VERTEBRATE ZOOLOGY

© Senckenberg Gesellschaft für Naturforschung, 2020.

70 (4): 547–569

2020

SENCKENBERG

Taxonomic reassessment of the *Pareas margaritophorus-macularius* species complex (Squamata, Pareidae)

Gernot Vogel[1,*], Tan Van Nguyen[2,*], Hmar Tlawmte Lalremsanga[3], Lal Biakzuala[3], Vanlal Hrima[4] & Nikolay A. Poyarkov[5,6,*]

[1] Society for Southeast Asian Herpetology, Im Sand 3, 69115 Heidelberg, Germany; email: gernot.vogel@t-online.de — [2] Save Vietnam's Wildlife Centre, Nho Quan, Ninh Binh, Vietnam; e-mail: tan@svw.vn — [3] Department of Zoology, Mizoram University, Tanhril 796 004, Aizawl, Mizoram, India; e-mail: htlrsa@yahoo.co.in — [4] Biodiversity and Nature Conservation Network, Mission Veng, Aizawl, Mizoram, India, 796001 — [5] Department of Vertebrate Zoology, Biological Faculty, M. V. Lomonosov Moscow State University, Moscow 119234, Russia; e-mail: n.poyarkov@gmail.com — [6] Joint Russian-Vietnamese Tropical Research and Technological Center, Nghia Do, Cau Giay, Hanoi, Vietnam — * Corresponding authors

Submitted June 5, 2020.
Accepted September 10, 2020.
Published online at www.senckenberg.de/vertebrate-zoology on October 2, 2020.
Published in print Q4/2020.

Editor in charge: Uwe Fritz

Abstract

In the present paper we reassess the taxonomy of the *Pareas margaritophorus-macularius* species complex based on an integrative approach including morphological and molecular data from type, historical, and newly collected specimens. The name *Pareas andersonii* Boulenger, 1888 is revalidated for the populations of Myanmar (Kachin, Chin, Shan states and Sagaing, Mandalay divisions), India (Mizoram and Nagaland states), and China (Yunnan Province). The name *Pareas modestus* Theobald, 1868 is revalidated for populations in southern Myanmar (Yangon Division) and India (Mizoram State). Molecular and morphological data further re-confirm the full species status of *P. macularius* Theobald, 1868. We provide an identification key to the species of the *Pareas margaritophorus-macularius* complex. Our results further underline that the taxonomy of the genus *Pareas* species has not yet been fully assessed, especially in widely distributed taxa often representing complexes of cryptic or morphologically similar species. Our work brings the total number of species recognized within the genus *Pareas* to 19.

Key words

Distribution, morphology, mtDNA, *Pareas andersonii*, *P. macularius*, *P. margaritophorus*, *P. modestus*, Southeast Asia, taxonomy.

Introduction

The taxonomy of the Asian snail-eating snake genus *Pareas* remains in a state of flux and has been frequently revised with several new species being described or resurrected in several recent morphological and molecular studies (e.g. Guo *et al*., 2011; You *et al*., 2015; Vogel, 2015, Wang *et al*., 2020). Species complexes with wide distributions and several lineages with an unclear taxonomic status like the *Pareas hamptoni-formosensis* complex or the *P. carinatus-nuchalis* complex remain especially challenging (Guo *et al*., 2011; You *et al*., 2015).

One of the groups which has received comparatively little attention from the taxonomists is the *Pareas margaritophorus-macularius* species complex widely distributed from Sumatra, Singapore, and Malaysia Peninsular to Indochina, Thailand, Myanmar, northeast India and southern China (see Hauser, 2017; Nguyen *et al*., 2020). Until recently, this species complex was either regarded as a single species, *Pareas margaritophorus* (Jan, 1866) (see You *et al*., 2015), or as two species, *P. margaritophorus* and *P. macularius* Theobald, 1868 (see Hauser, 2017). However, morphological and molecular differentiation, as well as the extent of distribution of the lineages comprising this complex remains unclear; further progress in clarifying it is hampered by common misidentifications of the complex members in a number of recent molecular works (e.g. Zaher *et al*., 2019; Li *et al*., 2020). In the present paper we provide a reassessment of this species complex, examining morphological and molecular differentiation of snakes previously referred to as *Pareas margaritophorus* or *P. macularius*. This species complex is characterized by the following morphological attributes: purplish-gray or brownish-gray coloration of dorsum with or without numerous bicolored black-and-white spots; loreal not contacting eye; vertebral scales not enlarged; subocular and postocular scales regularly fused forming a crescent-shaped scale; and elongated temporal scales (Boulenger, 1896; Hauser, 2017; this study).

Pareas margaritophorus was the first species to be described in this group by Jan in Bocourt (1866) from "Siam" (now Bangkok Capital, Thailand) under the name *Leptognathus margaritophorus*. Two years later *P. macularius* was described from Tenasserim in Burma (now Tanintharyi Divison, Myanmar) by Theobald in 1868. The type specimens of both species were characterized by the presence of bicolored black-and-white spots. Subsequently three additional morphologically similar slug-eating snakes were described, and all of them were considered as valid species in Boulenger's review (1896): *Pareas modestus* Theobald, 1868 from "Rangun" [sic], Pegu, Burma (now Yangon Division, Myanmar), *Pareas moellendorffi* Böttger, 1885 from Guangdong Province, southeastern China, and *Pareas andersonii* Boulenger, 1888 from Kachin State, northern Myanmar. In 1935 *Amblycephalus tamdaoensis* Bourret, 1935 – another slug snake with bicolored spots was described from Tam Dao Mountain in Vinh Phuc Province, northern Vietnam (Bocourt, 1866; Boulenger 1888, 1896; Bourret, 1935; Theobald, 1868). Bourret (1936) recognized 5 full species in this complex and used the characters of the size of the frontal scale and the loreal scale and the keeling of the scales to separate them in his key. He did not mention *P. modestus* and likely just overlooked this name. Wall (1922) synonymized *P. modestus* and *P. andersonii* with *P. macularius* but accepted *P. moellendorffi* as valid species (Bourret, 1936; Wall, 1922).

Smith (1943) followed Wall in this taxonomy but also synonymized *A. moellendorffi* with *P. margaritophorus*, and also put *A. tamdaoensis* in synonymy of *P. macularius*, however without providing morphological justification or any comments for these decisions. After the work of Smith (1943) of the six previously recognized species of spotted slug snakes only two were regarded as valid species. Sixty years later the situation has become even more confusing when Huang (2004) regarded *P. macularius* as a junior synonym of *P. margaritophorus* based on a review of data from previous studies, but without proper morphological justification or examination of any type specimens or additional materials. After the work of Huang (2004) only one species of spotted slug snakes remained valid (*P. margaritophorus*). Recently, Hauser (2017) reviewed morphological variation of this complex in Thailand and demonstrated that *P. macularius* and *P. margaritophorus* represent distinct valid species, which are separated both by morphological characters, coloration and natural history. More recently, the species-level differentiation between *P. macularius* and *P. margaritophorus* was assumed based on molecular analyses of a limited material from China (Wang *et al*., 2020) and Thailand (Suntrarachun *et al*., 2020). However, a careful comprehensive taxonomic analysis of the status of the lineages within this group, integrating data from both morphology and DNA, is still lacking. Taxonomically the most important is that all recent reviews of the *P. margaritophorus-macularius* complex were based on a small number of specimens originating from a certain region (southern China or Thailand), and without examination of type materials and the specimens from the whole of the distribution area. Thus, an integrative taxonomic review of the complex has never been done.

In the present paper, based on an examination of collection material and newly collected specimens of the *P. margaritophorus-macularius* complex we present a review of morphological variation within the group supported by the data on molecular differentiation from the analyses of cytochrome *b* mtDNA gene sequences. Herein we confirm the species level differentiation of *P. macularius* and *P. margaritophorus*, and also resurrect the full species status for *Pareas andersonii* Boulenger, 1888 and *P. modestus* Theobald, 1868.

Materials and Methods

Specimens examined

For this study, a total 92 preserved specimens were examined for their external morphological characters [including: 15 specimens of *P. andersonii* (except for lectotype and paralectotype which were only photo recorded), 9 specimens of *P. modestus* (except for holotype, data given in reference to WALL, 1909), 15 specimens of *P. macularius*, 51 specimens of *P. margaritophorus*, 2 specimens of *P.* cf. *macularius* (see Table 1); geographic location of examined populations presented in Fig. 1] and on several photographed specimens. A total of 40 morphological characters were recorded for each specimen (following Vogel, 2015). Measurements were taken with a slide-caliper to the nearest 0.1 mm, except body and tail lengths, which were measured to the nearest of one millimeter with a measuring tape. The number of ventral scales was counted according to Dowling (1951). Half ventrals were counted as one. The first enlarged shield anterior to the ventrals was regarded as a preventral and was present in all examined specimens. The first scale under the tail meeting its opposite was regarded as the first subcaudal, and the terminal scute was not included in the number of subcaudals. The dorsal scale rows were counted at one head length behind head, at midbody, and at one head length before vent. In the number of supralabials touching the subocular, those only

Table 1. Measurements and scale counts of *Pareas andersonii*, *P. modestus*, *P. macularius*, and *P. margaritophorus*. Abbreviations are listed in the Materials and methods. (*= holotype; **= holotype of *Pareas moellendorffi*; ***= syntype of *Amblycephalus tamdaoensis*; measurements: # from Wall (1909); ? = not available). For sampling localities see Fig. 1. (Continues on the next page).

Species	Number	Locality	Sex	SVL	TaL	KMD	VEN	SC	SL	IL	At	Pt	SoO	PoO
Pareas andersonii	NHM(UK) 1904.4.26.14	Mogok, Mandalay, Myanmar	M	332	73	7	152	47	7/7	7/7	2/2	3/3	1/1	1/1
	NHM(UK) 1925.12.22.1	Shweli, Mongmit, Shan, Myanmar	M	233	45	5	144	40	7/7	7/7	2/2	3/3	1/1	1/1
	NHM(UK) 1926.3.17.9	Kalaw, Taunggyi, Shan, Myanmar	M	262	57	7	141	42	7/7	7/7	2/2	3/2	1/1	1/1
	CAS 235359	Mindat, Chin, Myanmar	M	266	56	?	153	46	6/7	8/8	2/1	3/2	1/1	1/1
	CAS 245296	Khandi, Sagaing, Myanmar	M	346	70	?	153	42	7/7	8/8	2/2	3/2	1/1	1/1
	CAS 245377	Khandi, Sagaing, Myanmar	M	307	58	?	153	41	7/7	8/8	2/2	3/3	1/1	0/0
	NHM(UK) 1901.9.14.11	Kyatpyin, Mandalay, Myanmar	F	382	76	5	159	45	7/7	8/8	2/2	3/3	1/1	1/1
	NHM(UK) 1904.4.26.13	Mogok, Mandalay, Myanmar	F	381	65	7	159	40	7/7	7/7	2/2	4/3	1/1	1/1
	NHM(UK) 1908.6.23.94	Myanmar	F	387	69	9	162	43	7/7	7/8	2/2	3/3	1/1	1/1
	CAS 235218	Mindat, Chin, Myanmar	F	367	67	?	155	41	7/7	8/7	?	?	?	?
	CAS 241270	Myitkyina, Kachin, Myanmar	F	271	42	?	160	35	7/7	7/8	2/2	3/3	1/1	1/1
	CAS 233330	Haka, Chin, Myanmar	F	407	74	5	155	36	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 916	Mizoram, India	F	297	53	5	156	40	7/7	7/7	2/2	3/3	1/1	1/1
Pareas modestus	ZSI 8028*,#	Yangon, Myanmar	?	?	?	5	156	37	7/7	?	2/2	3/3	1/1	1/1
	MZMU 274	Mizoram, India	M	424	71	3	157	42	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 1293	Mizoram, India	M	226	52	5	156	46	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 1487	Mizoram, India	M	267	53	5	155	45	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 1537	Mizoram, India	M	310	75	5	151	46	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 275	Mizoram, India	F	406	56	5	153	38	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 1193	Mizoram, India	F	357	53	5	157	35	7/7	7/7	2/2	2/2	1/1	1/1
	MZMU 1604	Mizoram, India	F	304	57	5	156	37	7/7	7/7	2/2	3/3	1/1	1/1
	MZMU 1665	Mizoram, India	F	310	54	5	159	38	7/7	7/7	2/2	2/2	1/1	1/1
Pareas cf. *mac-ularius*	MNHN 1994.743	Northern Laos	F	407	75	6	156	44	7/7	8/7	2/2	3/3	1/1	1/2
	MNHN 2005.0232	Long Nai, Phongsaly, Laos	F	363	62	7	162	41	7/7	7/8	2/2	2/3	1/1	1/1
Pareas macularius	CAS 206620	Bago, Bago, Myanmar	M	355	73	9	166	49	7/7	7/7	2/2	3/3	1/1	0/1
	CAS 247899	Dawei, Tanintharyi, Myanmar	F	331	58	?	173	44	7/7	8/8	3/3	3/2	1/1	1/0
	CIB 10155 (725035)	Jianfengling, Hainan, China	M	322	80	9	151	51	7/7	8/7	2/2	3/3	1/1	1/1
	NHM(UK) 1946.1.20.8*	Martaban, Tanintharyi, Myanmar	M	333	70	?	161	50	7/7	8/8	2/2	2/3	1/1	0/0
	NHM(UK) 1947.1.1.14	Lam Dong, Vietnam	F	403	71	5	152	39	7/7	8/8	2/2	3/3	2/2	0/0
	DTU 479	Ba Vi, Ha Noi, Vietnam	M	363	79	7	154	45	7/7	8/8	2/2	3/3	1/1	1/1
	DL 2019.07.29012	Jiangcheng, Yunnan, China	F	392	72	7	156	43	7/7	6/6	2/2	3/3	1/1	1/1
	FMNH 135331	Dansai, Loei, Thailand	M	209	43	9	161	53	7/7	7/8	2/2	3/3	1/1	1/1
	FMNH 175332	Ngan Son, Bac Kan, Vietnam	F	270	49	5	160	43	7/7	7/7	2/2	3/3	1/1	1/1
	MNHN 1938.89***	Tam Dao, Vinh Phuc, Vietnam	M	281	57	7	152	53	7/7	8/7	2/2	3/3	1/1	1/1

Table 1 continued.

