsileanus</i> "giant"							
ZFMK	63175	Ranomafana	920	215	233	0.23	77 41
ZFMK	60500	Marojejy	920	255	234	0.28	93 ?
MRSN	R1975	Masoala	948	285	231	0.30	88 0
MRSN	R1976	Masoala	945 (205)	236 (0.22)	(64)	0	
MNHN	1996.7432	uncertain	985	305	233	0.31	103 49

Tab. 1. Measurements (in mm) and meristic data of *Stenophis* specimens examined. Abbreviations used: HT, holotype; PT, paratype; ST, syntype; SVL, snout-vent length; TaL, tail length; V, number of ventral scales; SC, number of subcaudal scales; CB, number of crossbands on body and tail. Values in parentheses refer to incomplete data, mostly due to mutilated tails.

Morphometrische (in mm) und meristische Angaben zu den untersuchten *Stenophis*-Exemplaren. Verwendete Abkürzungen: HT, Holotypus; PT, Paratypus; ST, Syntypus; SVL, Kopf-Rumpflänge; TaL, Schwanzlänge; V, Anzahl Ventralia; SC, Anzahl Subcaudalia; CB, Anzahl von Querbändern auf Körper und Schwanz. Zahlen in Klammern beziehen sich auf unvollständige Angaben, meist bei Individuen mit unvollständigen Schwänzen.

Stenophis inornatus BOULENGER, 1896

As indicated by its name, this species has a uniform colouration without crossbands. The origin of the type is uncertain, but one MNHN specimen comes from Zampongotra, indicating a distribution in western Madagascar. From data in Tab. 2 it is conspicuous that this species has no convincing meristic differences to *S. pseudogranuliceps*, although the relative tail length of *S. inornatus* is slightly larger. *S. inornatus* differs from *S. inopiniae* by at least partially divided subcaudals.



Fig. 3. Head portraits of species of *Stenophis* / Kopfportraits verschiedener *Stenophis*-Arten. (a) *Stenophis gaimardi*, Marojejy (UADBA); (b) *Stenophis granuliceps*, Montagne des Français (ZSM 550/2000); (c) *Stenophis* sp., Benavony (ZSM 404/2000); (d) *Stenophis citrinus*, Kirindy (ZFMK 59794); (e) *Stenophis arctifasciatus*, Andasibe (ZSM 231/2002); (f) *Stenophis arctifasciatus*, Tsararano (MRSN R1971); (g) *Stenophis variabilis*, Kirindy (UADBA); (h) *Stenophis betsileanus*, Andohahela (MRSN R1145); (i) *Stenophis betsileanus*, “giant” specimen, Marojejy (ZFMK 60500).

Stenophis guentheri BOULENGER, 1896

This species is known from southern and central Madagascar. Among the species with 17 dorsals, it is recognizable by its lack of distinct crossbands (only vertebral markings), and low number of ventrals (the lowest number in any *Stenophis*). Beside the holotype from SW-Madagascar, two MNHN specimens with locality data were available for examination (from Itremo and Ambovombe), and NUSSBAUM et al. (1999) quote the species from Beraketa.

Stenophis citrinus DOMERGUE, 1995

This is certainly the most distinctive *Stenophis* species (Fig. 1f). Its bright yellow colour with comparatively few (50-57) deep black crossbands leave no possibility of misidentification. The iris is black as well. Besides Beroboka and Kirindy, the species has been recorded from a third site in western Madagascar, the Tsingy de Bemaraha (SCHIMMENTI & JESU 1997). VENCES et al. (1998) reported on live-bearing in this snake.

Subgenus *Phisalixella* DOMERGUE, 1995

According to DOMERGUE (1995) this subgenus is recognized by 17-25 rows of dorsal scales, the vertebral row and some paravertebral rows being distinctly enlarged in comparison to the other dorsal rows. Subcaudals are undivided (except for *S. iarakaensis*) and a biapical trilobed hemipenis is present in at least three species. The tail is relatively long (38-54 % of SVL if *S. inopinae* is excluded, see Tab. 1)

Stenophis arctifasciatus (DUMÉRIL, BIBRON & DUMÉRIL, 1854)

This species is characterized by 21 dorsal scale rows, a rather distinct blackish crossband around the neck and indistinct dark crossbands at the rest of the body and tail (Fig. 2a). The live colouration is yellowish to reddish, and the iris has a reddish-orange shade as well. This species is known from central-eastern Madagascar (Andasibe-Moramanga region). A specimen from the north-east (Tsararano Forest) is also attributed to this species although differing by a larger number of crossbands (142 vs. 100-124 in the other specimens). However, this specimen fits the remaining characters, and thus is here assigned to *S. arctifasciatus*. RAXWORTHY (1988) further reports on a finding from Nosy Mangabe on the east coast.

