On the Validity of *Pareas macularius* Theobald, 1868 (Squamata: Pareidae) as a Species Distinct from *Pareas margaritophorus* (Jan in Bocourt, 1866)

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**Abstract.**– The genus *Pareas* Wagler, 1830, consists of about fifteen species of small snail-eating snakes distributed in China, South and Southeast Asia. Until recently, two *Pareas*-species ornamented with characteristic bicolored spots were recognized, *P. margaritophorus* (Jan in Bocourt, 1866) and *Pareas macularius* Theobald, 1868. However, *P. macularius* was synonymized with *P. margaritophorus* by Huang (2004), reducing the speciosity of the bicolored-snail-eaters to a single species. This claim was tested by examining more than 60 fresh road-killed specimens of bicolored-snail-eaters from northern Thailand. They were either completely smooth-scaled, or had rows of weakly keeled dorsals. The smooth-scaled specimens differed significantly from the keeled-scaled in a number of characters. The holotype of *P. margaritophorus* corresponded closely to the smooth-scaled specimens, whereas the holotype of *Pareas macularius* corresponded to the keeled-scaled ones. It was, thus, shown that *P. macularius* is a valid species and the synonymization as claimed by Huang (2004) was refuted. *P. macularius* is distinguished from *P. margaritophorus* by having the 7–13 most median rows of dorsal scales feebly keeled at midbody, by the form and color of the nuchal collar, its larger size, the larger number of ventral shields, and the high incidence of an intense black blotch on the last, largest supralabial. A preliminary distribution map for the two species is provided.

**KEY WORDS:** northern Thailand, *Pareas macularius*, *Pareas margaritophorus*, Southeast Asia, taxonomy

**INTRODUCTION**

The snail-eating snakes of South, East and Southeast Asia are presently considered to constitute the distinct family of Pareidae together with two other genera (Pyron et al., 2011; Wiens et al., 2012; Reptile Database; see Savage [2015] for the correct spelling of the family name). Most species have a number of adaptations related to preying on snails and slugs (Wall, 1909), such as a blunt snout, and a specialized feeding-apparatus, including an asymmetric dentition related to extracting (dextral) snails from their shells (Parker and Grandison, 1977; Hosot et al., 2007, 2010; Danaisawadi et al., 2015, 2016). Another morphological characteristic is the lack of a central mental groove separating the paired chin shields. Pareid snake taxonomy is an ongoing controversy. The genus *Pareas* differs from the other genera of the family by having 15 rows of dorsal scales, the presence of pre- and suboculars (in most species), and characteristics of the chin shields (Grossman and Tillack, 2003). It consists of 14 recognized species at present (Reptile Database).

Three of them, *Pareas carinatus* Boie, 1828, *P. hamptoni* (Boulenger, 1905), and *P. margaritophorus* (Jan in Bocourt, 1866) are currently recognized from northern Thailand (Reptile Database). Besides these, *P. macularius* Theobald, 1868 had previously been recognized in this and adjacent regions as well, but Huang (2004)
synonymized this nominal species with *P. margaritophorus*.

Prior to Huang’s (2004) synonymization, *P. margaritophorus* and *P. macularius* had been considered to occur throughout much of mainland Southeast Asia and parts of southern China. Both were described as purplish-grey or brownish-grey snakes, rarely exceeding 60 cm in total length. In visual appearance, they are particularly conspicuous by having an ornamentation of numerous black-and-white spots. These spots are exactly the size of a dorsal scale: the anterior tip of such a scale is white, and the remaining, posterior portion is black. These bicolored spots contrast conspicuously with the ground color of the skin which is greyish (densely speckled with fine dark grains). Some bicolored spots appear to be completely black, since the tiny white anterior tip of each scale is completely covered by the posterior black portion of the preceding scale. These bicolored spots are not randomly distributed, but usually form a number of rather narrow, transverse series. Even when both *P. margaritophorus* and *P. macularius* were considered as valid, they could not be distinguished by the shape or distribution of these spots. Superficially, therefore, the two nominal species showed considerable morphological similarity by the presence of at least a good number of conspicuous bicolored spots.

These spots have given rise to the scientific names of both *Pareas margaritophorus* (the specific nomen meaning ‘pearl carrier’) and *Pareas macularius* (the specific nomen meaning ‘spotted’). Confusing colloquial English and Thai names also referred to these spots: In English, *P. margaritophorus* was known as ‘White-spotted Slug Snake’ (e.g. Cox 1991; Cox *et al.* 2012) or ‘Black-spotted Slug Snake’ (Nabhitabhata *et al.* 2004); the colloquial Thai names *ngu kin thak chut khao* (‘White-spotted Slug-eating Snake’) for *P. margaritophorus* and *ngu kin thak chut dam* (‘Black-spotted Slug-eating Snake’) for *P. macularius* (Cox 1991; Jintakune 2000) are translations of those confusing English names.

The original descriptions of the two nominal species in the mid-19th century were not very clear. The description of *Pareas macularius* (Theobald, 1868) was particularly confusing because two of the five specimens examined by Theobald did not appear to represent bicolored-spotted slug snakes at all (Sclater, 1891; Das *et al.*, 1998). However, in the classic work of Boulenger (1896), *P. margaritophorus* and *P. macularius* emerged as two clearly distinct species. In the meantime, three rather similar species of snail-eaters were described and considered valid in Boulenger’s work. Another bicolored spotted snail-eater was also added to the list published in 1935 by R. Bourret.