Species	Number	Locality	Sex	SVL	TaL	KMD	VEN	SC	SL	IL	At	Pt	SoO	PoO
Pareas macularius	MNHN 1938.148***	Tam Dao, Vinh Phuc, Vietnam	F	388	79	5	156	44	7/7	8/7	2/2	4/3	1/1	1/0
	NMW 39964.1	Tam Dao, Vinh Phuc, Vietnam	F	432	85	7	154	41	7/7	7/7	2/2	3/3	1/1	1/1
	ZFMK 82925	Nghe An, Vietnam	M	280	67	11	?	49	7/7	8/7	2/2	3/3	1/1	1/1
	ZFMK 86446	Phong Nha-Ke Bang, Quang Binh, Vietnam	F	370	76	9	156	45	7/7	8/7	2/2	3/3	1/1	2/2
	ZMMU R-16629	Ban Mauk, Sagaing, Myanmar	F	304	64	7	159	44	7/7	7//7	2//2	3//3	1//1	2//2
Pareas margaritophorus	CAS 14949	Hainan, China	F	215	40	0	160	44	7/7	8/8	2/2	2/1	1/1	0/0
	CIB 10160 (705015)	Yuling, Hainan, China	M	253	71	0	145	49	6/7	7/5	2/2	2/2	1/1	0/0
	CIB 83792 (665082)	Diaoluo Shan, Hainan, China	F	287	57	0	150	44	7/7	8/8	2/2	2/2	1/1	0/0
	CIB 10157 (665081)	Diaoluo Shan, Hainan, China	F	327	65	0	155	43	7/7	8/7	2/2	2/2	1/1	0/0
	CIB 10158 (665080)	Diaoluo Shan, Hainan, China	F	317	60	0	157	40	7/7	7/7	2/2	2/2	1/1	0/0
	CIB 10162 (64III5159)	Wuzhi Shan, Hainan, China	F	278	49	0	156	41	7/7	6/8	2/2	4/4	1/1	0/0
	DTU 475	Pu Mat, Nghe An, Vietnam	F	300	50	0	149	41	7/7	7/7	2/2	3/3	1/1	0/0
	DTU 476	Cuc Phuong, Ninh Binh, Vietnam	F	262	67	0	133	47	7/7	7/7	2/2	3/3	1/1	0/0
	DTU 477	Cuc Phuong, Ninh Binh, Vietnam	F	300	49	0	140	40	7/7	7/7	2/2	3/3	1/1	0/0
	DTU 478	Cuc Phuong, Ninh Binh, Vietnam	F	249	65	0	133	44	7/7	7/7	2/2	3/3	1/1	0/0
	FMNH 71704	Da Lat, Lam Dong, Vietnam	M	249	65	0	135	47	7/7	7/8	2/2	1/1	1/1	0/0
	FMNH 71705	Da Lat, Lam Dong, Vietnam	M	252	63	0	137	45	7/7	7/6	2/2	2/1	1/1	0/0
	FMNH 256973	Hong Kong, China	M	274	77	0	138	49	7/7	6/7	2/2	2/2	2/1	1/1
	FMNH 263022	Siem Pang, Stung Treng, Cambodia	M	175	42	0	145	50	7/7	8/7	2/2	1/3	1/1	1/1
	FMNH 6661	Hainan, China	F	258	48	0	149	42	7/7	8/7	2/2	2/2	1/1	0/0
	FMNH 66621	Hainan, China	F	245	43	0	145	40	7/7	7/7	2/2	2/2	1/1	0/0
	FMNH 71137	Hong Kong, China	F	243	52	0	143	42	6/7	7/6	2/2	2/3	1/1	0/0
	FMNH 178389	Pattani, Thailand	F	241	45	0	144	39	7/7	7/7	2/2	1/1	1/1	0/0
Pareas margaritophorus	FMNH 178390	Chiang Mai, Thailand	F	265	48	0	152	38	7/7	7/8	2/2	2/2	1/1	0/0
	FMNH 180219	Nakhon Ratchasima, Thailand	F	268	48	0	143	36	8/8	8/8	2/2	1/2	1/1	0/0
	FMNH 180220	Nakhon Ratchasima, Thailand	F	330	59	0	138	36	7/7	7/7	2/2	2/2	1/1	0/0
	FMNH 233357	Pahang, Malaysia	F	235	47	0	148	42	6/7	7/7	2/2	2/1	1/1	0/0
	FMNH 252128	An Khe, Gia Lai, Vietnam	F	202	35	0	149	39	7/7	8/8	2/2	2/2	1/1	0/0
	FMNH 263791	Na Di, Prachinburi, Thailand	F	282	48	0	145	35	7/7	8/7	2/2	3/3	2/2	0/1
	FMNH 267738	Areng Chum Noab, Koh Kong, Cambodia	F	274	52	0	155	42	7/7	7/7	2/2	2/2	1/1	0/0
	MNHN 599*	Thailand	M	241	66	0	139	51	7/7	8/9	2/2	2/2	1/1	1/1
	NMW 28128:2	Vietnam	M	192	48	0	143	52	7/7	7/7	2/2	3/3	1/1	0/0
	NMW 28128:5	Vietnam	M	252	70	0	138	49	7/7	7/8	2/3	2/2	1/1	0/0
	NMW 28128:8	Phuoc Son, Quang Nam, Vietnam	M	223	63	0	134	48	7/7	7/7	2/3	2/2	1/1	0/0
	NMW 28128:9	Phuoc Son, Quang Nam, Vietnam	M	182	50	0	140	51	8/8	7/7	2/3	2/2	1/1	0/0
	NMW 28128:10	Phuoc Son, Quang Nam, Vietnam	M	267	75	0	146	51	8/9	7/7	2/2	3/3	1/1	0/0
	NMW 28128:12	Phuoc Son, Quang Nam, Vietnam	M	172	41	0	143	54	9/8	8/7	2/2	3/3	1/1	0/0
	NMW 28128:3	Vietnam	F	274	?	0	145	?	7/7	9/8	2/2	2/3	1/1	0/0

Table 1 continued.

Species	Number	Locality	Sex	SVL	TaL	KMD	VEN	SC	SL	IL	At	Pt	SoO	PoO
Pareas margaritophorus	NMW 28128:4	Cambodia	F	313	58	0	145	39	8/8	7/8	2/2	3/2	1/1	0/0
	NMW 28128:6	Phuoc Son, Quang Nam, Vietnam	F	250	46	0	152	41	8/8	7/7	2/2	2/2	1/1	0/0
	NMW 28129:3	Vietnam	F	270	53	0	148	40	7/7	8/7	2/2	2/2	1/1	0/0
	NMW 39964.1	Nahe Ibok, Trengganu, Malaysia	F	265	55	0	152	40	7/7	7/7	2/1	2/2	1/1	0/0
	SMF 20792	Hong Kong, China	M	222	58	0	136	46	7/7	7/7	2/2	2/2	1/1	0/0
	SMF 20790**	Lo Fou Shan, Guangzhou, China	F	244	43	0	149	37	7/7	7/6	2/2	3/3	1/1	0/0
	SMF 20791	Hong Kong, China	F	286	51	0	149	37	7/7	7/7	2/2	2/2	1/1	0/0
	ZFMK 76107	Mesa, Chiang Mai, Thailand	M	232	65	0	138	48	7/7	7/7	2/2	3/3	1/1	0/0
	ZFMK 80664	Phong Nha-Ke Bang, Quang Binh, Vietnam	M	197	51	0	141	48	8/7	8/8	2/2	3/3	1/1	0/0
	ZFMK 82924	Nghe An, Vietnam	M	233	52	0	139	46	7/7	8/7	2/2	2/2	1/1	0/0
	ZFMK 92637	Phnom Kulen, Siem Reap, Cambodia	M	244	70	0	141	49	7/7	7/7	2/2	1/1	1/1	0/0
	ZFMK 92636	Phnom Kulen, Siem Reap, Cambodia	M	262	76	0	136	48	7/7	7/7	2/2	2/1	1/1	0/0
	ZFMK 70584	Kuala Lumpur, Malaysia	F	210	46	0	148	43	7/7	7/7	2/2	4/3	1/1	0/0
	ZFMK 81479	Ke Go, Ha Tinh, Vietnam	F	337	57	0	153	38	7/7	7/7	2/2	1/1	1/1	0/0
	ZFMK 90378	Phnom Kulen, Siem Riep, Cambodia	F	276	46	0	149	35	7/7	7/7	2/2	2/2	1/1	0/0
	ZFMK 95197	Bai Tu Long, Quang Ninh, Vietnam	F	315	56	0	147	38	8/7	7/7	2/2	2/1	1/1	0/0
	ZMB 50680	Perak, Malaysia	M	230	63	0	138	49	7/7	7/7	2/2	3/3	1/1	1/1
	ZSM 22710	Vietnam	M	247	61	0	145	47	7/8	8/8	2/2	3/2	1/1	1/1

touching the presubocular were not included. Infralabials were considered being those shields that were completely below a supralabial and bordering the mouth gap. Usually the last supralabial shield was a very large shield, much larger than other supralabials. Smaller shields behind this enlarged shield do not border the mouth gap (only the connecting muscle) and were excluded in the sublabial scales count, despite the fact that they were covered by the supralabials. The first sublabial was defined as the scale that starts between the posterior chin shield and the infralabials and that borders the infralabials. Values for paired head characters were recorded on both sides of the head, and were reported in a left / right order. The sex was determined by dissection of the ventral tail base. Morphological measurements (all in mm) and counts included: SVL: Snout-vent length; TaL: Tail length; TL: Total length; TaL/TL: Relative tail length; VEN: Ventral scales; SC: Subcaudal scales; SL: Supralabials; IL: Infralabials; KMD: Number of keeled dorsal scale rows at midbody; At: Anterior temporal; Pt: Posterior temporal. Other abbreviations: N.P.: National Park; a.s.l.: above sea level; SoO: Suboculars PoO: Postocular.

Museum abbreviations

AUP: School of Agriculture and Natural Resources, University of Phayao, Phayao, Thailand; **NHM(UK)**: The Natural History Museum, London, UK; **BNHS**: Bombay Natural History Society, Mumbai, India; **CAS**: California Academy of Sciences Museum, California, USA; **CIB**: Chengdu Institute of Biology, Chengdu, People's Republic of China; **DTU**: Duy Tan University, Da Nang, Vietnam; **DL**: Ding Lee's private collection, Chengdu, China; **FMNH**: Field Museum of Natural History, Chicago, USA; **HS**: Song Huang's private collection, College of Life Sciences, Anhui Normal University, Wuhu, Anhui, China; **LSUHC**: La Sierra University Herpetological Collection, La Sierra University, Riverside, California, USA; **KIZ**: Museum of the Kunming Institute of Zoology, Yunnan, China; **MNHN**: Muséum national d'Histoire naturelle, Paris, France; **MSNG**: Museo Civico di Storia Naturale "Giacomo Doria," Genova, Liguria, Italy; **MZM**U: Departmental Museum of Zoology, Mizoram University, Mizoram, India; **NMNS**: National Museum of Natural Science, Taichung, Taiwan; **NMW**: Naturhistorisches Museum Wien, Vienna, Austria; **SMF**: Naturmuseum Senckenberg, Frankfurt am Main, Germany; **ZFMK**: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; **ZMB**: Zoologisches Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany; **ZMMU**: Zoological Museum of Lomonosov Moscow State University, Moscow, Russia; **ZSM**: Zoologische Staatssammlung, München, Germany.

Molecular methods

For those specimens for which tissue samples were available, we performed molecular phylogenetic analyses to test for correlation with the morphological data (summarized in Table 2; see Fig. 1, 2). For molecular analyses, total genomic DNA was extracted from ethanol-preserved liver or muscle tissue using standard phenol-chloroform-proteinase K extraction procedures with consequent isopropanol precipitation (protocols followed HILLIS *et al*., 1996; SAMBROOK & RUSSEL, 2001). The isolated total genomic DNA was visualized in agarose electrophoresis in the presence of ethidium bromide. DNA concentration was measured in 1 µl using NanoDrop 2000 (Thermo Scientific), and adjusted it to ca. 100 ng DNA/µL. We amplified 1127 bp long fragment of mtDNA cytochrome *b* (cyt *b*), which was widely applied in biodiversity surveys in snakes, including the family Pareidae (e.g. LAWSON *et al*., 2005; GUO *et al*., 2011; LOREDO *et al*., 2013; YOU *et al*., 2015; DEEPAK *et al*., 2020; LI *et al*., 2020). DNA amplification was performed in 20 µl reactions using ca. 50 ng genomic DNA, 10 nmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl2, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl2 and 0.01% gelatine) and 1 U of Taq DNA polymerase. Primers used in PCR and of cyt *b* gene followed YOU *et al*., (2015) and included: L14910 (5'-GACCTGTGATM TGAAAAACCAYCGTTGT-3') and H16064 (5'-CTTTGGTTT-ACAAGAACAATGCTTTA-3') (DE QUEIROZ *et al*., 2002). The PCR conditions followed YOU *et al*., (2015) and included denaturation at 94°C for 3 min, followed by 35 cycles at 94°C for 30 s, 52°C for 40 s and 72°C for 90 s, with a final extension at 72°C for 10 min using an iCycler Thermal Cycler (Bio-Rad).

Table 2. Sequences and voucher specimens of *Pareas* and outgroup taxa used in molecular analyses for this study. For sampling localities see Fig. 1. (Continues on the next page).