Stenophis jaosoloa DOMERGUE, 1995 was described from Andasibe in central-eastern Madagascar, based on a single large specimen that in the original description was already said to be closely related to *S. arctifasciatus*. Actually, the meristic characters of this species fall within the range of *S. arctifasciatus*. The only difference, according to the original description, is the shape of the temporal scale that is “*unique très étroite, serrée entre la pariétale et les 6è et 7è labiales supérieures qui sont particulièrement hautes.*” Upon examination, we did not observe any pattern of head scalation that would be so striking to justify placing this specimen into a different species. Because *S. arctifasciatus* also occurs at Andasibe, we here consider *S. jaosoloa* as a junior synonym of that species. It should be mentioned that a wrong catalogue number of the *jaosoloa* holotype was given in the original description (MNHN 1988.360 instead of the correct number MNHN 1988.323).

Stenophis variabilis BOULENGER, 1896

One of the type specimens (BMNH 1946.1.7.10) has a variable number of scale rows at midbody (23-25) and the anal scale is divided in some specimens but undivided in others (a unique trait in *Stenophis*). This unusual variability probably explains the name of this species. The colour pattern of the types is similar to *S. arctifasciatus* (Fig. 2b).

Stenophis tulearensis DOMERGUE, 1995 was described from western and south-western Madagascar. The holotype and other specimens in the MNHN collection assigned by C.A. DOMERGUE to this species largely agree with the *S. variabilis* types in pattern and meristic characters (although the holotype has a higher number of ventrals). We therefore herein consider *S. tulearensis* as a junior synonym of *S. variabilis*. Two inconsistencies of the original description of *S. tulearensis* should be mentioned. The name *tulearensis* refers to Toliara in south-western Madagascar, although the holotype was not collected in this area; specimens from Toliara were intended to become paratypes as obvious from the MNHN catalogue, but were not listed in the original description. The original description mentions the holotype and six studied specimens; it is not clear whether this number includes the holotype or not, and which specimens are referred to. More research in the MNHN collection is necessary to understand which specimens can be considered to be paratypes of *S. tulearensis*. Furthermore, the catalogue number of the holotype given in the original description (MNHN 1988.379) is wrong and a misspelling of 1988.319.

A questionable specimen with 23 dorsals, but in a rather bad state of preservation (colour completely faded) is known from Nosy Be (MNHN 1950.371).

Species	N	D	V	SC	CB	A	SC div	SUPL	INFL	POOC	PROC	LOR
<i>S. carleti</i>	3	17	252-258	97	77-90	2	no or partly	8	9	3	1	1
<i>S. gaimardi</i>	7	17	266-284	105-117	72-86	2	no or partly	7-8	9	2-3	1-2	1
<i>S. sp.</i>	1	17	238	(45)	(68)	2	no	8	8	3-4	2	1
<i>S. pseudogramuliceps</i>	16	17	220-239	75-118	67-99	2	all	7-8	6-10	2-3	1-2	1
<i>S. granuliceps</i>	7	17	224-245	99-122	99-113	2	all	8-9	9-10	3	1-2	1
(<i>S. capuroni</i> HT)	1	17	257	(96)	100	2	all	8	10	3	2	1
<i>S. guentheri</i>	4	17	185-209	70-94	86-105	2	partly or all	8-9	9	3	1-2	0-1
<i>S. inornatus</i>	3	17	210-234	106-114	0	2	partly or all	8	9-10	3	1	1
<i>S. citrinus</i>	3	17	239-254	111-126	50-58	2	no or partly	8	9	3	2	1
<i>S. arctifasciatus</i>	7	21	214-247	144-179	100-142	2	no	7-9	10-13	3	1-2	1
(<i>S. jaosoloa</i> HT)	1	21	234	158	104	2	no	8	9-11	3	1	1
<i>S. variabilis</i>	6	23-25	244-275	151-166	105-132	1-2	no	8	10-12	2-3	1-2	1
(<i>S. tulearensis</i> HT)	1	25	278	(98)	—	2	no	9	12	2-3	1	1
<i>S. inopiniae</i>	4	17	223-248	108-113	75-111	2	no	8-9	9-10	3	1-2	1
<i>S. iarakaensis</i>	1	19	235	157	129	2	all	7-8	10-11	5-6	3	1
<i>S. betsileanus</i> "small"	4	23	209-229	93-105	44-52	2	all	6-8	10	2	2	0
<i>S. betsileanus</i> "giant"	5	23	231-236	77-103	41-49	2	all	7-8	10	2	2	0

Tab. 2. Summary of meristic data of *Stenophis* species, based on material examined by us only (Tab. 1). Abbreviations used: N, number of specimens studied; D, number of dorsal scale rows at midbody; V, number of ventral scales; SC, number of subcaudal scales; CB, number of crossbands on body and tail; A, anal scale (2, divided; 1, undivided); SC div, divided state of subcaudals; SUPL, number of supralabials; INFL, number of infralabials; POOC, number of postoculars; PROC, number of preoculars; LOR, number of loreals. Values in parentheses refer to incomplete data due to mutilated tails. Values of the holotypes (HT) of *S. capuroni*, *S. jaosoloa* and *S. tulearensis* are given separately in parentheses to show that they largely fall within the range of *S. granuliceps*, *S. arctifasciatus* or *S. variabilis* of which these taxa are herein considered to be synonyms.