The situation was completely reversed when Smith (1943) synonymized one of these newer species with *P. margaritophorus*, and three others with *P. macularius*. Of the previous six species of ‘spotted snail-eaters’, only two remained. The final blow to the speciosity of the spotted snail-eaters came sixty years later when Huang (2004) synonymized *P. macularius* with *P. margaritophorus*, resulting in only one valid species. This complex history is summarized in Fig. 1.

Huang’s synonymization coincided with another publication, in which the authors also ‘believe that *Pareas macularius* Theobald, 1868, is a synonym of *P. margaritophorus* (Jan, 1866)’ (Guo and Zhao, 2004). Authors of these works seem
to have paid little attention, if any, to Smith (1943), and most of other subsequent works, including Taylor (1965), in which *P. margaritophorus* and *P. macularius* were apparently well-defined against each other. In Chan-ard *et al.* (1999), six pictures of spotted snail-eating snakes were published, each of which was identified correctly as either *P. margaritophorus* or *P. macularius*. In this period, the validity of each of the two species was not questioned by any taxonomists. Living specimens that before Huang’s (2004) synonymization would have been identified as *P. margaritophorus* and *P. macularius*, are shown in Fig. 2, respectively Fig. 3.

Huang’s synonymization was made solely on the basis of information from Smith’s (1943) description and data from Chinese specimens, i.e., without examining holotypes of *P. margaritophorus* and *P. macularius*, despite their non-Chinese origins (“Siam” [Thailand] and Martaban [southeastern Myanmar], respectively). Nevertheless, Huang’s (2004) account was adopted in most subsequent Chinese studies, such as Guo and Deng (2009) and Guo *et al.* (2011), although a few others continued to recognize *P. macularius* as valid (e.g., Yang and Rao, 2008). In the meantime, Vogel (2009) expressed his conservative stance against Huang’s (2004) claim due to the absence of examination of type materials therein. Notwithstanding these views, the synonymization has been gradually and broadly approved by authors in subsequent publications, leading to the removal of *P. macularius* from most recent lists of recognized *Pareas* species, including that in the reputed Reptile Database (see above). In a number of collections, specimens initially identified as *P. macularius* were renamed *P. margaritophorus*. In at least one study, such renamed specimens were subjected to DNA extraction and analysis, resulting in the conclusion that ‘*Pareas margaritophorus*’
showed remarkably large sequence divergences (Guo et al., 2011).

In the present paper, I resurrect *P. macularius* as a valid species based on the analysis of morphological data of many road-killed specimens found in northern Thailand.

**MATERIALS AND METHODS**

Sixty-one relatively intact, freshly road-killed (DOR) specimens, showing characteristics of *P. margaritophorus* sensu Huang (2004), were collected during the rainy seasons of 2011-2015. They all originated from northern Thailand (the provinces of Chiang Mai, Chiang Rai, Lampang, Lamphun, Mae Hong Son, Nan, and Phayao), including the ‘lower north’ (the provinces of Phetchabun, Phitsanulok, and Tak), a region close to the localities from which the holotypes of *P. margaritophorus* and *P. macularius* had originated.

Each specimen was photographed on detection at the collecting site, and the presence or absence of keeled dorsal-scale rows was determined by carefully screening the dorsal surface with a magnifying glass. The total length (TL) and tail length (TaL, from the tail tip to the posterior edge of the anal shield) of most fresh specimens were measured (in mm), and the relative tail lengths, TaL/TL (in %), were calculated for comparisons. Specimens with aborted eggs beside them were considered females, while specimens with one or both hemipenes everted from the vent were scored as males. For the remaining specimens (the majority), the tail was squeezed and massaged from its center towards the vent, which resulted in evertion of hemipenes in a good number of them. In damaged specimens, this procedure often fails to result in evertion of hemipenes. However, the sex of many specimens could be determined with high probability by the relative tail length.

Subsequently, a note was made on the habitat of the collecting site, which was specified as the distance (by road) in kilometers to the nearest large village or district town (e.g. Highway 1095, 5 km northwest of Mae Sae, Mae Taeng District, Chiang Mai Province). The elevation of the collecting sites could later be estimated with the help of maps (1:50,000) from the *Krom Phaen Thi Thahan* of the *Kong Bancha Kan Thahan Sung Sut* (“Thai Army Maps”) on which 25-meter jumps in elevation are visualized by a dense network of lines. The less detailed 1:250,000 Thai Army Maps of the same publisher have been useful for provinces of which no 1:50,000 maps were available. It was later shown that elevations estimated using these methods were usually within the range of measurements with GPS ± 100 meter.

The specimens were temporarily stored in 70% ethanol and, after several days, were transferred to 8-10% formalin. After fixation in formalin for a varying period, all were transferred again to 70 % ethanol.

The following characters could be rated in nearly all specimens:

- The number of ventral shields (V): Counted following Dowling (1951). This corresponds closely to the scale count starting from the second scale of the throat twice as wide as long until and including the ventral shield just before the anal shield. The first scale of the throat also twice as wide as long, was considered a preventral shield and, thus, was excluded from the count together with the anal shield.
The number of subcaudal pairs (SC): Counted with an exclusion of the terminal scute.

Special attention was given to the form and color of the nuchal collar in the fresh material, as two different collar types could be distinguished, a sulphur (pale yellow), pink or reddish collar without speckling (Type I) and an often characteristic W-shaped collar with fine brown speckling (Type II).