#	GenBank A.N.	Specimen ID	Species	Locality	Reference
1	MT968756	ZMMU NAP-02839	*Pareas margaritophorus*	Vietnam, Lam Dong, Loc Bao	*this work*
2	MT968757	ZMMU R-14036	*Pareas margaritophorus*	Vietnam, Binh Phuoc, Bu Gia Map N.P.	*this work*
3	MT968758	V11 (tissue)	*Pareas margaritophorus*	Vietnam, Binh Phuoc, Bu Gia Map N.P.	*this work*
4	MT968759	V12 (tissue)	*Pareas margaritophorus*	Vietnam, Binh Phuoc, Bu Gia Map N.P.	*this work*
5	KJ642195	M01 (tissue)	*Pareas margaritophorus*	Vietnam, Binh Phuoc, Bu Gia Map N.P.	You *et al*., 2015
6	KJ642196	M02 (tissue)	*Pareas margaritophorus*	Vietnam, Binh Phuoc, Bu Gia Map N.P.	You *et al*., 2015
7	MT968760	ZMMU R-16645	*Pareas margaritophorus*	Vietnam, Gia Lai, Kon Ka Kinh N.P.	*this work*
8	MT968761	ZMMU R-16646	*Pareas margaritophorus*	Vietnam, Gia Lai, Kon Ka Kinh N.P.	*this work*
9	MT968762	ZMMU R-16197	*Pareas margaritophorus*	Vietnam, Gia Lai, Kon Ka Kinh N.P.	*this work*
10	MT968763	ZMMU R-16146	*Pareas margaritophorus*	Malaysia, Pahang, Kuala Tahan	*this work*
11	MT968764	ZMMU R-14790	*Pareas margaritophorus*	Vietnam, Quang Binh, Tuyen Hoa	*this work*
12	MT968765	ZMMU R-16418	*Pareas margaritophorus*	Vietnam, Nghe An, Pu Mat N.P.	*this work*
13	MT968766	ZMMU R-16431	*Pareas margaritophorus*	Vietnam, Nghe An, Pu Mat N.P.	*this work*
14	MT968767	C11 (tissue)	*Pareas margaritophorus*	China, Hong Kong	*this work*
15	KJ642197	M03 (tissue)	*Pareas margaritophorus*	China, Hong Kong	You *et al*., 2015
16	MK201376	CHS 273	*Pareas margaritophorus*	China, Hainan	Li *et al*., 2020
17	MK201480	CHS 699	*Pareas margaritophorus*	China, Guangdong, Heishiding	Li *et al*., 2020
18	JF827675	—	*Pareas margaritophorus*	China, Hainan	Guo *et al*., 2011
19	MK135097	GP4410	*Pareas margaritophorus*	China, Guangxi, Cangwu	Wang *et al*., 2020
20	MK135098	GP4837	*Pareas margaritophorus*	China, Guangxi, Cangwu	Wang *et al*., 2020
21	MK135100	GP4465	*Pareas margaritophorus*	China, Guangxi, Cangwu	Wang *et al*., 2020
22	MK135099	GP4437	*Pareas margaritophorus*	China, Guangxi, Cangwu	Wang *et al*., 2020
23	MK557848	—	*Pareas margaritophorus*	Thailand, Nakhon Ratchasima	Suntrarachun *et al*., 2020
24	AY425805	—	*Pareas margaritophorus*	Laos, Xe Kong	unpublished
25	AF471082	CAS 206620	*Pareas macularius*	Myanmar, Bago	Lawson *et al*., 2005
26	MT968768	AUP 00175	*Pareas macularius*	Thailand, Chiang Mai	*this work*

Table 2 continued.

#	GenBank A.N.	Specimen ID	Species	Locality	Reference
27	MT968769	ZMMU R-16627	*Pareas macularius*	Vietnam, Gia Lai, Kon Ka Kinh N.P.	*this work*
28	MK557847	—	*Pareas macularius*	Thailand, Chiang Mai	Suntrarachun *et al.*, 2020
29	MT968770	ZMMU R-16628	*Pareas macularius*	Laos, Xaisomboun, Longcheng	*this work*
30	MK201500	CHS 747	*Pareas macularius*	China, Guangxi, Daoyaoshan	Li *et al.*, 2020
31	MT968771	ZMMU R-16629	*Pareas macularius*	Myanmar, Sagaing, Ban Mauk	*this work*
32	MK135101	GP815	*Pareas macularius*	China, Hainan	Wang *et al.*, 2020
33	MK135102	GP2110	*Pareas macularius*	China, Hainan	Wang *et al.*, 2020
34	MK135103	GP2147	*Pareas macularius*	China, Hainan	Wang *et al.*, 2020
35	MK135104	GP4660	*Pareas macularius*	China, Hainan	Wang *et al.*, 2020
36	MK135105	GP4715	*Pareas macularius*	China, Yunnan, Jingdong	Wang *et al.*, 2020
37	MK135106	GP4699	*Pareas macularius*	China, Yunnan, Jingdong	Wang *et al.*, 2020
38	MN970039	—	*Pareas andersonii*	India, Nagaland, Khonoma	Deepak *et al.*, 2020
39	MK201238	CHS 015	*Pareas andersonii*	China, Yunnan, Longchuan	Li *et al.*, 2020
40	MT968772	CAS 235359	*Pareas andersonii*	Myanmar, Chin, Natmataung Mt.	*this work*
41	MT968773	MZMU 1293	*Pareas modestus*	India, Mizoram, Aizawl, Tanhril	*this work*
42	MT968774	MZMU 1665	*Pareas modestus*	India, Mizoram, Aizawl, MZU campus	*this work*
43	MT968775	MZMU 1487	*Pareas modestus*	India, Mizoram, Aizawl, Selesih	*this work*
44	KJ642182	NMNS 05618	*Pareas komaii*	Taiwan, Taitung, Lijia	You *et al.*, 2015
45	KJ642160	I05-ISG3	*Pareas iwasakii*	Japan, Okinawa, Ishigaki	You *et al.*, 2015
46	KJ642122	NMNS 05594	*Pareas atayal*	Taiwan, Yilan, Beiheng Rd.	You *et al.*, 2015
47	MT968776	CAS 248147	*Pareas vindumi*	Myanmar, Kachin, Chipwi, Lukpwi	*this work*
48	MK201455	CHS 656	*Pareas nigriceps*	China, Yunnan, Gaoligongshan	Li *et al.*, 2020
49	KJ642151	NMNS 05652	*Pareas formosensis*	Taiwan, Taitung, Lijia	You *et al.*, 2015
50	MT968777	CAS 221489	*Pareas hamptoni*	Myanmar, Kachin, Naung Mon	*this work*
51	MK135113	GP1294	*Pareas mengziensis*	China, Yunnan, Mengzi	Wang *et al.*, 2020
52	JN230704	HM 2007-S001	*Pareas stanleyi*	China, Guangxi, Guilin	Guo *et al.*, 2011
53	JF827678	KIZ 09965	*Pareas boulengeri*	China, Hubei, Enshi	Guo *et al.*, 2011
54	JF827691	CIB 098269	*Pareas chinensis*	China, Sichuan, Tianquan	Guo *et al.*, 2011
55	MN970038	ADR507	*Pareas monticola*	India, Assam, Orang	Deepak *et al.*, 2020
56	MK135113	GP1292	*Pareas menglaensis*	China, Yunnan, Mengla	Wang *et al.*, 2020
57	JF827677	DL 2008-S039	*Pareas carinatus*	Malaysia (peninsular)	Guo *et al.*, 2011
58	MT968778	CAS 247982	*Pareas carinatus*	Myanmar, Tanintharyi, Yaephyu	*this work*
59	JF827673	KIZ 011963	*Aplopeltura boa*	Malaysia (peninsular)	Guo *et al.*, 2011
60	AY425808	—	*Asthenodipsas tropidonotus*	Indonesia	unpublished
61	KC916755	LSUH C9098	*Asthenodipsas lasgalenensis*	Malaysia, Pahang, Fraser's Hill	Loredo *et al.*, 2013
62	AY425807	—	*Asthenodipsas vertebralis*	Malaysia (peninsular)	unpublished
63	KX660468	FMNH 241296	*Asthenodipsas laevis*	Malaysia, Sabah, Lahad Datu	Figueroa *et al.*, 2016
64	KX660469	FMNH 273617	*Asthenodipsas borneensis*	Malaysia, Sarawak, Bintulu	Figueroa *et al.*, 2016
65	MK340914	BNHS 3376	*Xylophis captaini*	India, Kannam, Kottayam	Deepak *et al.*, 2020

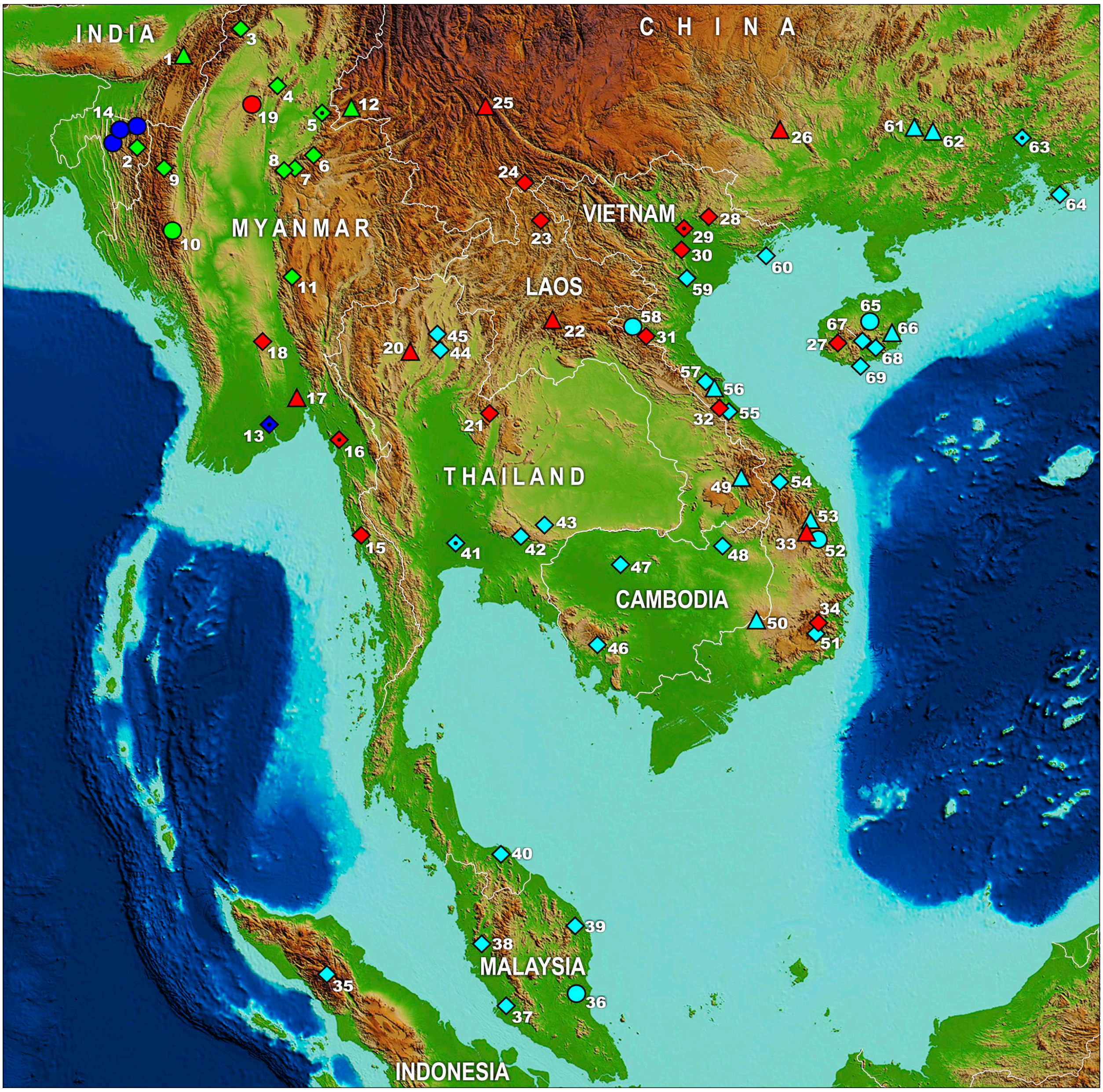


Fig. 1. Map showing distribution of *Pareas margaritophorus-macularius* species complex and location of studied populations. Circles denote localities for which both DNA and morphological data were examined; diamonds denote localities for which only morphological data were available; triangles denote populations for which only DNA data were available; dot in the center of an icon indicate type locality. **Localities**. ***Pareas andersonii*:** India: 1 – Khonoma, Kohima Dist., Nagaland; 2 – Mission Vengthlang, Aizawl, Mizoram; Myanmar: 3 – Laung Nguk, Lahe, Khandi , Sagaing; 4 – Indawgyi N.R., Myitkyina , Kachin; 5 – Bhamo, Kachin (type locality of *Pareas andersonii* Boulenger, 1888); 6 – Shweli, Mongmit, Shan; 7 – Mogok, Mandalay; 8 – Kyatpyin, Mandalay; 9 – Hakha, Chin; 10 – Mindat, Chin; 11 – Kalaw, Taunggyi, Shan; China: 12 – Longchuan, Yunnan; ***Pareas modestus*:** Myanmar: 13 – "Rangun" (Yangon) (type locality of *Pareas modestus* Theobald, 1868); India: 14 – Mizoram (three localities); ***Pareas macularius*:** Myanmar: 15 – Yebyu, Dewei, Tanintharyi; 16 – "Martaban" (Mottama), Mon (type locality of *Pareas macularius* Theobald, 1868); 17 – Bago; 18 – Bago Yoma, Bago; 19 – Banmauk, Sagaing; Thailand: 20 – Doi Inthanon, Chiang Mai; 21 – Dansai, Loei; Laos: 22 – Longcheng, Xaisomboun; 23 – Long Nai, Phongsaly; China: 24 – Jiangcheng, Yunnan; 25 – Jingdong, Yunnan; 26 – Daoyaoshan, Guangxi; 27 – Jianfengling, Hainan; Vietnam: 28 – Ngan Son, Bac Kan; 29 – Tam Dao N.P., Vinh Phuc (type locality of *Amblycephalus tamdaoensis* Bourret, 1935); 30 – Ba Vi N.P., Hanoi; 31 – Nghe An; 32 – Phong Nha-Ke Bang N.P., Quang Binh; 33 – Kon Ka Kinh N.P., Gia Lai; 34 – Lam Dong; ***Pareas margaritophorus*:** Indonesia: 35 – Gunung Leuser N.P., Bukit Lawang, North Sumatra (see Nguyen *et al*., 2020); Malaysia: 36 – Pahang; 37 – Kuala Lumpur; 38 – Perak; 39 – Nahe Ibok, Terengganu; Thailand: 40 – Pattani; 41 – Bangkok (type locality of *Leptognathus margaritophorus* Jan, 1866); 42 – Nadi Bu Phram, Prachin Buri; 43 – Nakhon Ratchasima; 44 – Chiang Mai; 45 – Mae Sa, Chiang Mai; Cambodia: 46 – Areng Chum Noab, Koh Kong; 47 – Phnom Kulen, Siem Reap; 48 – Siem Pang, Stung Treng; Laos: 49 – Xe Kong; Vietnam: 50 – Bu Gia Map N.P., Binh Phuoc; 51 – Da Lat, Lam Dong; 52 – Kon Ka Kinh N.P. and An Khe Dist., Gia Lai; 53 – Kon Chu Rang N.P., Gia Lai; 54 – Phuoc Son, Quang Nam; 55 – Phong Nha-Ke Bang N.P., Quang Binh; 56 – Thanh Thach, Tuyen Hoa, Quang Binh; 57 – Ke Go, Ha Tinh; 58 – Pu Mat N.P., Nghe An; 59 – Cuc Phuong N.P., Ninh Binh; 60 – Bai Tu Long N.P., Quang Ninh; China: 61 – Cangwu, Guangxi; 62 – Heishiding, Guangdong; 63 – Lo Fou Shan, Guangzhou, Guangdong (type locality of *Pareas moellendorffi* Böttger, 1885); 64 – Hong Kong; 65 – "Hainan"; 66 – Haikou, Hainan; 67 – Wuzhi Shan, Hainan; 68 – Diaoluo Shan, Hainan; 69 – Yulin, Hainan.