Zusammenfassung meristischer Daten bei *Stenophis*-Arten, basierend auf den von uns untersuchten Exemplaren (Tab. 1). Verwendete Abkürzungen: N, Anzahl untersuchter Exemplare; D, Anzahl Dorsalia; V, Anzahl Ventralia; SC, Anzahl Subcaudalia; CB, Anzahl Querbändern auf Körper und Schwanz; A, Analschuppe (2, geteilt; 1, ungeteilt); SC div, Vorhandensein geteilter Subcaudalia; SUPL, Anzahl Supralabialia; INFL, Anzahl Infralabialia; POOC, Anzahl Hinteraugenschuppen; PROC, Anzahl Schuppen vor dem Auge; LOR, Anzahl Lorealschuppen. Angaben in Klammern beziehen sich auf Exemplare mit unvollständigem Schwanz. Die Werte der Holotypen (HT) von *S. capuroni*, *S. jaosoloa* und *S. tulearensis* werden (in Klammern) separat angegeben, um zu zeigen, dass sie weitgehend innerhalb der Variabilität von *S. granuliceps*, *S. arctifasciatus* beziehungsweise *S. variabilis* liegen, als deren Synonyme sie hier aufgefasst werden.

Stenophis inopiniae DOMERGUE, 1995

This species was described without locality data, but according to the MNHN catalogue the holotype originates from Antongo[n]bato (located in the Antsiranana region according to an unpublished manuscript of C.A. DOMERGUE and apparently identical with Antongobato or Antongombato, both apparently synonyms and located at 12°22'S, 49°13'E, 147 m alt [<http://www.calle.com/world/>]). Further specimens tentatively assignable to this species come from Ankarana and Montagne des Français (Fig. 2 c-d). This is the only species assigned to the subgenus *Phisalixella* with 17 rows of dorsal scales. This assignment by DOMERGUE (1995) apparently purely relied on its enlarged vertebral scale row, but the significance of this character to place *S. inopiniae* apart from other species with 17 dorsals (in the nominal subgenus *Stenophis*) is uncertain. In life, *S. inopiniae* is characterized by a yellowish to light brown colour with a row of dark vertebral spots (Fig. 2c) that can be almost unrecognizable in some specimens (Fig. 2d).

Stenophis iarakaensis DOMERGUE, 1995

This is the only *Stenophis* with 19 rows of dorsal scales, beside the enigmatic *Stenophis maculatus* which is of unknown origin (BOULENGER 1896). The single specimen was described from Hiaraka [= Iaraka or Iharaka], near Maroantsetra in north-eastern Madagascar. It is the only *Phisalixella* in which all subcaudals are divided. It has a relatively large number of dark crossbands (129). The holotype is a juvenile of small size. Apart from the meristic characters, it is rather similar in colouration to *S. arctifasciatus*, namely to the specimen MRSN R1971 from Tsararano (a locality not so far from Hiaraka). The holotype of *S. iarakaensis* shares a typical nuchal collar, which reminds that visible in MRSN R1971. However, its deviant number of dorsals, the fully divided subcaudals (all undivided in *S. arctifasciatus*), and the high number of postoculars and preoculars (unique in the genus, see Tab. 2) may be significant characters corroborating the specific status of *S. iarakaensis*.

Subgenus *Parastenophis* DOMERGUE, 1995

This subgenus was erected for a single species, *S. betsileanus*, which is the only one with constantly 23 dorsal scale rows, the vertebral and paravertebral rows not being distinctly enlarged. Subcaudals are divided and the hemipenis is thick and biapical (DOMERGUE 1995). The tail is short (23-31 % of SVL, see Tab. 1).

Stenophis betsileanus (GÜNTHER, 1880)

This species can be recognized by the absence of a loreal scale (or, defined in a different way, by the loreal being in contact with the eye). It is also the only species (besides some specimens of *S. variabilis*) with 23 dorsal scale rows. Typically the species has a black to dark brown colour with 41-52 white narrow crossbands (Fig. 2f). The iris is black (Fig. 3). Among the specimens available to us, there is a huge gap in size classes (see also GLAW & VENCES 1996). Some specimens measure 920-985 mm in snout-vent length, whereas others measure 275-315 mm. It is uncertain whether there small specimens of *Stenophis betsileanus* are actually adults. However, it can be excluded that the differences reflect a simple sexual dimorphism. Both groups contain males as recognizable by everted hemipenes (MNHN 1978.1423, 315 mm SVL, and MRSN R1975, 948 mm SVL), although in the smaller specimens these organs are relatively small. Whereas the small specimens always have distinct white bands on a blackish body (Fig. 2f), the large specimens are usually more brownish and often lack