For determining the type of collar, color pictures of fresh specimens were essential, because the coloration of the Type I-collar rapidly faded during preservation in alcohol or formalin.

The amount and pattern of spots, speckles and blotches on ventral scales were rated by the author from 1 to 5: 1 = sparsely speckled, anteriorly almost completely white with small spots restricted to the lateral edges of the ventral scales; 3 = moderately speckled, more and larger speckles than in 1, posteriorly some blotches as wide as half the width of the ventral scale; 5 = densely speckled, speckles and blotches dominating, posteriorly with numerous large blotches often shaped like the blades of knives. All other ratings are estimates in between these three values.

No attention was paid to the head scalation as head shields were badly damaged in most specimens, making it impossible to observe or precisely count infra- and supralabials, oculars, and temporals. Even so, the presence or absence of a large, conspicuous solid, intensely black blotch (IBB) that covers much (30-60%) of the last (usually 7th) supralabial was recorded.

This blotch could be easily distinguished, when present, in most specimens including those with seriously damaged heads. Greyish, diffuse, or speckled blotches on this shield were rated as absence of blotch.

The dorsal scale row formula examined in a large number of specimens (and as given in literature) was always 15:15:15 and was, therefore, discarded for the analyses. As anal shields were consistently entirely, this character was also ignored.

All specimens had numerous bicolored spots and their presence was not listed. The size of the vertebrals relative to adjacent scales (enlarged versus normal) was also excluded from the analyses, because the state of this character was extremely difficult to quantify exactly. Likewise, it was nearly impossible to quantify the body shape (round versus laterally compressed) in the DOR-material. Thus, variation in this character was also ignored.

Dentition and hemipenal structure were not examined for practical reasons. Examination of the former in such small animals as snail-eaters would be technically difficult and required too much time. Moreover, the dentition was apparently severely damaged in many road-killed specimens. In the majority of specimens in which the base of the tail was damaged, hemipenes could only be partly everted, or not at all. In just a few specimens, the hemipenes could be everted completely and were photographed. In specimens preserved in alcohol or formalin, this tiny, hollow structure was usually shrunk.

All 61 preserved specimens used in this study were deposited in the collection of the Queen Saovabha Memorial Institute (QSMI) in Bangkok, Thailand.
Supportive specimens

A large number of photographs of spotted *Pareas*-specimens in museum and private collections, as well as those in herpetological publications, were examined. The holotypes of *Leptognathus margaritophorus* (Jan in Bocourt, 1866) and *Pareas macularius* Theobald, 1868 were particularly important to this study. The relevant data of these specimens were extracted from photographs and literature (e.g., Boulenger, 1896).

Abbreviations of museums and other collections

BM(NH)-British Museum (of Natural History), London, UK; CAS-California Academy of Sciences, San Francisco, California, USA; CIB-Chinese Institute of Biology, Chengdu, China; EHT-HMS-E.H. Taylor, private collection; FMNH-Field Museum of Natural History, Chicago, USA; HNU-Hainan Normal University, Hainan, China; IEBR-Institute of Ecology and Biological Resources, Hanoi, Vietnam; LSUHC-La Sierra University Herpetological Collection, La Sierra, California, USA; LSUDPC-La Sierra University Digital Photo Collection, La Sierra, California, USA; MNHN-Muséum National d’Histoire Naturelle, Paris, France; NHW-Naturhistorisches Museum Wien, Vienna, Austria; QSMI-Queen Saovabha Memorial Institute, The Thai Red Cross Society, Bangkok, Thailand; SHPC-Sjon Hauser’s Private Collection, Chiang Mai, Thailand; SKKCC-Stan Klaassens’ Ko Chang Collection, Ko Chang, Trat, Thailand; SMF-Senckenberg Museum Frankfurt, Frankfurt am Main, Germany; THNHM-Thai Natural History Museum, Nakhon Pathom, Thailand; ZFMK-Zoologisches Forschungsinstitut und Museum Alexander König, Bonn, Germany; ZRC-Zoological Reference of the Raffles Museum of Biodiversity at the National University of Singapore, Singapore.

FIGURE 2. A living specimen of the smooth-scaled type of the spotted snail-eater (SHPC12.12.12-01) from lowland in Mueang District, Chiang Mai Province, Northern Thailand.
RESULTS

Fresh material from northern Thailand

Of more than 120 fresh DOR-specimens collected and briefly examined, the 61 most intact specimens were preserved and used for this study. Of these, 37 had completely smooth dorsal scales, while the remaining 24 had keeled dorsal scales in 7-11 of the invariably 15 rows. The presence or absence of keels strongly correlated with other characters (Table 1).

Body size and scale counts

Specimens with the presence of keeled dorsal scales were larger in TL than those with only smooth dorsal scales. Also, the former had higher numbers of ventral shields than the latter (Table 1). These differences are graphically illustrated in histograms (Figs. 4, 5).

The larger body size of the keeled-scaled specimens and their higher number of ventral scales are not attributable to differential male/female ratio between the two groups, because, although females tended to have larger bodies with more ventrals in either group of specimens, the keeled specimens contained a slightly lower proportion of females (58%) than the smooth-scaled specimens (60%). The males of the keeled-scaled specimens were larger and had more ventrals than the smooth-scaled males, whereas the keeled-scaled females were also larger with more ventrals than the smooth-scaled females (Table 1).