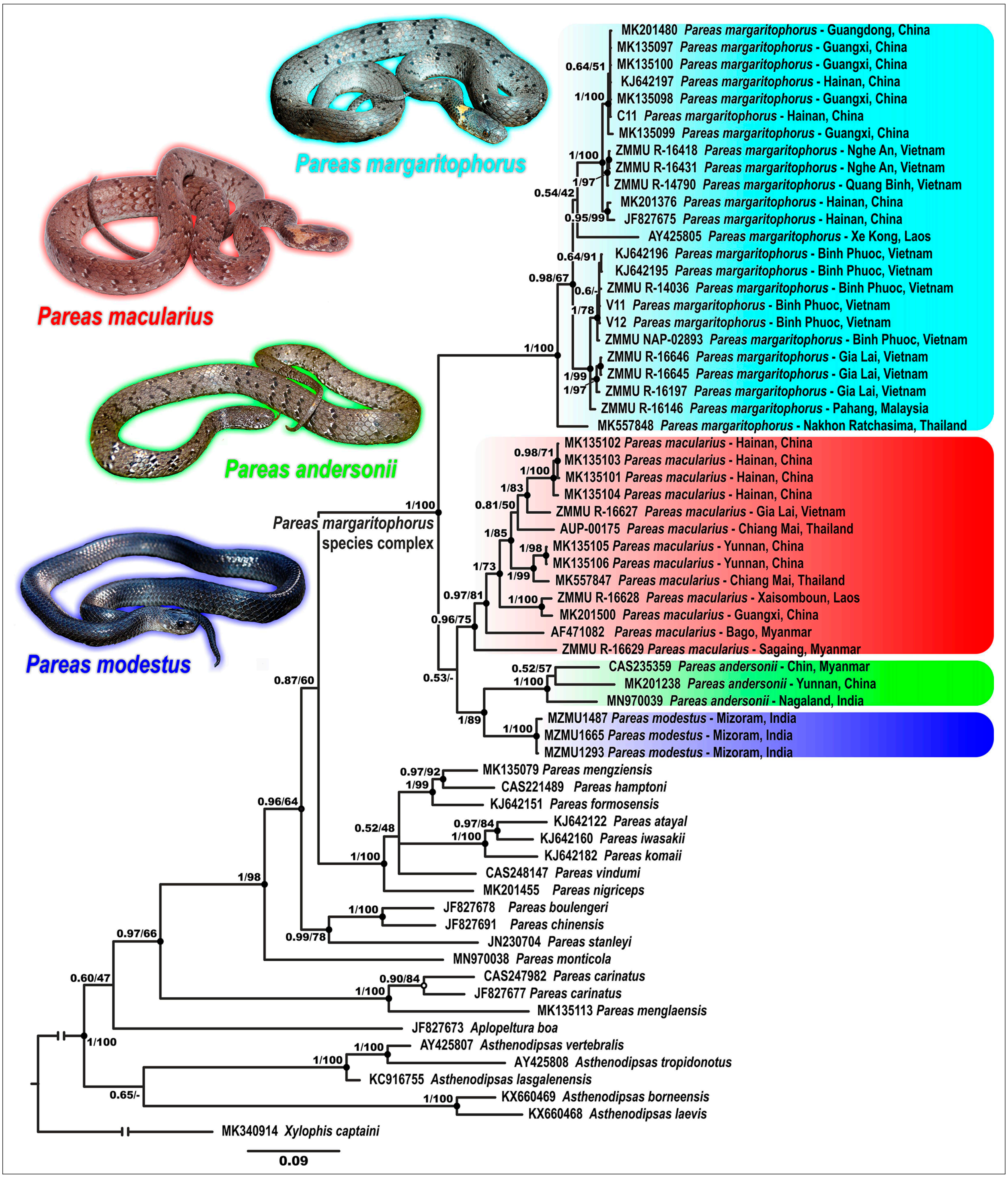


Fig. 2. Bayesian inference tree of *Pareas margaritophorus-macularius* species complex derived from the analysis of 1127 bp of cyt *b* gene fragment. For voucher specimen information and GenBank accession numbers see Table 2. Red, light blue, dark blue, and green color denotes *Pareas macularius*, *P. margaritophorus*, *P. modestus*, and *P. andersonii*, respectively (see Figure 1). Numbers at tree nodes correspond to PP/BS support values, respectively. Photos on thumbnails by N. A. Poyarkov (*Pareas macularius* and *P. margaritophorus*), V. Hrima (*P. modestus*), and by R. Hmar (*P. andersonii*).

PCR products were loaded onto 1.5% agarose gels in the presence of ethidium bromide and visualized in agarose electrophoresis. Successful targeted PCR products were outsourced to Evrogen® (Moscow, Russia) for PCR purification and sequencing; sequence data collection and visualization was performed on an ABI 3730xl Automated Sequencer (Applied Biosystems). The newly obtained sequences were deposited in GenBank under the accession numbers MT968756–MT968778 (see Table 2 for details).

Phylogenetic analyses

To estimate the matrilineal genealogy of the genus *Pareas*, we used the newly obtained cyt *b* sequences together with previously published sequences of *Pareas margaritophorus*, *P. macularius* and *P. andersonii*, as well as representative sequences of 14 other species of *Pareas*, five species of *Asthenodipsas* and *Aplopeltura boa*; the sequence of *Xylophis captaini* was used to root the tree following the results of DEEPAK *et al.* (2019) (see Table 2). In total, cyt *b* sequences for 65 Pareidae specimens were included in the final analysis, including sequences of all currently recognized *Pareas* species except *P. nuchalis*, and 43 sequences of *Pareas margaritophorus-macularius* complex members representing all nominal species within the group.

Nucleotide sequences were initially aligned in MAFFT v.6 (KATOH *et al.*, 2002) with default parameters, and subsequently checked by eye in BIOEDIT 7.0.5.2 (HALL, 1999) and adjusted. The mean uncorrected genetic *p*-distances between sequences were determined with MEGA 6.0 (TAMURA *et al.*, 2013). The optimal evolutionary models for the data set were estimated in MODELTEST v.3.6 (POSADA & CRANDALL, 1998). The best-fitting models of DNA evolution for both BI and ML analyses were HKY+I+G for the 1st and 2nd codon-partitions, and GTR+I+G for the 3rd codon-partition as suggested by the Akaike Information Criterion (AIC).

The matrilineal genealogy of the Pareidae was inferred using Bayesian inference (BI) and Maximum Likelihood (ML) approaches. BI was conducted in MRBAYES 3.1.2 (RONQUIST & HUELSENBECK, 2003); Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for 50 million generations and sampled every 1000 generations. Two independent MCMCMC runs were performed and checked to be sure the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER v1.6 (RAMBAUT *et al.*, 2007). We excluded the first 25% of trees as burn-in before the loglikelihood scores stabilized. The confidence in tree topology was assessed by the posterior probability (PP) (HUELSENBECK & RONQUIST, 2001). The ML tree was generated using the IQ-TREE webserver (NGUYEN *et al.*, 2015); preceded by the selection of substitution models using the Bayesian Information Criterion (BIC) in MODELFINDER (KALYAANAMOORTHY *et al.*, 2017), which supported TrN+I+G for cyt *b* codon positions 1 and 2, and GTR+F+I+G for position 3. Confidence in tree topology for ML analysis was assessed by 1000 bootstrap replications (BS). We a priori regarded the tree nodes with BS values 75% or above and PP values over 0.95 as

Table 3. Uncorrected *p*-distance (percentage) between the sequences of cyt *b* mtDNA fragment (below the diagonal), estimate error (above the diagonal), and intraspecific genetic *p*-distance (on the diagonal, in bold) of the *Pareas* species included in phylogenetic analyses.

No.	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	*P. margaritophorus*	**3.7**	1.3	1.6	1.5	1.7	1.8	1.6	1.8	1.9	1.7	1.5	1.6	1.8	1.5	1.8	1.9	2.0	1.9
2	*P. macularius*	14.8	**7.6**	1.3	1.1	1.6	1.6	1.5	1.6	1.7	1.5	1.5	1.5	1.7	1.5	1.6	1.8	1.9	1.9
3	*P. andersonii*	17.2	15.1	**9.0**	1.3	1.7	1.8	1.6	1.7	1.6	1.6	1.7	1.6	1.7	1.5	1.6	1.8	2.0	2.0
4	*P. modestus*	14.9	11.6	12.5	**0.2**	1.7	1.8	1.6	1.7	1.7	1.5	1.6	1.5	1.7	1.6	1.8	1.8	2.1	1.9
5	*P. mengziensis*	20.7	20.1	20.8	19.2	—	1.2	0.9	1.7	1.6	1.6	1.3	1.3	1.7	1.6	1.7	1.5	1.9	1.8
6	*P. hamptoni*	22.0	20.5	21.7	20.4	8.4	—	1.2	1.7	1.8	1.9	1.5	1.5	1.8	1.7	1.8	1.6	1.9	2.2
7	*P. formosensis*	19.2	18.7	20.2	19.0	7.0	9.4	—	1.5	1.5	1.6	1.3	1.3	1.4	1.6	1.6	1.5	1.8	1.9
8	*P. atayal*	20.2	20.0	21.1	17.8	16.4	17.1	16.4	—	1.1	1.3	1.6	1.6	1.7	1.8	1.7	1.7	1.8	1.7
9	*P. iwasakii*	20.7	20.7	20.7	19.9	15.9	16.4	15.9	8.0	—	1.3	1.6	1.6	1.7	1.8	1.7	1.7	1.9	1.8
10	*P. komaii*	20.0	18.6	19.5	17.1	17.1	18.8	15.9	10.4	10.8	—	1.6	1.5	1.9	1.8	1.7	1.7	1.8	1.8
11	*P. vindumi*	19.8	19.5	21.8	19.5	12.1	13.2	12.0	16.6	16.6	16.8	—	1.4	1.8	1.8	1.8	1.7	2.0	1.8
12	*P. nigriceps*	18.6	18.4	18.6	16.4	12.7	13.2	12.7	15.7	16.1	16.2	12.3	—	1.8	1.6	1.8	1.6	1.9	1.9
13	*P. boulengeri*	18.9	17.5	19.2	17.3	16.9	16.4	14.5	17.8	16.9	17.6	17.4	16.9	—	1.3	1.6	1.8	2.0	2.0
14	*P. chinensis*	18.4	16.9	18.4	17.0	16.4	18.3	15.7	18.5	18.3	18.3	17.1	16.2	8.9	—	1.6	1.8	1.9	2.1
15	*P. stanleyi*	19.4	18.3	19.2	18.3	19.8	19.7	19.3	19.2	19.2	17.4	19.5	19.0	14.2	14.2	—	1.9	2.0	2.2
16	*P. monticola*	22.2	19.8	21.1	19.4	19.2	20.0	18.5	20.7	20.7	20.2	19.3	19.2	19.0	17.1	19.8	—	1.9	2.0
17	*P. carinatus*	24.5	23.0	24.0	24.3	23.1	23.6	22.2	23.4	24.5	24.6	23.5	23.0	21.6	22.5	24.4	21.6	**6.5**	1.7
18	*P. menglaensis*	24.9	23.0	23.7	23.0	23.6	24.4	23.9	23.3	23.4	24.1	23.6	23.3	22.9	23.4	25.8	22.9	13.7	—

sufficiently resolved; BS values between 75% and 50% and PP values between 0.95 and 0.90 were regarded as tendencies; while lower values were regarded as lack of node support (Huelsenbeck & Hillis, 1993).

Results

Sequence variation

Among the 1127 bp of the final cyt *b* alignment, 458 sites were conserved and 668 sites exhibited variation, of which 558 were found to be parsimony-informative. The transition-transversion bias (R) was estimated as 4.16. Nucleotide frequencies were A = 29.77%, T = 26.69%, C = 31.20%, and G = 12.34% (data given for ingroup only).

MtDNA genealogy

Bayesian inference (BI) and maximum likelihood (ML) analyses resulted in essentially identical topologies, differing only in two poorly supported nodes (Fig. 2). Our phylogenetic analyses were generally concordant with the earlier phylogenies of the group by Guo *et al*. (2011) and You *et al*. (2015), and suggest monophyly of the genus *Pareas* with respect to other Pareinae genera (0.97/66; hereafter nodal support values given for PP/BS, respectively); monophyly of the genus *Asthenodipsas* received no support (0.65/-, see Fig. 2).

Within the genus *Pareas*, *P. carinatus* and *P. menglaensis* formed a sister lineage to all other species included in the analysis with strong support (1.0/98). Within the remaining species of *Pareas*, *P. monticola* formed a distant lineage sister to all other species with moderate values of node support (0.96/64). The remaining species of *Pareas* clustered in three well-supported monophyletic groups; however, the order of branching between them was not fully resolved. The first clade (*P. chinensis* group; 0.99/78) included *P. chinensis*, its sister species *P. boulengeri* (1.0/100), and a more distant *P. stanleyi*. The second clade (*P. hamptoni* group; 1.0/100) included *P. hamptoni*, its sister species *P. mengziensis* (0.97/92), and a more distant *P. formosensis* (1.0/99), a clade of East Asian island species *P. atayal*, *P. iwasakii*, and *P. komaii* (1.0/100); and *P. vindumi* with *P. nigriceps*; phylogenetic relationships between the two clades and the remaining species of *P. hamptoni* group remain unresolved (Fig. 2). Finally, the third clade joined the members of *P. margaritophorus-macularius* species complex (1.0/100), and was represented by four strongly supported species-level subclades, representing *P. macularius* (0.96/75), *P. andersonii* (1.0/100), *P. modestus* (1.0/100), and *P. margaritophorus* (1.0/100) (Fig. 2). *Pareas andersonii* and *P. modestus* were suggested as sister species with strong support (1.0/89), phylogenetic relationships between these species, plus *P. macularius* and *P. margaritophorus* were essentially unresolved.