Species	Crossbands	Crossbands dark vs. light	Ventral colour (belly)	Ventral colour (tail)
<i>S. carleti</i>	distinct; not bordered by white	equal or less wide	uniform or indistinctly spotted	with dark markings
<i>S. gaimardi</i>	distinct; usually not bordered by white	less wide	uniform light or indistinctly spotted	uniform light or with dark markings
<i>S. sp. (Benavony)</i>	distinct; not bordered by white	less wide	dirty spotted	dirty spotted
<i>S. pseudogranuliceps</i>	distinct; sometimes bordered by white	usually wider or equal	uniform light	with dark markings
<i>S. granuliceps</i>	irregular; bordered by white	less wide	usually uniform light	with dark markings
<i>S. guentheri</i>	vertebral spots only; not bordered by white	less wide	uniform light	with dark markings
<i>S. inornatus</i>	largely inexistant	largely inexistant	uniform light	uniform light
<i>S. citrinus</i>	very distinct, not bordered by white	equal	regular crossbands continued from dorsum	regular crossbands continued from dorsum
<i>S. arcifasciatus</i>	indistinct, not bordered by white	less wide	uniform light or dark marbling	uniform light or dark marbling
<i>S. variabilis</i>	indistinct, not bordered by white	less wide	uniform light	uniform light or dark marbling
<i>S. inopiniae</i>	vertebral spots only; not bordered by white	less wide	uniform light	uniform light
<i>S. iarakensis</i>	distinct, not bordered by white	less wide	uniform light	with dark markings
<i>S. betsileanus</i> "small"	very distinct, white	wider or less wide	regular crossbands continued from dorsum	regular crossbands continued from dorsum
<i>S. betsileanus</i> "giant"	absent or distinct, white	if present, wider	uniform brownish or crossbands continued	uniform brownish or crossbands continued

Tab. 3. Summary of relevant colour characters of *Stenophis* species / Zusammenfassung wichtiger Färbungs- und Zeichnungsdaten der als valide angesehenen *Stenophis*-Arten.

distinct crossbands (Fig. 2e) although bands are present in two out of five specimens. The number of ventral scales is higher in the available sample of large specimens (231-236 vs. 209-229). The holotype of *S. betsileanus* (BMNH 1946.1.2.51) measures 310 mm SVL and has 227 ventrals, thus perfectly agreeing with our sample of small specimens (GLAW & VENCES 1996). We were unable to find any additional meristic difference between the two groups. Both large and small specimens are known from a rather large area in eastern Madagascar: Andohahela, Ambositra, Masoala, Nosy Mangabe (small specimens), Ranomafana, Masoala, Marojejy (large specimens). We consider the locality Nosy Be given on a MNHN label for one large specimen (MNHN 1996.7432) as in need of confirmation. A further locality is Andasibe (RAXWORTHY 1988).

4 Discussion

The data provided here show that the systematics of *Stenophis* is far from being resolved. Three recently described species are considered as junior synonyms of other, well established species: *Stenophis capuroni* as a synonym of *S. granuliceps*, *S. jaosoloa* of *S. arctifasciatus*, and *S. tulearensis* of *S. variabilis*. The status of *S. carleti* is still uncertain because its differences to *S. gaimardi* are relatively low and the differentiation between *S. granuliceps* and *S. pseudogranuliceps* is weak as well, although we tend to consider these two as distinct species. On the other hand, a number of additional species may be recognized in the future. As an example, the unassigned *Stenophis* from Benavony in north-western Madagascar may represent a local endemic, and the presence of specimens of distinctly different size and slightly different number of ventrals within *S. betsileanus* claims for an explanation either in terms of taxonomy or of unusual natural history patterns.

The low number of specimens available (a total of 73 individuals of 12-14 species) points to a main dilemma. *Stenophis* are difficult to discover in the wild, and therefore only single specimens from most localities are available. All *Stenophis* individuals captured by us were found at night: in most cases on branches and twigs in the vegetation or climbing on tree trunks or walls, but mainly on the ground for large *S. betsileanus*. The only species with a more or less representative sample size was *S. pseudogranuliceps* (16 individuals). This renders reliable assessments of intraspecific variability impossible and hinders the identification of diagnostic characters. This is not so unusual in Malagasy forest snakes, for which the abundance is often low (ANDREONE & LUISELLI, 2000).

Also the knowledge of the basic natural history of these snakes is still very rudimentary, and little information is available on food, predation and habitat. Although most records of *Stenophis* refer to primary forest, we found a juvenile *S. granuliceps* close to Antsiranana (deposited in the UADBA) on a big tree in a largely degraded area. Furthermore, some specimens of "giant" *S. betsileanus* from Masoala were captured on the ground just within Ambatoledama Village, in an area where the forest is heavily cut (ANDREONE & RANDRIANIRINA, 2000). THORSTROM & DE ROLAND (2000) describe two instances of predation on undetermined *Stenophis* species by the Madagascar serpent-eagle (*Eutriorchis astur*). RAXWORTHY (1988) found a chameleon (*Furcifer willsi*) in the stomach of a *S. betsileanus*, and hypothesized that *Stenophis* may mainly feed on smaller chameleons when these are sleeping at night. Also GLAW & VENCES (1996) observed chameleon-eating in *Stenophis*: a large *S. betsileanus* female (ZFMK 63175) was found during heavy rain at night on a road, just eating an adult female *Furcifer balteatus*. NUSSBAUM & RAXWORTHY (2000b) report on the finding

of a gecko, *Paroedura tanjaka*, in the stomach of a *Stenophis* (reported as *Lycodryas gaimardi*).