As a whole, the keeled-scaled snakes also had relatively longer tails than the smooth-scaled snakes, and this is also true when the male and female specimens were separately compared between the two types.

For the relative tail length, there was no significant difference between the smooth-scaled and the keeled-scaled specimens, when both sexes were combined for comparison. However, smooth-scaled males had longer relative tail lengths than the keeled-scaled males, whereas the smooth-
scaled females had shorter relative tail lengths than the keeled-scaled females. There was no significant difference in the number of subcaudal pairs between the smooth-scaled and keeled-scaled specimens, when males and females were combined for comparison. This was also true when the smooth-scaled males were compared with the keeled-scaled males. However, the keeled-scaled females had higher numbers of subcaudal pairs than the smooth-scaled females.

**Shape, color, and extent of speckling of the collar**

Based on the shape, color, and extent of speckling of the collars, the specimens could be divided into two types. A Type I-collar was an entire band or a band partially or completely broken into three dots (tripartite or triple dot), of which the two lateral dots were often inconspicuous: the central dot was usually conspicuous, but sometimes reduced to a small dot or even to a narrow stripe. In this type the collar was almost always white, cream, yellowish, pink or reddish/orange without fine speckles: however, there sometimes were a few black spots.

A Type II-collar was usually shaped like a gothic letter W, or butterfly-shaped, often with two black round blotches enclosed. Its shape could also be amoeboïd. Occasionally, these collars had two “tails” stretching posteriorly. The Type II-collar was speckled with fine brown pigment; the speckling might be very dense, so that the collar was hardly distinct from the surroundings. The appearance was whitish when the fine brown speckling was very sparse (or sometimes even absent), and, more often, light brown when the speckling was moderate, or dark brown when it was dense. Various forms of both collar-types are illustrated in Figs. 6, 7 and 8.

**Table 1.** A summary of selected data from 37 smooth-scaled and 24 keeled-scaled specimens of bicolored-spotted snail-eaters.

<table>
<thead>
<tr>
<th>Sex ratio (% males)</th>
<th>Average TL in mm and STDEV</th>
<th>Average TaL in mm and STDEV</th>
<th>Average TaL/TL (%) and STDEV</th>
</tr>
</thead>
<tbody>
<tr>
<td>smooth-scaled males</td>
<td>100% 335.4 ± 38.2</td>
<td>69.8 ± 9.0</td>
<td>20.8 ± 0.9</td>
</tr>
<tr>
<td>keeled-scaled males</td>
<td>100% 448.3 ± 41.7 p&lt;0.01</td>
<td>86.6 ± 12.7 p&lt;0.005</td>
<td>19.25 ± 1.36 p&lt;0.01</td>
</tr>
<tr>
<td>t-test (2,3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>smooth-scaled females</td>
<td>0% 363.0 ± 42.4</td>
<td>52.6 ± 5.4</td>
<td>14.5 ± 0.72</td>
</tr>
<tr>
<td>smooth-scaled males</td>
<td>0% 423.1 ± 63.9 p&lt;0.01</td>
<td>64.4 ± 10.4</td>
<td>15.2 ± 0.74</td>
</tr>
<tr>
<td>t-test (2,3)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>smooth-scaled (males+females+sex unknown)</td>
<td>40% 353.7 ± 42.3</td>
<td>59.9 ± 10.9</td>
<td>17.1 ± 3.1</td>
</tr>
<tr>
<td>keeled-scaled (males+females+sex unknown)</td>
<td>42% 433.6 ± 119.0</td>
<td>68.3 ± 15.8</td>
<td>16.9 ± 2.3</td>
</tr>
<tr>
<td>t-test (2,3)</td>
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</tbody>
</table>

TABLE 1. A summary of selected data from 37 smooth-scaled and 24 keeled-scaled specimens of bicolored-spotted snail-eaters.
Nearly all of the smooth-scaled specimens (97%) had a Type I-nuchal collar, but this type was not found in the keeled-scaled specimens. On the other hand, nearly all of the keeled-scaled specimens (94%) had a Type II-nuchal collar, whereas such a collar was absent in the smooth-scaled specimens. In a few specimens (3% of the smooth-scaled and 6% of the keeled-scaled), no collar could be distinguished.

**Intensive black blotches and belly speckling**

In the keeled-scaled specimens, there was a very high incidence of an IBB on the posterior part of the spoon-shaped, last supralabial (98%), whereas it was very low (3%) in the smooth-scaled specimens.

The speckling and mottling of the belly appeared to be much denser in the keeled-scaled specimens. For objective comparison, however, this character further needs an appropriate quantification procedure. Examples of sparse and dense belly speckling are illustrated in Fig. 9 and Fig. 10.

**Hemipenal structure**

In only a few specimens, for each of the smooth-scaled and the keeled-scaled types, hemipenes could be everted completely. The pictures of these hemipenes showed that they were deeply forked with numerous folds and papillae, and no spines. In the present observations, however, detailed morphology and arrangement of these folds or the shape and distribution of papillae remained obscure. I, thus, refrained from attempting to quantify possible differences in these characters between the smooth-scaled and keeled-scaled specimens.

**Conclusion**

From the analyses of the data as summarized in Table 1, it is obvious that the keeled-scaled and smooth-scaled populations represent two distinct species, each with a set of explicit diagnostic characters. Additional, indirect support for their distinctiveness comes from the localities.
where the specimens were collected: All smooth-scaled specimens were found at elevations below 800 m (150-800 m) a.s.l., while all keeled-scaled specimens were collected at elevations above 800 m a.s.l. (Fig. 11). These data show that the two species are sympatric in much of northern Thailand, but they are rarely syntopic.