The four species of *P. margaritophorus-macularius* complex demonstrated different levels of internal substructuring. Within *P. macularius* our analysis revealed a deep geographic structure: the sample from northern Myanmar (Sagaing) was found to be the most divergent forming a sister lineage with respect to all other samples (0.97/81), which included lineages from southern Myanmar (Bago), Laos + Guangxi, China (1.0/100), Thailand + Yunnan, China (1.0/99), central Vietnam and Hainan, China (1.0/83) (Fig. 2). *Pareas andersonii*, which was found to be strongly separated from genetically uniform *P. modestus*, was represented in our analysis by three populations from Myanmar (Chin), India (Nagaland) and China (Yunnan), each of them deeply divergent from another (Fig. 2). Finally, within *P. margaritophorus* a more shallow structure was observed, with the basal position occupied by a single specimen from Thailand forming a sister lineage to all remaining populations (0.98/67), which included the southern lineage (southern to central Vietnam + Peninsular Malaysia; 1.0/99), northern lineage (China + northern to central Vietnam; 1.0/100), and an orphaned sample from southern Laos (see Fig. 2).

Genetic distances

The uncorrected *p*-distances for the cyt *b* gene are shown in the Table 3. The interspecific distances within *Pareas* varied from $p = 8.0\%$ (between *P. iwasakii* and *P. atayal*) to $p = 25.8\%$ (between *P. menglaensis* and *P. stanleyi*). The interspecific differences among the members of *P. margaritophorus-macularius* species complex varied from $p = 11.6\%$ (between *P. macularius* and *P. modestus*) to $p = 17.2\%$ (between *P. andersonii* and *P. margaritophorus*). Intraspecific genetic differentiation was high in *P. andersonii* ($p = 9.0\%$) and *P. macularius* ($p = 6.6\%$), but was notably lower for *P. margaritophorus* ($p = 3.8\%$) and *P. modestus* ($p = 0.2\%$) (see Table 3).

Taxonomy

On the basis of morphological analysis, we could identify a major level of separation between the four taxa of the *P. margaritophorus-macularius* species complex both in morphology and mtDNA cyt *b* gene sequences. Species in this group can be consistently distinguished from each other by the characteristics of pholidosis, body shape and color, namely by the number of keeled dorsal scale rows, numbers of ventral and subcaudal scales, coloration of the nuchal collar, presence or absence of cross-bands consisting of bicolored spots, and belly pattern (see below).

At the same time, the molecular phylogenetic analyses demonstrated the presence of four well-supported clades within *P. margaritophorus-macularius* species complex, fully coinciding with the recognized morphospecies in this group. Our integrative data confirm the distinctiveness of *P. macularius* from *P. margaritophorus* in concordance with the molecular data, which was previously demonstrated only from morphological line of evidence (HAUSER, 2017). Furthermore, phylogeny clearly indicates that a specimen of *P. andersonii* from Myanmar is distinct from both *P. macularius* from *P. margaritophorus*, and is grouped together with two more specimens of *P. andersonii* from Nagaland (India) and Yunnan (China), originally misidentified as *P. macularius* (see DEEPAK *et al*., 2020) and *P. margaritophorus* (see LI *et al*., 2020), respectively. These data strongly suggest that *P. andersonii* is a valid species and clarifies its distribution. *P. andersonii* seems to occur through Myanmar, northeast India and the westernmost part of Yunnan Province of China. Finally, our molecular phylogenetic analyses confirmed the species-level divergence of the uniform dark-colored *Pareas* from Mizoram State of India, identified herein as *P. modestus*. Phylogenetically *P. modestus* is suggested as the sister species of *P. andersonii*, the stable morphological differences in coloration and body scalation confirm its distinctiveness from the three remaining members of the species complex. Hence, based on integrative analysis of morphological and molecular characters, we demonstrate that the *P. margaritophorus-macularius* complex is comprised of four distinct species, including *P. andersonii* and *P. modestus* resurrected herein. Below we provide detailed taxonomic accounts and revised diagnoses for these two poorly known species of *Pareas*.

Taxonomic accounts

Pareas andersonii Boulenger, 1888
Anderson's slug snake

Figures 3, 4A–F, 7A, 8A–B.

Chresonymy.
Pareas macularius – (in part) SMITH (1943).
Pareas macularius – (in part) WOGAN *et al*. (2008).
Pareas macularius – (in part) WALLACH *et al*. (2014).
Pareas margaritophorus – BIAKZUALA & LALREMSANGA (2019).
Pareas macularius – (in part) DEEPAK *et al*. (2020).
Pareas margaritophorus – (in part) LI *et al*. (2020).

Lectotype. MSNG 30861, **Paralectotype.** MSNG 30860, designated by CAPOCACCIA (1961).

Type locality. Bhamò and Kakhinen Hills, Burma (now Kachin State, Myanmar).

Taxonomic comment. BIAKZUALA & LALREMSANGA (2019) recorded *Pareas margaritophorus* from Mizoram, India based on specimen number MZMU 916 however lacking detailed morphological description. Re-examination of this specimen demonstrated that it belongs to *P. andersonii* resurrected herein (Fig. 4e, f).

Material examined. Males (*n* = 6). **Myanmar:** NHM(UK) 1904.4.26.14 in Mandalay Division; NHM(UK) 1925.12.22.1 in Shweli Town, Mongmit Township, Shan State; NHM(UK) 1926.3.17.9 (elevation ca. 1680 m a.s.l.) in Kalaw Township, Taunggyi District, Shan State; CAS 235359 collected on 8 Jun 2004 by A.K. Shein and T. Nyo in Tin Myo's house, near Natnataung NP. office, Old Kanpetlet township, Mindat District, Chin State (21.204639°N, 94.035528°E; elevation ca. 1810 m a.s.l.); CAS 245296 collected on 15 May 2009 by M. Hlaing, S.L. Oo, Z.H. Aung, and Y.M. Win in Luang Nguk Village, Lahe Township, Khandi Distinct, Sagaing Division (26.156222°N, 95.533278°E; elevation ca. 830 m a.s.l.), and CAS 245377 collected on 21 May 2009 by M. Hlaing, S.L. Oo, Z.H. Aung and Y.M. Win in Luang Nguk Village, Lahe Township, Khandi Distinct, Sagaing Division (26.154944°N, 95.521472°E; elevation ca. 1110 m a.s.l.). **Females** (*n*=7). **Myanmar**: NHM(UK) 1901.9.14.11 (elevation ca. 1340 m a.s.l.), and NHM(UK) 1904.4.26.13 in Mandalay Division; CAS 235218 collected on 14 May 2006 by A.K. Shein and L. Shein in Ke Har Stream, Kanpatlat Town, Mindat District, Chin State (21.205611°N; 94.050306°E; elevation ca. 1310 m a.s.l.), CAS 233330 collected on 12 August 2003 by K.S. Lwin, A.K. Shein and H. Tun in Haka Township, Chin State (22.798333°N, 93.563222°E; elevation ca. 1600 m a.s.l.); CAS 241270 collected on 20 July 2008 by J.A. Wilkinson, J.V. Vindum, S.L. Oo, K.T. Kyaw and M. Win in vicinity Kyang Kyar Village, Indawgyi Lake Wildlife Sanctuary, Moenyin Township, Myitkyina District, Kachin State (25.303472°N, 96.354167°E; elevation ca. 260 m a.s.l.); NHM(UK) 1908.6.23.94 (specific locations not available); **India**: MZMU 916 collected on 5 October 2016 by S. Lallianzela in south Vanlaiphai, Lunglei District, Mizoram State (22.80351°N, 92.99543⁰E; elevation ca. 1231 m a.s.l.).

Diagnosis. *Pareas andersonii* differs from all other members of the genus by the combination of the following characters: slender grayish body; medium size (total length 278–481 mm); two anterior temporals, elongated; frontal scale is hexagonal with shield-shaped with the lateral sides converging posteriorly; anterior pair of chin shields are longer than broad; loreal not contacting the eye; prefrontal contacting the eye; one subocular elongate, crescent and one postocular; median vertebrals not enlarged; 7–8 infralabial scales; 15 dorsal scale rows with 5–9 rows slightly keeled at midbody; 141–162 ventrals; 35–47 subcaudals, divided; body color grey to dark grey, dorsal pattern consists of irregularly scattered black and white bicolored spots not forming cross-bands; no markings on the head, no collar; belly with rows of squarish, black blotches.

Description and variation. Medium sized (TL: 396.67 ± 68.74 mm, our longest specimen was a female of 481 mm [CAS 233330]). Body stout, round. Head slight distinct from neck, slightly rounded and thick, distinctly compressed laterally and oval in dorsal view. Rostral scale slightly visible from above; single nasals; two internasals, widely in contact with each other with a diagonal suture; two large irregular pentagonal prefrontals, much larger than internasals and with a slightly diagonal suture between; one frontal scale is hexagonal with shield-shaped with the lateral sides converging posteriorly, smaller than parietals; parietals very large, subequal in length to its distance from internasals; presubocular absent; usually one subocular scale elongated and crescent-shaped and one postocular (occasionally subocular and

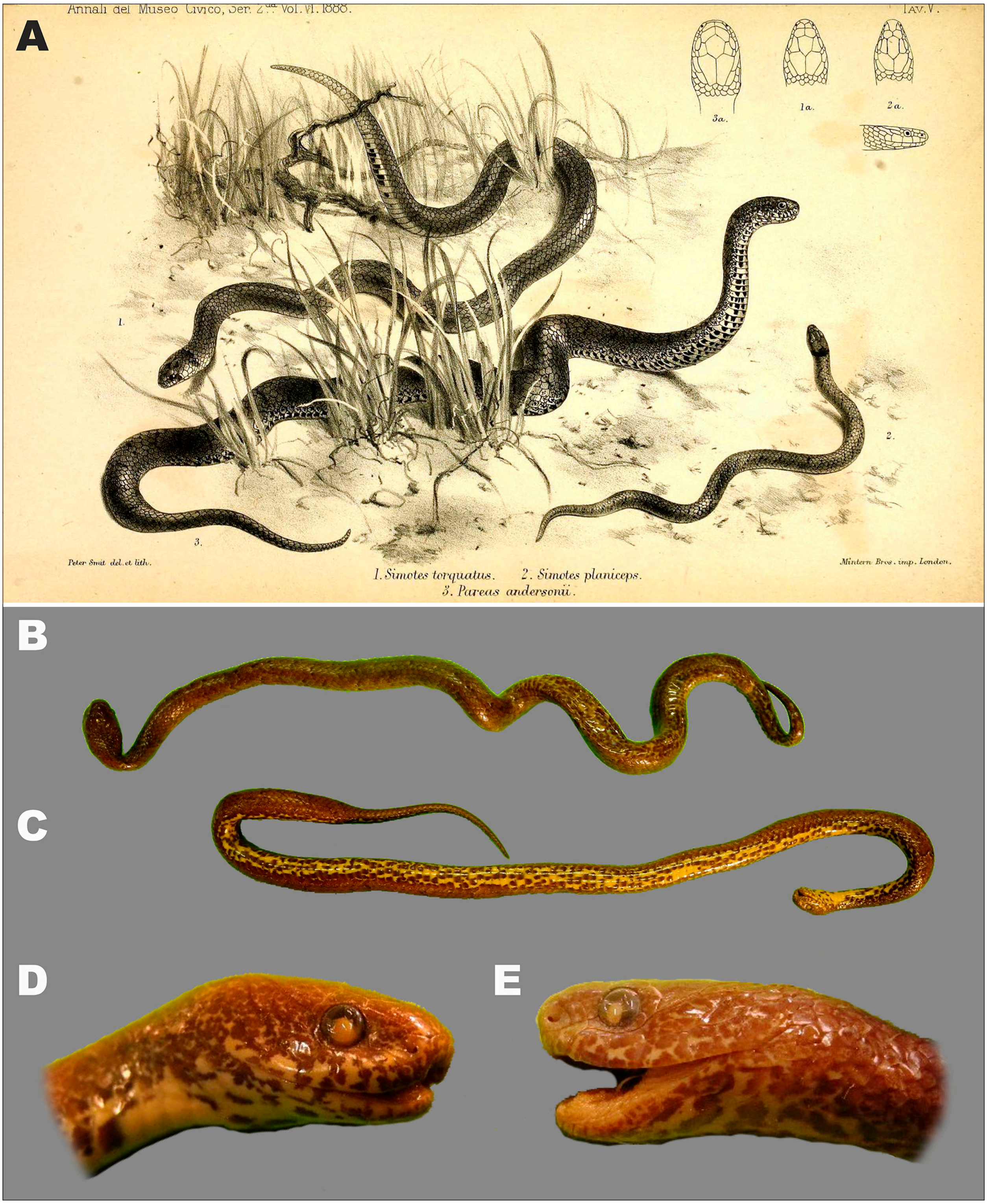
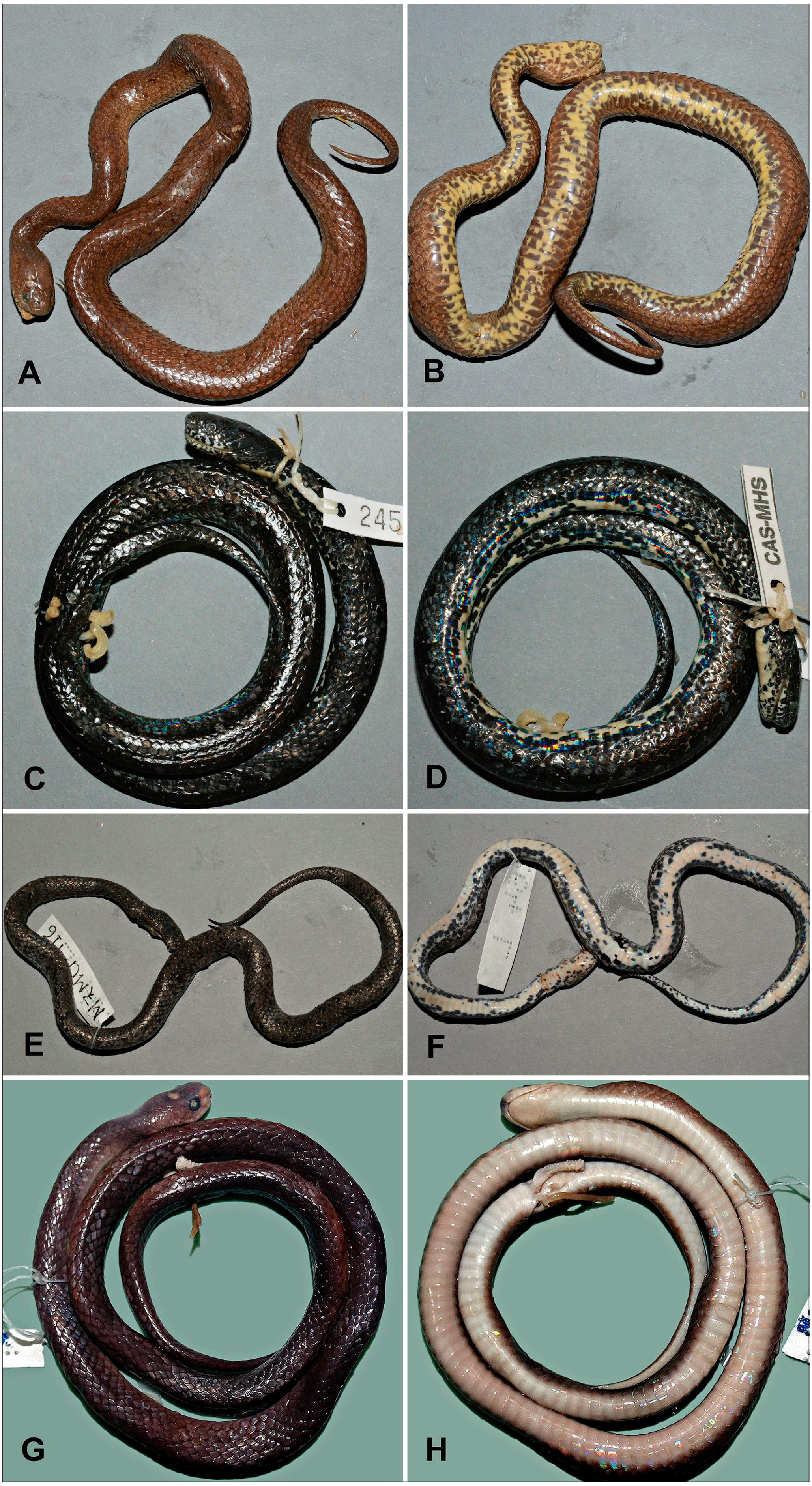