Clarification of *Stenophis* phylogeny and of the relationships of these snakes to the Comoroan *Lycodryas* has to await more detailed studies using hemipenial morphology, karyology and DNA sequences. However, a number of phenetic hypotheses can be drawn already at the present state. Within the subgenus *Stenophis*, it seems quite obvious that *Stenophis gaimardi* and *S. carleti* are sister taxa, as are *S. granuliceps* and *S. pseudogranuliceps*. All these four species are similar in morphology and colour patterns and may form a monophyletic group. In the subgenus *Phisalixella*, colour patterns of *Stenophis arctifasciatus* and *S. variabilis* are similar. This similarity extends also to live colouration, especially of the iris (Fig. 3). Despite the differences in numbers of dorsal scale rows we believe that these two species are closely related, as are probably *S. arctifasciatus* and *S. iarakaensis*. The classification of *Stenophis inopinae* in the subgenus *Phisalixella* by DOMERGUE (1995) appears doubtful: the number of dorsal scale rows (17), the low number of subcaudal scales, the relatively short tail length, and the iris colouration indicate that this species may belong to the subgenus *Stenophis* rather than to *Phisalixella*. *S. inopinae* shares with *S. guentheri* and *S. inornatus* a relatively small size (SVL < 500 mm) and the lack of distinct dark crossbands, possibly indicating closer relationships of these three species.

Analysing the collection sites of the presumably related species, they apparently all have allopatric distributions. In the subgenus *Stenophis* the presumably related species are distributed in the east (*S. gaimardi*), south-east (*S. carleti*), west (*S. pseudogranuliceps*) and north-west (*S. granuliceps*). Only in the Sambirano region *Stenophis* sp. (from Benavony) occurs next to the distribution area of *S. granuliceps*, and in this area sympatric occurrence of these two taxa is likely. A similar allopatric distribution is found within *Phisalixella*, with *S. arctifasciatus* in the east, *S. iarakaensis* in the north-east and *S. variabilis* in the west. The origin of these species may have been allopatric vicariant speciation in forest refuges. Assembling more data on the phylogenetic relationships among them and on their exact distribution areas bears the potential to better understand speciation mechanisms in Malagasy reptiles and the historical changes of climate and vegetation cover of Madagascar.

Acknowledgements

We are grateful to WOLFGANG BÖHME (Bonn), BARRY CLARKE (London), GIULIANO DORIA (Genova), ALAIN DUBOIS (Paris), RICCARDO JESU (Genova), GUNTHER KÖHLER (Frankfurt), and ANNEMARIE ÖHLER (Paris) for allowing examination of specimens held in their care. MORITZ GRUBENMANN, THOMAS HAFEN, JÖRN KÖHLER and BILL LOVE provided photographs. GENNARO APREA, MEIK LANDSBERGER, FABIO MATTIOLI, NIRHY RABIBISOA, LILIANE RAHARIVOLONIAINA, DOMOINA RAKOTOMALALA, OLIVIER RAMILISON, HERILALA RANDRIAMHAZO, JASMIN E. RANDRIANIRINA, KATHRIN SCHMIDT, ILDIKO SOMORJAI, and DENIS VALLAN assisted during fieldwork. We are grateful to the Malagasy authorities for issuing research and export permits. This work has partly been financially supported by the Deutscher Akademischer Austauschdienst (DAAD) and the Deutsche Forschungsgemeinschaft (DFG). Logistic assistance was provided by Wildlife Conservation Society, CARE and WWF.

Eine Übersicht über die madagassischen Baumschlangen der Gattung *Stenophis* (Colubridae)

Einleitung

Unter den Colubriden Madagaskars stehen die nachtaktiven Baumschlangen der Gattung *Stenophis* besonders hervor. Aufgrund ihrer sehr versteckten Lebensweise ist ihre Systematik

bislang nur sehr unzureichend bekannt, und ihre Biologie ist kaum erforscht. Bis vor kurzem wurden diese Schlangen in die Gattung *Lycodryas* eingeordnet, doch DOMERGUE (1995) schlug vor, die Verwendung dieses Gattungsnamens auf die Arten des Komoren-Archipels zu beschränken. Für die madagassische Fauna beschrieb er in Form von sehr kurzen Diagnosen acht neue *Stenophis*-Arten und teilte die Gattung in drei Untergattungen ein. In der vorliegenden Arbeit akzeptieren wir diese Gattungs- und Untergattungseinteilung in vorläufiger Weise. Wir fassen unsere Feldbeobachtungen zu *Stenophis* und den Kenntnisstand zu jeder der Arten kritisch zusammen. Wir beschreiben morphologische und meristische Merkmale der meisten uns bekannten Exemplare (inklusive namenstragenden Typen aller Arten mit Ausnahme von *S. betsileanus*; Tab. 1-2) und dokumentieren die Lebendfärbung von acht Arten (Abb. 1-3). Die Validität verschiedener kürzlich beschriebener Arten ist zweifelhaft, und drei dieser Arten werden hier als jüngere Synonyme anderer Arten aufgefasst.