The holotype of *Leptognathus margaritophorus* Jan in Bocourt, 1866

The holotype of *Leptognathus margaritophorus* Jan in Bocourt, 1866, deposited in the Muséum Naturelle d’Histoire Naturelle in Paris, France, as MNHH 599, is labeled as having originated from “Siam” (=Thailand). Careful
examination of pictures, which show the dorsal surface of the specimen, revealed complete absence of keeled scales thereon. There was a narrow, wavy (“almost tripartite”) “white” collar that lacked dark speckles and could have been yellowish or pink in life (thus, most likely representing the Type I pattern). The ventral scale count, 140, fell within the range of the smooth-scaled specimens, and was distinctly lower than the range of the keeled-scaled specimens. An IBB is absent on the 7th supralabial.

These results make the specimen unequivocally fit to the smooth-scaled type
of the bicolored-spotted snail-eaters from northern Thailand. Thus, the smooth-scaled specimens are identified as *Pareas margaritophorus*.

**The holotype of *Pareas macularius* Theobald, 1868**

The holotype of *Pareas macularius* Theobald, 1868, deposited in The Natural History Museum, London, U.K., as BM 1946.1.20.8, was ambiguously labeled with two name cards: *Amblycephalus macularius* and *Pareas margaritophorus*, with the record of its collection locality as Martaban in Myanmar, a locality close to western Thailand. Several median rows of dorsal scales in this specimen were feebly keeled, and a large, compact brown blotch on the 7th supralabial seemed to have been intensely black in life. The number of ventral shields, 160 (given as 164 by Boulenger, 1896, who might have incorporated the preventral and anal shields to the ventral shields), fell within the range of the ventral counts in the keeled-scaled specimens, but was beyond the range in the smooth-scaled specimens. Despite the discolorations due to long preservation, a W-shaped nuchal collar, with fine brown speckles, obviously representing the Type II pattern, is conspicuous.

These characters correspond perfectly to those of the keeled-scaled type of the bicolored-spotted snail-eaters from northern Thailand, but deviate from those of the smooth-scaled type. All 24 keeled-scaled specimens are, thus, identified as *P. macularius*. The name should, therefore, be resurrected as a valid species distinct from *P. margaritophorus*.

The differences between *Pareas margaritophorus* and *P. macularius*, as revealed in this study, using specimens from northern Thailand, are summarized below.

- **Pareas margaritophorus.** Dorsal scales entirely smooth; nuchal region usually with pink, cream or yellow entire or tripartite collar or spot without fine brown speckling; IBB usually absent on the 7th supralabial (very rarely present); ventral shields usually fewer than 158; belly speckling usually sparse, in particular anteriorly, and no large blotches are present.

- **Pareas macularius.** Dorsal scales forming the median 7-13 rows weakly keeled; nuchal region often with a butterfly- or W-shaped collar with moderate or dense speckling; IBB usually present on the 7th supralabial (rarely absent); ventral shields usually more than 148; belly speckling usually dense, often large blotches are present.

**Distribution in the whole range**

Owing to the newly described discriminant characters of *P. margaritophorus* and *P. macularius*, bicolored-spotted snail-eaters could be easily identified to the species level in photographs of museum specimens or in herpetological publications. A number of obvious misidentifications and doubtful identifications consequently elucidated are listed in Appendix II.

Dozens of specimens, for which the origins had been known, could be identified as either *P. margaritophorus* or *P. macularius* with some degrees of certainty, sometimes even solely on the basis of brief descriptions of external features. For example, when the description includes ‘pink collar is evident’, the snake in question is highly likely to belong to *P. margaritophorus*. The distributions of *P.*
margaritophorus and P. macularius as revealed in this preliminary survey are mapped in Fig. 12. The sources (literature, and museum and private collections) are given in the caption of the map.

Variations in discriminant characters for the two species are discussed below, based on the results of the analysis of the 61 road-killed specimens and a large number of the supportive specimens correctly identified as either P. margaritophorus or P. macularius.

**DISCUSSION**

This study shows that two distinct species of bicolored-spotted snail-eating snakes occur widely in northern Thailand, of which the one with 7-13 median rows of feebly keeled dorsal scales at midbody is identified as Pareas macularius Theobald, 1868, and the other, with entirely smooth dorsal scales, as P. margaritophorus (Jan in Bocourt, 1866). The synonymy of P. macularius with P. margaritophorus by Huang (2004) is refuted. The present analyses demonstrated that the two species have a good number of discriminant characters and their combination, excluding any noise from extreme variation in individual character, offer reliable identifications. Smith (1943), studying a smaller number of specimens, had come to the same conclusion. The discriminant characters in his study included body size (total length), number of ventral scales, and the presence or absence of keeled dorsal scales, as well as hemipenal structure. In the present study, the shape and color of the nuchal collar, the presence or absence of IBBs, and the state of specklings on the belly, were shown to be additional effective discriminant characters.
Both species are broadly sympatric in mainland Southeast Asia (Thailand, Laos and Vietnam) and Hainan in southeastern China (Fig. 12).

**Variation in *Pareas margaritophorus***

Dorsal scales in this species were invariably smooth. Specimens usually had a large number of bicolored spots arranged in distinct cross-bands. In some specimens, many of the spots appeared to be black, because the anterior white portion of each scale was covered by the posterior black portion of the preceding scale.