Fig. 3. Type series of *Pareas andersonii* Boulenger, 1888 (Kachin Sate, Myanmar). **A.** Original figure illustrated by Boulenger, 1988; **B, E**: paralectotype MSNG 30860 general view and lateral view of head, respectively; **C, D**: lectotype MSNG 30861 general view and lateral view of head, respectively. Photos by G. Vogel.

postocular fused into a scale); one loreal not contacting the eye; prefrontal contacting the eye; temporals usually 2 + 3, crescent-shaped, elongated; supralabials usually 7, not touching eye; 7 – 8 infralabials, three pairs of chin shields interlaced, no mental groove under chin and throat, anterior pair of chin shields are longer than broad; dorsal scales in 15 – 15 – 15 rows around body, slightly keeled in 5 – 9 scale rows at midbody; ventrals 141 – 153 (149.33 ± 5.39, n = 6) in males and 155 – 162 (158.00 ± 2.71, n = 7) in females, slight angulate laterally; preventrals usually 1; cloacal scale undivided; subcaudals 40 – 47 pairs (43.00 ± 2.83, n = 6) in males and


A
B
245
C
CAS-MHS
D
E
F
G
H

35–45 pairs (40.00 ± 3.56, *n* = 7) in females; relative tail length on 0.170 ± 0.009 in males (0.159–0.180, *n* = 6) and 0.151 ± 0.010 in females (0.134–0.166, *n* = 7).

Colouration. In life dorsum and body sides with glossy-grey background coloration with bluish tint (see Fig. 8A, B), covered with numerous black spots of one scale in size posteriorly edged with white; dorsal black and white spots form few irregular rows anteriorly, and are scattered randomly at midbody and posteriorly; head dark grey, dorsally with numerous black spots and vermiculations, light nuchal spot or collar absent, laterally head with dense white mottling, labial scales white with dark spots marking the edges; ventral surfaces of head white with black spots; ventral surfaces of body and tail with light beige background densely covered with numerous rectangular spots on every ventral shield; dark spots form a line on the ventralmost row of dorsals edging the lighter coloration of ventrals. In preservative (based on MSNG 30860-30861) head and dorsal glossy blackish dorsum with few bicolored spots, not clear; upper labials, loreal region mottled white; ventral cream with rows of rectangular, black blotches (Fig. 3).

Comparison. *Pareas andersonii* shares most morphological characters with the closely related species of the *P. margaritophorus-macularius* complex (Table 4, Fig. 7, 8).

P. andersonii differs from *P. macularius* by having: slightly smaller size (maximum to 481 mm vs. 517 mm), lower number of subcaudals (41.38±3.48 vs. 46.20±4.33); nuchal collar colour and pattern (indistinct vs. usually distinct W or butterfly-shaped whitish or brown); few cross-bands of bicolored spots (vs. many); body grey to dark grey (vs. brownish-grey); belly with squarish black blotches (vs. dense speckling); head thicker, rounded (vs. compressed, oval); head slightly distinct from neck (vs. clearly distinct); anterior temporal elongated and long (vs. shorter).

P. andersonii differs from *P. modestus* (see below) by having: a slight larger size (maximum to 482 mm vs. 357 mm); dorsals slightly keeled in 5–9 rows at midbody (vs. 3–5 rows), body grey to dark grey with few bicolored spots (vs. uniform greyish black to blackish); belly with squarish black blotches (vs. uniform whitish).

P. andersonii differs from *P. margaritophorus* by having a larger size (391.08 ± 68.74 mm vs. 310.18 561± 43.48 mm), a higher number of ventrals (158.33 ± 6.24 vs. 144.67 ± 6.63), 5–9 dorsal rows slightly keeled at midbody (vs. all rows smooth), nuchal collar colour and pattern (indistinct vs. usually cream or pinkish, speckles); without cross-bands of bicolored spots (vs. present); body grey to dark grey (vs. brownish-grey); belly with squarish black blotches (vs. sparse speckling).

Distribution. *P. andersonii* is presently known from Myanmar (Kachin, Chin, Shan states and Sagaing, Mandalay divisions); India (Mizoram and Nagaland states) and China (Longchuan, Yunnan Province) (see Fig. 1).

Phylogenetic position. A member of *P. margaritophorus-macularius* species complex; sister species of *P. modestus* Theobald, 1868 (genetic divergence in cyt *b* gene *p* = 12.5%). Significant genetic differentiation among the samples of *P. andersonii* from Myanmar, India and China requires further studies.

Natural history. Because this population was not recognized as an independent taxon until now, little is known about its natural history apart from knowledge pertaining to the genus as a whole. Wogan *et al*. (2008) report *P. andersonii* sympatric with *P.* cf. *monticola* in Chin State. New specimens in Myanmar (CAS) were found between 9:00–22:13h in bush, 3 m above ground. The air temperatures at the times of collection ranged from 20–30°C and relative humidity from 65–91%. This species is distributed within the elevation ca. 260–1810 m a.s.l. (see http://portal.vertnet.org/o/cas/herp?id=urn-catalog, accessed in May 2020).

Pareas modestus Theobald, 1868

Black slug snake

Figures 4G–H, 7B, 8C.

Chresonymy.

Pareas modestus – Boulenger 1896.
Pareas macularius – Wall (1909).
Pareas macularius – (in part) Smith (1943).
Pareas macularius – (in part) Wallach *et al*. (2014).

Holotype. ZSI 8028 (lost, see below)

Type locality. Rangun [sic], Pegu, Burma (now Yangon Division, Myanmar).

Taxonomic comment: The description of *P. modestus* by Theobald, 1868 is not especially short for that time period, but most basic characters are missing. Theobald gave no length, no ventral and no subcaudals count for his new species. The holotype was deposited in the "Museo Soc. Asiaticae Bengalensis", today the collection of the Zoological Survey of India in Kolkata. It is lost according to Das (1998) who mentioned the register entry from 13 May 1921 for the holotype, registered as ZSI 8028 as: "Stolen from almirah in lab". So the type specimen is lost. However, a redescription of the holotype was made by Wall (1909). Despite the fact that the description is quite detailed, he did not give the length of

Fig. 4. Dorsolateral and ventral aspects of *Pareas andersonii* – **A, B**: NHM(UK) 1904.4.26.13 (Mandalay Division, Myanmar); **C, D**: CAS 245296 (Sagaing Division, Myanmar), **E, F**: MZMU 916 (Mizoram State, India); and *Pareas modestus*: **G, H**: MZMU 274 (Mizoram State, India). Photos by G. Vogel (A-F) and HT. Lalremsanga (G, H).

Table 4. Comparison of measurements and meristic characters in *Pareas andersonii*, *P. modestus*, *P. macularius*, and *P. margaritophorus*.

Characters		*P. andersonii*	*P. modestus*	*P. macularius*	*P. margaritophorus*
TL	Min – Max	278 – 481	226 – 357	252 – 517	213 – 394
	Mean ± SD	387.92 ± 66.80	304.25 ± 40.86	406.12 ± 69.23	310.18 ± 43.48
	n	13	8	15	49
TaL/TL	Min – Max	0.13 – 0.18	0.13 – 0.19	0.15 – 0.20	0.14 – 0.22
	Mean ± SD	0.16 ± 0.01	0.17 ± 0.02	0.17 ± 0.01	0.18 ± 0.03
	n	13	8	15	49
SL	Min – Max	6 – 7	7	7	6 – 9
	Mean ± SD	6.96 ± 0.14	7.00 ± 0.00	7.00 ± 0.00	7.13 ± 0.40
	n	13	9	15	51
IL	Min – Max	7 – 8	7	6 – 8	5 – 9
	Mean ± SD	7.42 ± 0.45	7.00 ± 0.00	7.40 ± 0.54	7.23 ± 0.50
	n	13	8	15	51
VEN	Min – Max	141 – 162	151 – 159	151 – 173	133 – 160
	Mean ± SD	154.00 ± 6.00	155.56 ± 2.35	157.93 ± 6.06	144.67 ± 6.63
	n	13	9	14	51
SC	Min – Max	35 – 47	35 – 46	39 – 53	35 – 54
	Mean ± SD	41.38 ± 3.48	40.44 ± 4.33	46.20 ± 4.33	43.60 ± 5.07
	n	13	9	15	550
KMD	Min – Max	5 – 9	3 – 5	5 – 11	0
	Mean ± SD	6.25 ± 1.49	4.78 ± 0.67	7.46 ± 1.85	0
	n	8	9	14	52
Body shape		Stout, round	Slender, compressed	Slender, compressed	Slight stout, round
The ratio of head to neck		Slight distinct	Slight distinct	Clearly distinct	Clearly distinct
Coloration of the nuchal collar		Indistinct	None	W or butterfly-shaped whitish or brown	Cream or pinkish, no speckles
Cross-bands of bicolored spots		Indistinct	None	Distinct	Distinct
Body color		Grey to dark grey	Completely black	Brownish-grey	Brownish-grey
Pattern belly		Squarish black blotches	Uniform light greyish-white	Dense speckling	Sparse speckling
Distributions		Myanmar, India, China	Myanmar, India	India, Southern China, Myanmar, Thailand, Indochina	Southern China, Thailand, Myanmar, Indochina, Malaysia, Indonesia, Singapore (introduced)

the specimens or the length of the tail, so these data are unknown.

Material examined. Males (*n* = 4). Mizoram, India: MZMU 274 collected on 12 August 2011 by T.B.C. Lalbiaknunmawia in Sawleng Village, Aizawl District (23.981913°N, 92.931285°E; elevation ca. 1170 m a.s.l.); MZMU 1293 collected on 21 July 2018 by L. Rinsanga in Tanhril Village, Aizawl District (23.736575°N, 92.675996°E; elevation ca. 960 m a.s.l.); MZMU 1487 collected on 21 August 2019 by V. L. Hruaia in Selesih Village, Aizawl District (23.802727°N, 92.732751°E; elevation ca. 1136 m a.s.l.); MZMU 1537 collected on 12 August 2011 by V. Hrima in Khawrihnim, Mamit District (23.981913°N, 92.931285°E; elevation ca. 1170 m a.s.l.). **Females (*n* = 4): Mizoram, India:** MZMU 275 collected on 27 June 2010 by T.B.C. Lalbiaknunmawia in Sawleng Village, Aizawl District, India (23.979949°N, 92.924811°E; elevation ca. 1135 m a.s.l.); MZMU 1193 collected on 21 July 2018 by L. Rinsanga in Tanhril, Aizawl District (23.738443°N, 92.673363°E; elevation ca. 950 m a.s.l.); MZMU 1604 collected on 4 October 2019 by J.C. Lalmuanawma in Suangpuilawn Village, Aizawl District (23.952506°N, 93.041164°E; elevation ca. 1060 m a.s.l.); and MZMU 1665 collected on 14 June 2020 by HT Decemson at MZU campus main gate, Aizawl District (23.440112°N, 92.400458°E; elevation ca. 850 m a.s.l.).

Diagnosis. *Pareas modestus* differs from all other members of the genus *Pareas* by the combination of the following morphological characters: slender black body, small size (total length 226–357 mm); two anterior temporals, elongated; frontal scale is hexagonal with shield-shaped with the lateral sides converging posteriorly; anterior pair of chin shields is longer than broad; loreal not contacting the eye; prefrontal contacting the eye one subocular and one postocular; not enlarged median vertebral; 7 – 8 infralabial scales; 15 dorsal scale rows slightly keeled in 3 – 5 scale rows at midbody; 151 – 159 ventrals; 35 – 46 subcaudals, divided; body pattern uniform greyish black to black dorsum lacking cross-bands of bicolored spots and markings on the head; no collar; ventral surface uniform light greyish-white.

Description and variation. Small-sized (TL: 303.43 ± 44.06 mm, our longest specimen was a female with 402 mm [MZMU 274]). Body slender, notably flattened laterally. Head distinct from neck narrowly elongated, distinctly compressed laterally and oval in dorsal view.