Ergebnisse

Untergattung *Stenophis* BOULENGER, 1896

Diese Untergattung ist nach DOMERGUE (1995) durch 17 dorsale Schuppenreihen, eine nicht deutlich verbreiterte Vertebral-Schuppenreihe partiell oder vollständig geteilte Subcaudalia und einen tief gegabelten Hemipenis charakterisiert. Sie enthält die folgenden Arten:

Stenophis gaimardi (SCHLEGEL, 1837): Eine hellbraun gefärbte Art mit deutlichen dunkelbraunen Querbändern aus dem zentralen und nördlichen Ostmadagaskar (Fig. 1a)

Stenophis carleti DOMERGUE, 1995: Ähnlich der vorigen Art, unterscheidet sich durch eine geringere Anzahl Ventralschuppen. Der Artstatus dieses Taxons ist zweifelhaft.

Stenophis sp.: Ein Exemplar aus Benavony in Nordwestmadagaskar, das keiner der bekannten Arten eindeutig zugeordnet werden konnte (Fig. 1b). In der Färbung ähnlich den beiden vorigen Arten, in den Schuppenwerten wie *S. inopinae* (siehe unten).

Stenophis pseudogranuliceps DOMERGUE, 1995: Auch diese Art aus dem Westen Madagaskars ähnelt den vorigen in ihrer dunkelbraunen Querbänderung (Fig. 1e), die bei großen Tieren weiß gerändert sein kann. Sie hat jedoch wesentlich weniger Ventralschuppen als *S. gaimardi* und *S. carleti* (Tab. 1-2).

Stenophis granuliceps BOETTGER, 1877: Diese Art aus dem Nordwesten Madagaskars erinnert stark an *S. pseudogranuliceps* (Fig. 1c-d), besitzt aber weniger dunkle Querbänder (Tab. 2). Diese sind besonders bei großen Tieren sehr unregelmäßig und weiß gerändert. Wir fassen *Stenophis capuroni* DOMERGUE, 1995 als jüngeres Synonym von *S. granuliceps* auf, da der Holotypus außer einer höheren Zahl Ventralschuppen, dem Vorhandensein von Inter-Gularschuppen sowie untypischer Konfigurationen einer Supralabial-Schuppe keine Unterscheidungsmerkmale aufweist.

Stenophis inornatus BOULENGER, 1896: Diese Art scheint in Westmadagaskar verbreitet zu sein. Sie hat eine uniforme Färbung und scheint sich von *S. pseudogranuliceps* – außer der Färbung – nur in einer etwas größeren relativen Schwanzlänge zu unterscheiden.

Stenophis guentheri BOULENGER, 1896: Die *Stenophis*-Art mit der geringsten Anzahl Ventralschuppen, charakterisiert durch nur undeutliche Vertebraalflecken statt Querbänder. Bislang aus dem Süden und Westen Madagaskars bekannt.

Stenophis citrinus DOMERGUE, 1995: Die auffälligste und am einfachsten zu erkennende *Stenophis*-Art überhaupt. Sie ist leuchtend gelb mit schwarzer Querbänderung (Fig. 1f), und aus Westmadagaskar bekannt.

Untergattung *Phisalixella* DOMERGUE, 1995

Diese Untergattung ist nach DOMERGUE (1995) durch 17-25 Reihen von Dorsalschuppen, meist ungeteilte Subcaudalia und eine deutlich verbreiterte vertebrale Dorsalschuppen-Reihe charakterisiert. Der Hemipenis, soweit bekannt, ist dreigeteilt und biapical.

Stenophis arctifasciatus (DUMÉRIL, BIBRON & DUMÉRIL, 1854): Diese Schlange aus den Regenwäldern Ost- und Nordostmadagaskars zeichnet sich durch 21 Dorsalia, ein dunkles Nackenband und undeutliche dunkle Querbänder auf dem restlichen Körper aus (Fig. 2a). Wir betrachten *Stenophis jaosoloa* DOMERGUE, 1995, als jüngeres Synonym von *S. arctifasciatus*.

Stenophis variabilis BOULENGER, 1896: Das westmadagassische Pendant zu *S. arctifasciatus*, von der sich *S. variabilis* vor allem durch die variable Anzahl Dorsalia (23-25) unterscheidet. Färbung und Zeichnung sind bei beiden Arten sehr ähnlich (Fig. 2b). Wir betrachten *Stenophis tulearensis* DOMERGUE, 1995, als jüngeres Synonym von *S. variabilis*.

Stenophis inopiniae DOMERGUE, 1995: Diese Art aus Nordwestmadagaskar (Fig. 2c-d) teilt mehr Merkmale mit Arten der Untergattung *Stenophis* (17 dorsale Schuppenreihen, relativ kurzer Schwanz, wenige Subcaudalia, Iris-Färbung) als mit Arten der Untergattung *Phisalixella*, was die bisherige Klassifikation in Frage stellt.