More prominent variation was observed in the degree of belly specklings, which ranged from very light state, concentrated at the lateral edges of the ventral shields, to denser state with small blotches all over the ventrals shields. No geographic differences in the speckling variation were evident.

The shape and color of the nuchal collar, though also showing prominent variation, were invariably categorized as “Type I” (see above). No correlations were evident between the color or the shape of the collar of this type and the body size or sex of the specimen. Campden-Main (1969) speculated that only females have nuchal markings (collar or spot) in the southern Vietnamese populations of *P. margaritophorus*, but this needs verification on the basis of concrete data. Definitely, this is not true for northern Thailand populations. It has been suggested that juveniles of *P. margaritophorus* in peninsular Malaysia have an orange or red collar, which eventually changes to white or yellow in adulthood (www.nature-malaysia.com). Also, this is not true for the northern Thailand populations, because juveniles (i.e., small-sized specimens) had often white or cream collars and adults (i.e., large-sized specimens) bright pink collars, respectively. Specimens with a ‘rudimentary’ pink collar, including a central spot or a narrow stripe, often had pink scales at the edge with a little, black dot or streak. This suggests that a collar may be reduced in size and even disappear by the deposition of dark pigment at the edges, and that an entire nuchal band may be broken up into a tripartite collar by dark pigment.
deposition. In a similar manner, a central dot may be reduced in size to a rudimentary dot. However, presence of numerous small specimens with “rudimentary” nuchal markings and large specimens with entire nuchal bands contradict such a prediction of ontogenetic changes in coloration.

There seems to be some geographical consistency in color and shape of the collar. Specimens from Umphang Valley often had a bright pink or orange collar (entire band or tripartite), but occasionally specimens with a pale yellow collar were also seen. On the other hand, specimens from eastern Nan Province often had a “rudimentary” tripartite, dull pinkish collar.

Enigmatic as the Type I-nuchal collar may be, its presence easily identifies a specimen as *P. margaritophorus*. This may be even true for preserved specimens in which the red and yellow pigments have faded.

**Variation in Pareas macularius**

*Pareas macularius* always showed a large number of bicolored spots arranged in distinct cross-bands. Several median rows of weakly-keeled dorsal scales (mostly 7-11 rows at midbody) were always present, but the keels were often too weak to detect at a glance. In photographs, keels were only distinct when seen from the right angle. In specimens (both fresh and preserved) that were allowed to dry up, the outer keratin layers of the scale may be deformed, making the weak keels undetectable. Keels also seem to be sensitive to wear and tear, because in severely damaged road-killed specimens, distinctly keeled scales were often difficult to find.

The belly speckling of the species showed considerable variation. The data gathered in northern Thailand suggested that this variation is partly geographical. For instance, very dense speckling with many large blotches was prevalent in specimens from Doi Inthanon, while the speckling of specimens from the mountains of Tak Province was usually sparser.

Despite showing much variation, the nuchal collar of *P. macularius* was nearly always distinctly Type II. The ontogenetic development of this collar is poorly understood, yet appears to be less enigmatic than the Type I collar of *P. margaritophorus*.

Two ‘fully developed foetuses’ found in unhatched eggs from the same clutch (SHPC12.10.18-01 from Lampang Province) each showed a whitish, W-shaped collar which contrasted sharply with the grey color of the head and body. A 21 cm long juvenile from Loei Province (EHT-HMS No. 31798 in Taylor and Eibel, 1958 and Taylor, 1965) and a 22.2 cm long juvenile from Mae Hong Son Province (SHPC15.05.22-04, Fig. 6) possessed very similar collars. These collars showed very little fine speckling. In larger and older specimens, the collar is usually distinct, but moderately or densely filled with tiny brown grains. Speckling of the collar is rarely absent in adult specimens. This suggests that the collar gradually becomes more densely speckled during maturing, and, eventually, is nearly completely filled with pigment. However, the rate of pigment deposition seems to be variable, and in adult specimens the speckling is sometimes sparse. Inequally distributed pigment accumulation may gradually change the general shape of the W into a vague butterfly, or even an amoeboid shape.

Specimens from peninsular Thailand nearly always exhibited a slightly aberrant W-shaped collar with two ‘tails’ extending backwards. Such collars were rarely seen in other regions of Thailand. As the Isthmus of Kra has been an important zoogeographical
barrier (Inger and Vorris, 2001; Pauwels et al., 2003), character states, deviating to some degree from those in the other regions, were to be expected. However, in their other characters, these specimens correspond to those from the other regions.

*Pareas macularius* from northern Vietnam was originally described as *Amblycephalus tamdaoensis* Bourret, 1935. Its synonymization with *P. macularius* by Smith (1943) was followed by most authors. The status of a distinct subspecies *P. macularius tamdaoensis* for the northern Vietnamese specimens was suggested by Orlov et al. (2000), without any supporting evidence. The comparison of a number of northern Vietnamese specimens with those from Thailand did not support this subspecific status, but this should be confirmed.

**Geographic distribution**

*Pareas margaritophorus* is shown to occur throughout Thailand, in the northern part of peninsular Malaysia, in most of Cambodia, most of Vietnam, and in the very southeastern part of China, including Hainan. Throughout this distribution range, the species is usually restricted to lowlands, valleys, and low hills up to 800 m. No reports are known from Myanmar, but it almost certainly occurs in valleys and hills in Myanmar’s Shan State and Kayin State, as it is common in adjacent parts of Thailand.