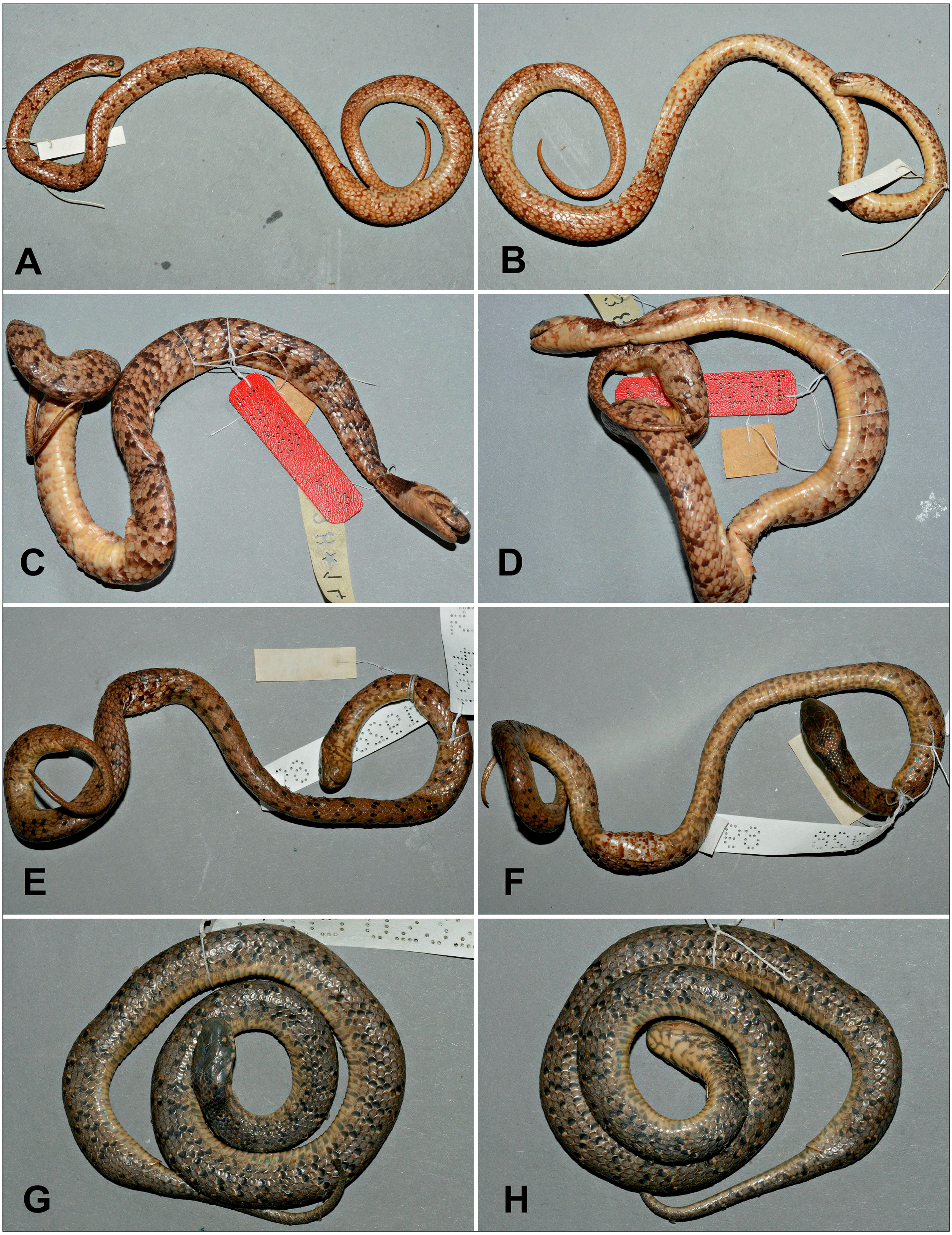


Fig. 5. Dorsal and ventral views of *Pareas macularius* – **A, B**: NHM(UK) 1946.1.20.8 (Holotype, Taninthary Divison, Myanmar), **C, D**: MNHN 1938.148 (syntype of *Amblycephalus tamdaoensis* Bourret, 1935, Tam Dao N.P., Vinh Phuc Province, Vietnam); **E, F**: MNHN 1994.743 (north Laos); **G, H**: MNHN 2005.0232 (Long Nai, Phongsaly Province, Laos). Photos by G. Vogel.

Rostral scale slightly visible from above; single nasals; two internasals, widely in contact with each other with a diagonal suture; two large irregular pentagonal prefrontals, much larger than internasals and with a slightly diagonal suture between; one frontal scale is hexagonal with shield-shaped with the lateral sides converging

Fig. 6. Dorsal and ventral view of *Pareas margaritophorus* – **A, B**: MNHN 599 (Holotype, Bangkok Capital, Thailand), **C, D**: SMF 20790 (Holotype of *Pareas moellendorffi* Böttger, 1885, Lo Fou Shan, Guangzhou Province, China). Photos by G. Vogel.

posteriorly, smaller than parietals; parietals very large, subequal in length to its distance from internasals; presubocular absent; one subocular scale elongated and crescent-shaped and one postocular (occasionally subocular and postocular fused into a scale); one loreal not contacting the eye; prefrontal contacting the eye; temporals usually 2+3 (occasionally 2+2), crescent–shaped, elongated; supralabials 7, not touching eye; 7 infralabials, three pairs of chin shields interlaced, no mental groove under chin and throat, anterior pair of chin shields are longer than broad; dorsal scales in 15–15–15 rows around body, slightly keeled in 3–5 scale rows at midbody; ventrals 151–157 (155.00±2.35, n=5) in males and 153–159 (156.25±2.50, n=4) in females, slight angulate laterally; preventrals 1; cloacal scale undivided; subcaudals 37–46 pairs (43.20±3.83, n=5) in males and 35–38 pairs (37.00±1.41, n=4) in females; relative tail length on 0.143–0.195 in males (0.173±0.023, n=4) and 0.121–0.158 in females (0.139±0.017, n=4).

Colouration (in life base MZMU 275)**.** Head and dorsal uniformly greyish-black to blackish dorsum with upper labials and temporals mottled in greyish-white; ventral shields up to the tail tip in uniform light greyish-white (Fig. 8C).

Distribution. Currently known from Yangon State, south Myanmar and Mizoram State, northeast India, it may be expected in neighboring states of Assam, Manipur and Nagaland (India) (Fig. 1).

Phylogenetic position. A member of *P. margaritophorus-macularius* species complex; sister species of *P. andersonii* Boulenger, 1888 (genetic divergence in cyt *b* gene p=12.5%).

Natural history. In contrast to the sympatric congener species *P. monticola*, *P. modestus* in Mizoram, India, is likely a crepuscular species according to our observations in captivity, and due to the fact that all of the specimens were collected during dawn and dusk. It is also presumed to be a secretive, predominantly terrestrial species since they were found on the ground and crevices of rocks in the vicinity of damp forested areas and water sources at an altitudinal range of ca. 850–1170 m a.s.l, whilst the other member of the genus are mostly arboreal. A semi-digested slug was recovered from the gut of one individual (MZMU 1604). The female MZMU 1665 contained 3 eggs (egg length 14.45–15.25 mm; width 6.54–6.75 mm).

Discussion

The mtDNA-based genealogy reported in the present paper has the most complete taxon sampling among the phylogenetic hypotheses published to date for *Pareas* and includes 18 of the 19 recognized nominal species of the genus. The only species which was not included

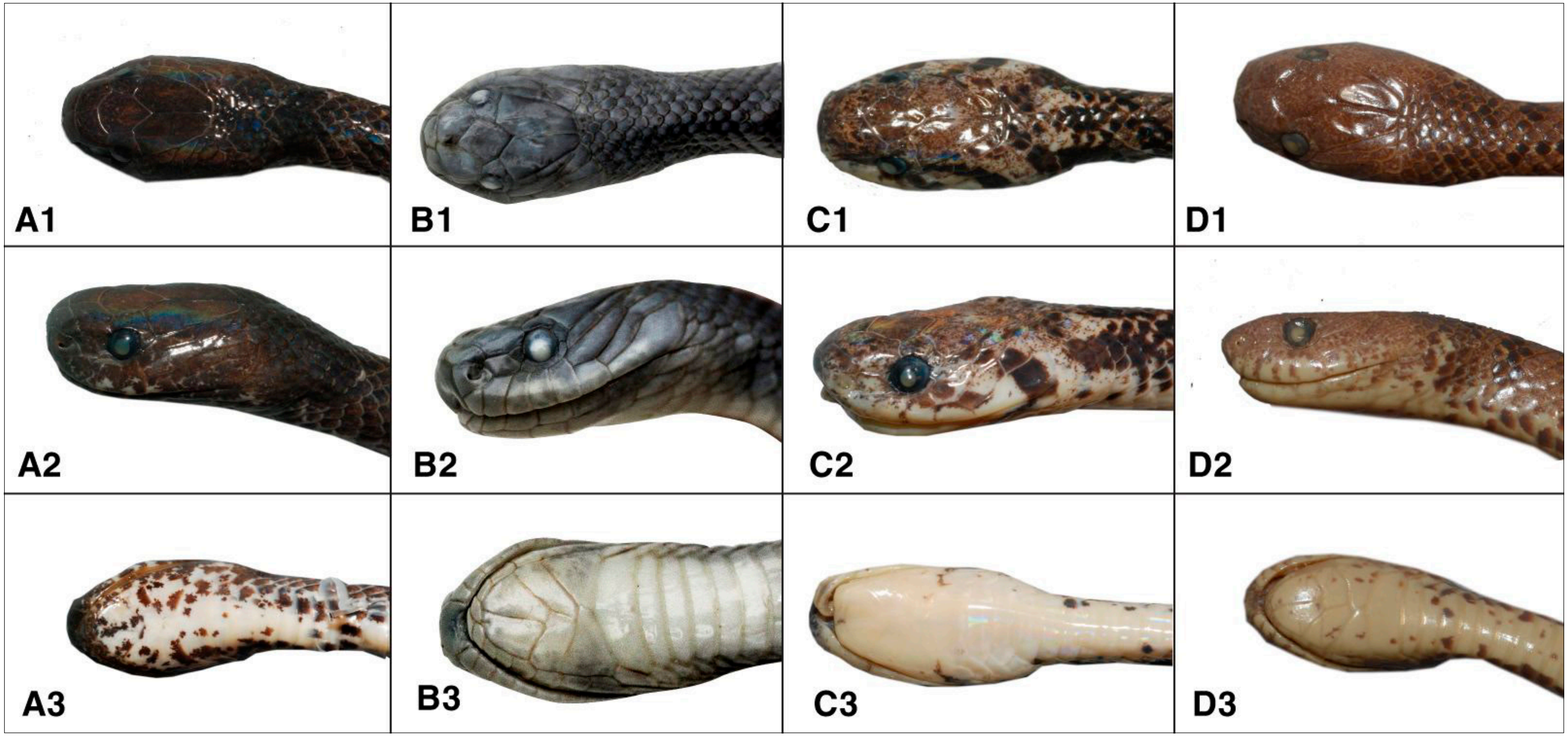


Fig. 7. Dorsal, lateral, and ventral view of head in *Pareas margaritophorus-macularius* complex members. **A**: *Pareas andersonii* (CAS 245296); **B**: *Pareas modestus* (MZMU 274); **C**: *Pareas macularius* CAS 206620; **D**: *Pareas margaritophorus* (SMF 20790, holotype of *Pareas moellendorffi* Böttger, 1885). Photos by G. Vogel (A, C, D) and HT. Lalremsanga (B).

Fig. 8. Photos in life of *Pareas margaritophorus-macularius* complex members. **A, B**: *Pareas andersonii* in Mizoram State, India (not collected); **C**: *Pareas modestus* in Mizoram State, India (MZMU 275); **D**: *Pareas macularius* in Sagaing Division, Myanmar (ZMMU NAP-09631); **E**: *Pareas macularius* in Xaisomboun Province, Laos (ZMMU NAP-09279); **F**: *Pareas macularius* in Yunnan Province, China (not collected); **G**: *Pareas margaritophorus* in Tak Province, Thailand (not collected), **H**: *Pareas margaritophorus* in Nghe An Province, Vietnam (DTU 475). Photos by R. Hmar (A, B), V. Hrima (C), N. A. Poyarkov (D, E), G. Vogel (F, G), and T. V. Nguyen (H).

due to the lack of comparative sequence data in GenBank is *P. nuchalis* of *P. cariantus* complex from Borneo (Malaysia and Indonesia). Our results also indicated a deep intraspecific divergence within *P. andersonii* and *P. macularius* (p=7.6%–9.0% in cyt *b* gene), which is comparable or even exceeds the interspecific distances between some of the recognized species (e.g. p=8.0% between *P. iwasakii* and *P. atayal*; p=8.9% between *P. boulengeri* and *P. chinensis* in cyt *b* gene) (You *et al*., 2015). This overlap might indicate that the taxonomy of *P. andersonii* and *P. macularius* may be still incomplete and additional research on phylogeography and geographic variation of these species is needed. Further increased taxon and gene sampling is required to achieve a better understanding of phylogenetic relationships and diversity of *Pareas* snakes.

Based on examination of the type material, our study provides strong support for *Amblycephalus tamdaoensis* Bourret as a subjective junior synonym of *P. macularius*; and *Pareas moellendorffi* Böttger as a subjective junior synonym of *P. margaritophorus*. Similar taxonomic conclusions were already reported earlier in the classic work of Smith (Smith, 1943), though without providing specific morphological evidence and comparative data confirming this taxonomy.

Two specimens of *Pareas* from Laos, MNHN 1994.743 (specific location not available) and MNHN 2005.0232 (from Long Nai, Phongsaly Province) shared certain morphological characteristics typical for *P. macularius* (butterfly-shaped whitish nuchal blotch with distinct cross-bands consisting of bicolored spots on body) and *P. andersonii* (body shape stout; head slightly distinct from neck; belly with rectangular black blotches). Unfortunately, molecular data are not available for these specimens, so we tentatively classify these specimens as *P.* cf. *macularius*. Additional sampling from Laos and other parts of Indo-Burma and molecular evidence are needed to clarify the taxonomic status of lineages within *P. macularius*.