Stenophis irakaensis DOMERGUE, 1995: Diese Art ist nur von einem Exemplar aus Ostmadagaskar bekannt, und zeichnet sich durch 19 Dorsalschuppenreihen sowie vollständig geteilte Subcaudalia aus.

Untergattung *Parastenophis* DOMERGUE, 1995

Diese monotypische Untergattung unterscheidet sich nach DOMERGUE (1995) deutlich von anderen *Stenophis* durch ihre 23 Dorsalschuppenreihen, die nicht verbreiterten Vertebraleschuppen, die ungeteilten Subcaudalia und den massiven, biapicalen Hemipenis.

Stenophis betsileanus (GÜNTHER, 1880): Das verfügbare Material beinhaltet große und kleine Individuen, wobei die Größenunterschiede sehr deutlich sind (275-315 vs. 920-985 mm Kopfrumpf-Länge). Alle kleinen und einige große Exemplare sind schwarz bis dunkelbraun mit weißen Querbändern, während einige andere der großwüchsigen Tiere einfarbig dunkelbraun gefärbt sind (Fig. 2e-f).

Diskussion

Unsere Ergebnisse, die nicht den Anspruch einer umfassenden Revision erheben, unterstreichen gleichwohl den lückenhaften Kenntnisstand über die Gattung *Stenophis*. Wir schlagen hier vor, drei Arten als Synonyme anzusehen, während gleichzeitig zwei weitere Formen (das Exemplar aus Benavony und die großwüchsigen Exemplare von *S. betsileanus*) unbeschriebene Arten oder Unterarten darstellen könnten. Ein Hauptproblem ist die Seltenheit von *Stenophis* in herpetologischen Sammlungen. Insgesamt standen uns lediglich 74 Individuen zur Verfügung, was in den meisten Fällen keine zuverlässigen Aussagen über die Variationsbreite von morphologischen Merkmalen zulässt.

Inwieweit diese Seltenheit von *Stenophis* real ist oder durch ihre versteckte (nachtaktive und überwiegend baumlebende) Lebensweise bedingt ist, lässt sich ohne weitergehende Untersuchungen nicht klären.

Mehrere, vermutlich eng verwandte Arten zeigen allopatrische Verbreitungsmuster: *Stenophis gaimardi* (Osten) und *S. carleti* (Südosten), *S. granuliceps* (Nordwesten) und *S. pseudogranuliceps* (Westen), *S. arctifasciatus* (Osten) und *S. variabilis* (Westen), was für künftige Untersuchungen über biogeografische Muster und Artbildungsprozesse in Madagaskar relevant sein könnte.

Schlagwörter: Squamata: Serpentes: Colubridae: *Stenophis*; Taxonomie; Verbreitung; Madagaskar.