Kuala Lumpur on peninsular Malaysia seems to be the southern limit of the species. It has been recorded in Singapore, but it is believed to have been introduced there (Baker and Lim, 2008; Tan and Lim, 2013). It has been reported to be common in Hong Kong (Smith, 1943) and around Pattani in the extreme south of Thailand (Taylor, 1965) and ‘not uncommon’ in the north of West Malaysia (Tweedie, 1953). It is probably common throughout much of its range. Surprisingly, neither Grossmann and Tillack (2000a, b), nor Pauwels et al. (2002), spotted the species during their surveys in Phang Nga Province in southern Thailand. It is common throughout northern Thailand, but is not often seen during the cool and dry months of January-March, when it seems to hibernate (unpublished data).

*Pareas macularius* is known from the highlands of northern, western, and northeastern Thailand; in southern Thailand, it occurs as far south as Nakhon Si Thammarat Province. It also occurs in northern Laos, and in northern and central Vietnam as far south as Kun Tom, but it has not been recorded in Cambodia. It is also known from Hainan (the very south of China). It probably occurs throughout the southern part of China’s Yunnan Province (most of the specimens listed in Yao and Datong, 2008). It occurs in southern and central Myanmar, and in the northern Kachin State. It probably also inhabits the mountains of the Shan State, as it is common in adjacent parts of the northern Thai mountains. Throughout its range, the species seems to be confined to elevations of more than 700 m a.s.l., with the exception of southern Thailand and southern Myanmar, where it is known to live at much lower elevations.

The species has been reported from Darjeeling and Sikkim in northern India (Smith, 1943; Sharma, 2003; Whitaker and Captain, 2004), giving rise to the colloquial English name ‘Darjeeling Snail Eater’. However, the identification of these snail-eaters as *P. macularius* is doubtful (see Appendix II).

**Habitat**

*Pareas margaritophorus* usually inhabits mixed deciduous forests and cultivated areas
in lowlands and low hills from 150-800 m (Fig.13). In southern Thailand, it is also known from tropical rainforest. Throughout its distribution range, it is a rather common snake, but in lowlands dominated by marshlands and rice paddies it is usually absent. Its commonness in northern Thailand is also suggested by many records.

**FIGURE 12.**
from the bowels of road-killed snakes; including *Bungarus fasciatus* (Schneider, 1801) and juvenile *Ophiophagus hannah* (Cantor, 1836) (unpublished data).

It is rarely found above 800 m. Ascending in northern Thailand’s mountains, *P. margaritophorus* is common in the low hills, but once the mixed deciduous forest with bamboo at about 600-900 m is replaced by hill evergreen forest (or montane forest), *P. margaritophorus* is rarely seen and *P. macularius* emerges.

Therefore, the colloquial English name ‘Mountain Slug Snake’ (Cox 1991; Cox *et al.*, 2012), or ‘Northern Mountain Slug Snake’ (Cox *et al.*, 1998), is rather inappropriate for the species. Interestingly, it is known to occur at an elevation of 1200 m a.s.l. in the Boloven Highlands, southern Laos (Teynié *et al.*, 2014).
2004). This might be due to the special conditions, including high precipitation (David, pers. com.), or the possible absence of *P. macularius*, allowing the species to extend its altitudinal range (Teynié, pers. com.). Also, in the Tam-Dao Mountain Range (northern Vietnam), the species thrives at slightly higher elevations, as Orlov et al. (2000) report its altitudinal range as 200 – 1100 m. In northern Thailand, the species was occasionally found at elevations of 1100 m, or even higher, when forest had been extensively cleared and converted into agricultural land (unpublished data).

*Pareas macularius*. In northern Thailand, *P. macularius* is usually found in hill-evergreen forest and agricultural land at elevations above 800 m (Fig. 14). It can be a very common snake species at elevations of 1200–1700 m, where hill evergreen and submontane forest prevail, often in association with *Pareas hamptoni* (Boulenger, 1905), *Oreocryptophis porphyraceus porphyraceus* (Cantor, 1839), *Gonyosoma prasinum* (Blyth, 1854), *Pseudoxenodon macrops macrops* (Blyth, 1854), and *Ovophis monticola* (Stoliczka, 1870). Specimens have been found in the bowels of *Naja kaouthia* Lesson, 1831 and *Sinomicrurus macclellandi macclellandi* (Reinhardt, 1844) (unpublished data). There is little overlap with the altitudinal range of *P. margaritophorus*. This is also true for areas where much of the forest has been converted into agricultural land. However, in the Tam-Dao Mountain Range, the species seems to occur at lower altitudes. Orlov et al. (2000) reported 400-1100 m as its altitudinal range there, which suggested that there is much overlap with the range of *P. margaritophorus* (200-1100 m).

In southern Thailand, at least one specimen of *P. macularius* (SHPC02.05.19-09) was collected at an elevation below 500 m, and in the extreme south of Myanmar,
CAS 247899 was collected at an elevation below 100 m a.s.l. This suggests that, in regions with high rainfall and high temperatures throughout the year, habitats at low elevations also suit the species, as is true for a number of other snake species, e.g. *Boiga cyanea* (Duméril, Bibron and Duméril, 1854), and *Rhabdophis nigrocinctus* (Blyth, 1855), which prefer higher elevations in northern Thailand.