We suggest that at present both newly revalidated species *P. andersonii* and *P. modestus* should be categorized as Data Deficient (DD) according to the IUCN Red List criteria (2016). Though these two species of *Pareas* are quite elusive, in northeast India they are often killed by local population being mistaken for venomous snakes like the black krait (*Bungarus niger*). Further research is required to clarify the extent of their distribution and conservation status.

Our work further underscores the western part of Indo-Burma (Myanmar and northeast India) as a herpetofaunal diversity hotspot, which remains still insufficiently studied compared to southwest China, Thailand, and Vietnam (Mulcahy *et al*., 2018; Platt *et al*., 2018; Zaw *et al*., 2019; Poyarkov *et al*., 2019). Further intensified field survey efforts along with integrative taxonomic analyses with application of molecular taxonomy techniques is required for further inventory and management of this poorly understood but diverse herpetofauna.

Updated key to the species of the *Pareas margaritophorus-macularius* complex

1a. Dorsal scales all smooth .... ***P. margaritophorus***
1b. Dorsal scales slightly keeled in 3–9 rows at midbody **2**
2a. Body uniform greyish black to black, belly uniformly colored .... ***P. modestus***
2b. Body shades of grey with distinct bicolored spots, belly with squarish black blotches or specklings ... **3**
3a. Few cross-bands of bicolored spots, belly with squarish black blotches .... ***P. andersonii***
3b. Multiple cross-bands of bicolored spots, belly with dense speckling .... ***P. macularius***

Acknowledgements

The authors are grateful to Thai Van Nguyen (SVW), Toan Quoc Phan (DTU), Andrey N. Kuznetsov (JRVTTC) for supporting our study. H.T. Lalremsanga acknowledges NMHS (Ref. No.: GBPNI/NMHS-2017/MG-22), Uttarakhand, DST-SERB (Ref.No.: EMR/2016/002391) and DBT (Ref. No.: DBT-NER/AAB/64/2017), Govt. of India, New Delhi for the financial support and the Chief Wildlife Warden of Environment, Forests and Climate Change Department, Govt. of Mizoram for the permission for herpetofaunal collection in Mizoram (No.A.33011/2/99-CWLW/22). He is also thankful to Romalsawma, S. Lallianzela, L. Rinsanga, T.B.C. Lalbiaknunmawia, V. L. Hruaia, Ht. Decemson and J.C. Lalmuanawma for their help and support during fieldwork. N.A. Poyarkov is grateful to Roman A. Nazarov (ZMMU) and Vladislav A. Gorin (MSU) for assistance, to Than Zaw and May Thu Chit (Mandalay University, Myanmar) for support during fieldwork in Myanmar; and to Chatmongkon Suwannapoom and Parinya Pawangkhanant (AUP) for support during fieldwork in Thailand and providing tissue samples from Thailand [collected with the permission of the Institutional Ethical Committee of Animal Experimentation of the University of Phayao (certificate number 610104022) and the Institute of Animal for Scientific Purposes Development Thailand (No. U1-01205-2558), both issued to Chatmongkon Suwannapoom]. Furthermore we want to thank the following people, who gave G. Vogel access to specimens in their care and helped while visiting their respective institutions: Colin McCarthy and Patrick Campbell (NHM(UK)), Jens Vindum and Alan Leviton (CAS), Yuezhao Wang, Xiaomao Zeng, Jiatang Li, and Ermi Zhao (CIB), Ding Lee (DL), Alan Resetar (FMNH), Alain Dubois, Ivan Ineich and Annemarie Ohler (MNHN), Valentina F. Orlova and Roman A. Nazarov (ZMMU), Irvan Sidik (MZB), Heinz Grillitsch, Silke Schweiger, and Richard Gemel (NMW), Gunther Köhler and Linda Acker (SMF), Dennis Rödder and Wolfgang Böhme (ZFMK), Mark-Oliver Rödel and Frank Tillack (ZMB), Valentina F. Orlova and Roman A. Nazarov (ZMMU), and Frank Glaw and Michael Franzen (ZSM). The authors are grateful to Ian Dugdale for proofreading of the paper. The authors thank Lee Grismer, Uwe Fritz and one anonymous reviewer for their useful comments and enormous work which helped us to improve the earlier draft of the manuscript.

This work was supported by the Russian Science Foundation [19-14-00050] for molecular analyses to N.A.P. (molecular and phylogenetic analysis, specimen collection, specimen examination).

References

Bocourt, F. (1866). Notes sur les reptiles. Les batraciens et les poissons recueillis pendant un voyage dans le Royaume de Siam. *Nouvelles Archives du Museum d'Histoire Naturelle De Paris*, **2**, 4–20 .

Boettger, F. (1885). Materialien zur herpetologischen Fauna von China I. *Berichte über die Thätigkeit des Offenbacher Vereins für Naturkunde*, **24–25**, 115–170.

Boulenger, G. A. (1888). An account of the Reptilia obtained in Burma, north of Tenasserim, by M. L. Fea, of the Genova Civic Museum. *Annali del Museo Civico di Storia Naturale di Genova*, **6**, 593–604.

Boulenger, G. A. (1896). *Catalogue of the Snakes in the British Museum* (*Natural History*). *Volume III, Containing the Colubridae* (*Opisthoglyphae and Proteroglyphae*), *Amblycephalidae*, *and Viperidae*. London, British Museum (Natural History).

Bourret, R. (1935). Notes herpétologiques sur l'Indochine Française X. Les serpents de la station d'altitude du Tam-dao. *Bulletin Général de l'Instruction Publique*, **15**, 259–271.

Bourret, R. (1936). *Les serpents de l'Indochine*. *Tome II*. *Catalogue systématique descriptif*. Toulouse, Henri Basuyau et Cie.

Capocaccia, L. (1961). Catalogo dei tipi di rettili del Museo Civico di Storia Naturale di Genova. *Annali del Museo Civico di Storia Naturale* "*Giacomo Doria*", **72**, 86–111.

Das, I., Dattagupta, B. & Gayen, N. C. (1998). History and catalogue of reptile types in the collection of the Zoological Survey of India. *Journal of South Asian Natural History*, **3**, 121–172.

De Queiroz, A., Lawson, R. & Lemos-Espinal, J. A. (2002). Phylogenetic relationships of North American garter snakes (*Thamnophis*) based on four mitochondrial genes: how much DNA is enough? *Molecular Phylogenetics and Evolution*, **22**, 315–329.

Deepak, V., Narayanan, S., Das, S., Rajkumar, K. P., Easa, P. S., Sreejith, K. A. & Gower, D. J. (2020). Description of a new species of *Xylophis* Beddome, 1878 (Serpentes: Pareidae: Xylophiinae) from the western Ghats, India. *Zootaxa*, **4755**, 231–250.

Dowling, H. G. (1951). A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, **1**, 97–99.

Guo, Y., Wang, G. & Rao, D. (2020). Scale microornamentation of five species of *Pareas* (Serpentes, Pareidae) from China. *Zootaxa*, **4742**, 565–572.

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic acids symposium series*. London: Information Retrieval Ltd; p. 95–98 (c1979–c2000).

Hauser, S. (2017). On the validity of *Pareas macularius* Theobald, 1868 (Squamata: Pareidae) as a species distinct from *Pareas margaritophorus* (Jan in Bocourt, 1866). *Tropical Natural History*, **17**, 147–174.

Hillis, D. M., Moritz, C. & Mable, B. K. (1996). *Molecular Systematics*. *Second Edition*. Massachusetts, Sinauer Associates.

Huang, Q. Y. (2004). *Pareas macularius* Theobald, 1868 should be a junior synonym of *Pareas margaritophorus* (Jan,1866). *Sichuan Journal of Zoology*, **3**, 207–208.

Huelsenbeck, J. P. & Hillis, D. M. (1993). Success of phylogenetic methods in the four-taxon case. *Systematic Biology*, **42**, 247–264

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

IUCN Standards and Petitions Subcommittee (2016). *Guidelines for Using the IUCN Red List Categories and Criteria*. *Version 12*. *Prepared by the Standards and Petitions Subcommittee*. http:www.iucnredlist.org/documents/RedListGuidelines.pdf

Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K., von Haeseler, A. & Jermiin, L. S. (2017). ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, **14**, 587.

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, **30**, 3059–3066.

Biakzuala, L. & Lalremsanga, H. T. (2019). Geographic distribution: *Pareas margaritophorus* (White-spotted slug-eating snake). *Herpetological Review*, **50**, 332.

Lawson, R., Slowinski, J. B., Crother, B. I. & Burbrink, F. T. (2005) Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution*, **37**, 581–601.

Li, J.-N., Liang, D., Wang, Y.-Y., Guo, P., Huang, S. & Zhang, P. (2020). A large-scale systematic framework of Chinese snakes based on a unified multilocus marker system. *Molecular Phylogenetics and Evolution*, **148**, 1–17.

Loredo, A. I., Wood, P. L., Quah, E. S. H., Anuar, S., Greer, L. F., Ahmad, N. & Grismer, L. (2013). Cryptic speciation within *Asthenodipsas vertebralis* (Boulenger, 1900) (Squamata: Pareatidae), the description of a new species from Peninsular Malaysia, and the resurrection of *A*. *tropidonotus* (Lidth de Jude, 1923) from Sumatra: an integrative taxonomic analysis. *Zootaxa*, **3664**, 505–524.

Mulcahy, D. G., Lee, J. L., Miller, A. H., Chand, M., Thura, M. K. & Zug, G. R. (2018). Filling the BINs of life: report of an amphibian and reptile survey of the Tanintharyi (Tenasserim) Region of Myanmar, with DNA barcode data. *ZooKeys*, **757**, 85–152.

Nguyen, L. T., Schmidt, H. A., Haeseler, A. & Bui, Q. M. (2015). IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, **32**, 268–274.

Nguyen, T. V., Nguyen, H. X. N., Agung, A. P. & Poyarkov, N. A. (2020). Geographic distribution: *Pareas margaritophorus* (White-spotted slug-eating snake). *Herpetological Review*, **51**(3): (in press).

Platt, S. G., Zug, G. R., Platt, K., Ko, W. K., Myo, K. M., Soe, M. M., Win, T., Win, M. M., Aung, S. H. N., Kyaw, N. W., Thu, H., Wint, K. T. Z., Van Dijk, P. P., Horne, B. D. & Rainwater, T. R. (2018). Field records of turtles, snakes and lizards in Myanmar (2009-2017) with natural history observations and notes on folk herpetological knowledge. *Natural History Bulletin of the Siam Society*, **63**, 67–114.

Posada, D. & Crandall, K. A. (1998). MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Poyarkov, N. A., Gorin, V. A., Zaw, T., Kretova, V. D., Gogoleva, S. S., Pawangkhanant, P. & Che, J. (2019). On the road to Mandalay: contribution to the *Microhyla* Tschudi, 1838 (Amphibia: Anura: Microhylidae) fauna of Myanmar with description of two new species. *Zoological Research*, **40**, 244–276.

Rambaut, A. & Drummond, A. J. (2007). Tracer V1.5. http://beast.bio.ed.ac.uk/Tracer.

Ronquist, F. & Huelsenbeck, J. P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.

Sambrook, J. & Russell, D. W. (2001). *Molecular cloning: a laboratory manual* (3rd edition). New York: Cold Spring Harbor Laboratory Press.

Smith, M. A. (1943). *The fauna of British India Ceylon and Burma*, *including the whole of the Indo-Chinese Sub-region*. *Reptilia and Amphibia*. *Vol*. *III*. *Serpentes*. London, Taylor and Francis.

Suntrarachun, S., Chanhome, L., Hauser, S., Sumontha, M. & Kanhya, K. (2020). Molecular phylogenetic support to the resurrection of *Pareas macularius* from the synonymy of *Pareas margaritophorus* (Squamata: Pareidae). *Tropical Natural History*, **20**, 182–190.

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013). MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, **30**, 2725–2729.

Theobald, W. (1868). Catalogue of the reptiles of British Birma, embracing the provinces of Pegu, Martaban, and Tenasserim;

with descriptions of new or little-known species. *Zoological Journal of the Linnean Society*, **10**, 4 – 67.
Vogel, G. (2015). A new montane species of the genus *Pareas* Wagler, 1830 (Squamata: Pareatidae) from northern Myanmar. *Taprobanica*, **7**, 1 – 7.
Wall, F. (1909). Remarks on some little known Indian Ophidia. *Records of the Indian Museum*, **3**, 145 – 150.
Wall, F. (1922). A review of the Indian species of *Amblycephalus*. *Records of the Indian Museum*, **24**, 19 – 27.
Wallach, V., Williams, K. S. & Boundy, J. (2014). *Snakes of the world: a catalogue of living and extinct species*. Boca Raton, CRC Press.
Wang, P., Che, J., Liu, Q., Li, K., Jin, J. Q., Jiang, K., Shi, L. & Guo, P. (2020). A revised taxonomy of Asia snail-eating snakes *Pareas* (Squamata, Pareidae): evidence from morphological comparison and molecular phylogeny. *ZooKeys*, **939**, 45 – 64.
Wogan, G. O. U., Vindum, J. V., Wilkinson, J. A., Koo, M. S., Slowinski, J. B., Win, H., Thin, T., Kyi, S. W., Oo, S. L., Lwin, K. S. & Shein, A. K. (2008). New country records and range extensions for Myanmar amphibians and reptiles. *Hamadryad*, **33**, 83 – 96.
You, C.-W, Poyarkov, N. A. & Lin, S.-M. (2015). Diversity of the snail-eating snakes *Pareas* (Serpentes, Pareatidae) from Taiwan. *Zoologica Scripta*, **44**, 349 – 361.
Zaher, H., Murphy, R. W., Arredondo, J. C., Graboski, R., Machado-Filho, P. R., Mahlow, K., Montingelli, G. G., Quadros, A. B., Orlov, N. L., Wilkinson , M., Zhang, Y.-P. & Grazziotin, F. G. (2019). Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE*, **14**, e0216148.
Zaw, T., Lay, P., Pawangkhanant, P., Gorin, V. A. & Poyarkov, N. A. (2019). A new species of crocodile newt, genus *Tylototriton* (Amphibia, Caudata, Salamandridae) from the mountains of Kachin State, northern Myanmar. *Zoological Research*, **40**, 151 – 174.

Zoobank Registration

at http://zoobank.org

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Commission on Zoological Nomenclature (ICZN). The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information can be viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org. The LSID for this publication is as follows:

urn:lsid:zoobank.org:pub:9723474C-BD17-4988-8138-7ACD08EB5331.