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Appendix: Material examined

Stenophis gaimardi: MNHN 3868 (holotype, Madagascar, QUOY and GAIMARD); MNHN 3869 (Madagascar, BERNIER); MNHN 1978.2916 (Maroantsetra, MONTSARRAT, 31.III.1971); MNHN 1978.2918 (probably Maroantsetra, C.A. DOMERGUE); MZUT R3564.1-2 (Moramanga 80 km East Tananarive; ZFMK 21819 (Toamasina, H. MEIER, I.1978). *Stenophis* sp.: ZSM 404/2000 (Benavony, J.E. RANDRIANIRINA, F. ANDREONE and M. VENCES, II.2000). *Stenophis carleti*: MNHN 1988.321 (holotype; Haute Mananoro [or Manavono], Manakara, M. CARLET, 12.X.1968 [according to a manuscript of DOMERGUE]); MNHN 1988.322 (paratype, col du Maningotra, Tolagnaro region, R. CAPURON, XII.1968 [according to a manuscript of DOMERGUE]); MNHN 1895.233 (SE coast, GRANDIDIER and LANTZ). *Stenophis pseudogranuliceps*: MNHN 1420 (Madagascar, GRANDIDIER, 1867); MNHN 1899.401 (around Toliara, GRANDIDIER, 30.V.1898); MNHN 1901.225 (Tolagnaro, ALLUAUD); MNHN 1901.392 (Befaisitra, Mandrare, DECORSE III.1901); MNHN 1906.119 (Toliara, bords du Fiherenana, GEAY); MNHN 1929.177 (Fiherenana valley, G. PETIT); MNHN 1929.178 (Maroamalona, G. PETIT); MNHN 1961.647 (Ampijoroa, PETTER); MNHN 1977.1061 (Ampijoroa, IX. 1956); MNHN 1978.42 (holotype, Ampijoroa, RN4 pK480, Dr. HOUIN, 12.I.1965); MNHN 1978.2917 and 1992.5329-5331 (Marofandilia, foret 20 km N Morondava, C.A. DOMERGUE, 10.VII.1969). *Stenophis granuliceps*: MNHN 1887.260 (Nosy Be, DEYROLLE); MNHN 1966.960 (Nosy Be, PICHON, 1964); MNHN 1988.325 (holotype *Stenophis capuroni*, forêts de l'Ankarana, sur plateaux calcaires profondément karstifiés, au sud de Diégo-Suarez (aujourd'hui Antsiranana), CAPURON, III.1964 [according to a manuscript of DOMERGUE]); MRSN R 1974 (Nosy Be, Lokobe, F. ANDREONE and J.E. RANDRIANIRINA 11.II.1999); MRSN R 1832 (Sahamalaza, F. ANDREONE, J.E. RANDRIANIRINA and M. VENCES 14.II.2000); ZFMK 17738 (Antsiranana, H. MEIER I 1976). ZSM 550/2002 (Montagne des Français, F. GLAW, K. SCHMIDT and M. VENCES, 14.III.2000); ZSM 553/2002 (Montagne des Français, 12°19'34"S, 49°20'09"E, 334 m alt., F. GLAW and K. SCHMIDT, 21.III.2000). *Stenophis inornatus*: BMNH 1946.1.7.9 (holotype; old number 94.2.27.8; Madagascar); MNHN 1421 (Madagascar, GRANDIDIER, 1867); MNHN 1977.1062 (Zampongotra, W Beloha, Karimbola plateau, C.A. DOMERGUE, 21.VI.1961). *Stenophis guentheri*: BMNH 1946.1.2.53 (holotype; old number BMNH 92.11.26.8; SW Madagascar); MNHN 1978.2914 (Itremo, A. PEYRIERAS and P. VIETTE, II.1974); MNHN 1950.161 (Ambovombe, DECARY); MNHN 7825 (Madagascar, GRANDIDIER). *Stenophis citrinus*: MNHN 1978.2790 (holotype, Beroboka, S. DE HAULME, IV.1970); ZFMK 59794 (Kirindy, F. GLAW, N. RABIBISOA and O. RAMILISON, I.1995); ZSM 923/2000 (pet trade, no locality data). *Stenophis arctifasciatus*: MNHN 3870 (holotype, Madagascar, QUOY and GAIMARD); MNHN 1901.72 (Moramanga, "La colonie [Exposition de 1900]"); MNHN 1930.372 (Tananarive, DECARY); MNHN 1950.162 (Madagascar, SALVAT); MNHN 1988.323 (holotype of *S. jaosoloa*, Andasibe (Périnet, III.1977, JAOSOLOA BESOA [according to a manuscript of DOMERGUE]); MRSN R 1971 (Tsararano, ANDREONE and J.E. RANDRIANIRINA); MRSN R 1972 (corridor between Moramanga and Zahamana, J.E. RANDRIANIRINA 17-21.I.1999); ZSM 231/2002 (Andasibe, I. SOMORJAI and L. RAHARIVOLONAINA, 8.XII.2001). *Stenophis variabilis*: BMNH 1946.1.7.10-11 (syntypes; old numbers 94.2.2.7 and 9; Madagascar); MNHN 1950.371 (Nosy Be, Lokobe, Ravenala axil, MILLOT); MNHN 1988.318 (Andranovory-Toliara, C.A. DOMERGUE); MNHN 1988.319 (holotype *S. tulearensis*, Ampijoroa, C.A. DOMERGUE, 9.I.1965); MNHN 1988.337 (Toliara, pK32, C.A. DOMERGUE, I.II.1981); MNHN 1994.3138 (Ankarafantsika, B. RICKLIN); UADBA (number unknown, Kirindy, F. GLAW, N. RABIBISOA and O. RAMILISON I.1995, for meristic data see GLAW & VENCES 1996). *Stenophis inopinae*: MNHN 1950.160 (holotype,

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Antongo[n]bato, région d'Antsiranana, LAUDAUDAN [according to a manuscript of DOMERGUE]; ZFMK 62200 (Ankarana, J. KÖHLER, 24.XI.1995); ZSM 551-552/2000 (Montagne des Français, 12°19'34"S, 49°20'09"E, 334 m alt., F. GLAW and K. SCHMIDT, 21.III.2000). *Stenophis iarakaensis*: MNHN 1988.320 (holotype, Iharaka, ANDRÉ PEYRIERAS, 1973 [according to a manuscript of DOMERGUE]). *Stenophis betsileanus*: MNHN 1903.225 (Ambositra, JOURDRAN); MNHN 1978.1423 (Madagascar, most probably Nosy Mangabe, A. PEYRIERAS, 5.XI.1968); MNHN 1996.7432 (locality uncertain, P. STRAUCH 1995); MRSN R 1145 (PN d'Andohahela, forest between the villages of Isaka Ivondro and Eminimihy, F. ANDREONE, J.E. RANDRIANIRINA and D. VALLAN 08.XI.1994); MRSN R1973 (Masoala Peninsula, Andasin'i Governora, F. ANDREONE and J.E. RANDRIANIRINA 3.XII.1999); MRSN R1975-1976 (Masoala Peninsula, ANDREONE and J.E. RANDRIANIRINA 11.XII.1998); ZFMK 60500 (Marojejy, F. GLAW and O. RAMILISON 4.III.1995); ZFMK 63175 (Ranomafana, F. GLAW, D. RAKOTOMALALA and F. RANAIVOJAONA 28.II.1996).

Manuscript received: 2 January 2003

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