The different elevational preferences of the two bicolored-spotted snail-eaters in northern Thailand are very similar to those of *Pareas hamptoni* and *P. carinatus*, two other, superficially very similar, snail-eating snakes in the region. In northern Thailand, *P. hamptoni* is found exclusively in evergreen and montane forests, and agricultural land at elevations above 900 m, while *P. carinatus* usually occurs at elevations of 400-1000 m, where it thrives in both mixed, deciduous and evergreen forests, orchards, gardens, and agricultural fields (unpublished data).

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APPENDIX I: MATERIAL EXAMINED (INCL. PICTURES)

**PAREAS MARGARITOPHORUS**

**China:** CIB 10160 (705015) “Yuling, Hainan”; SMF 20790 “Lo Fou Shan, Kanton”.

**Thailand:** MNHN 599 (Holotype of *Leptognathus margaritophorus*) “Siam/Thailande”.


**Central and Northeast:** QSMI-1321 “Nakhon Ratassima”; SKKCC-001 “Ko Chang, Trat”; SHPC14.09.13-06 “Thong Pha Phum, Kanchanaburi”. **South:** QSMI-0226 “Thung Song, Nakhon Si Thammarat”.

**Vietnam:** NMW28128:14 “Annam”.

**PAREAS MACULARIUS**

**China:** CIB 10155 “Hainan”.

**Laos:** MNHN 1994.743 “Haute Laos”; MNHN 2005.0232 “Long Nai Tai, Laos”. **Myanmar:** BM 1946.1.20.8 (Holotype of *Pareas macularius*) “Tenasserim”; BM 1974.901 “Num Kre, 26 01 N, 97 42 E”; CAS 206620 “Bago Division: Bago Yoma, N 18 52 59.8, E 95 52 44.9”; CAS 247899 “Tanintharyi Division: Dawei District, Yapeyu Township, TNR, Khodama military camp, Khodama stream, 14 43 56.9 N, 98 14 57.8 E, 260 ft”.

**Thailand:** **North:** Chiang Mai Province (north): SHPC12.10.21-02 “Doi Suthep, Mueang”; SHPC12.11.06-09 “Doi Ang Khang, Fang”; SHPC13.03.08-04 “Doi Saket”; QSMI-12.05.05-08 “Doi Inthanon, Chom Thong”; SHPC12.05.27-13 “Chiang Dao”; QSMI-13.06.09-10 “Doi

**PAREAS CARINATUS**

**Thailand:** QSMI-11.11.01-07 “Tha Song Yang District, Tak”; QSMI-13.05.27-06 “Mae Chan District, Chiang Rai”; SHPC13.08.17-09 “W of Phrao, Phrao District, Chiang Rai”; SHPC15.05.22-03 “Khun Yuam District, Mae Hong Son”.

**PAREAS HAMPTONI**

**Thailand:** QSMI 1013 “between Mae Sot and Umphang, Tak”; QSMI-12.11.06-08 “Doi Ang Khang, Fang District, Chiang Mai”; QSMI-13.07.18-03 “Doi Phu Kha, Bo Kluea District, Nan”; SHPC12.05.09-05 “Doi Inthanon, Chom Thong District, Chiang Mai”; SHPC12.08.16-04 “Doi Inthanon, Mae Wang District, Chiang Mai”; SHPC12.10.14-03 “Umphang District, Chiang Mai”; SHPC14.06.20-07 “4 km S of Umpiam, Umphang District, Tak”; SHPC14.08.04-03 “Doi Phu Kha National Park, Bo Kluea District, Nan”; SHPC15.05.22-03 “Khun Yuam District, Mae Hong Son”.
APPENDIX II: MISIDENTIFICATIONS AND DOUBTFUL IDENTIFICATIONS

- In Nutphan’s work on snakes in Thailand (Nutphan, 2001) *Parea macularius* (*sic*) is illustrated on p. 74 with pictures of a *P. margaritophorus* with a pale yellow tripartite (type I) collar.

- On the other hand, *Parea margaritophorus* (*sic*) in Nutphan (2001) is illustrated on p. 76 with pictures of *Asthenodipsas malaccana* Peters, 1864 and on p. 77 with a picture of *P. macularius* with a distinct W-shaped collar with “tails” densely speckled with brown (type II), a distinct IBB, and distinct keels in a number of dorsal scales.

- In their critical review of Nutphan’s work (Nutphan, 2001), David *et al.* (2004) present an exhaustive list of misidentifications and other errors, but in this review, the *P. macularius*-specimen in the picture on p. 77 of Nutphan (2001) is misidentified as *P. margaritophorus*.

- Following Smith (1943) and Sharma (2003), the Darjeeling Snail-eater, a rare snake known from Darjeeling and Sikkim in northern India, is identified as *P. macularius* in Whitaker and Captain (2004). An illustration undoubtedly shows *P. macularius*, but the snake originated from Thailand. Details in the description of the Darjeeling Snail-eater, however, cast some doubt on the identification, such as the ‘dark grey or black squarish spots’ on the underside and the occasional presence of a ‘white or yellow band on neck’.

- Six specimens of *Pareas margaritophorus*, collected on Hainan (southern China), are briefly described in Zhao *et al.* (2004/2005). Some of these specimens were completely smooth-scaled, others had 7-11 rows of feebly keeled dorsal scales. The keeled-scaled specimens have probably been misidentified, and are likely to represent *Pareas macularius*.

- In their study of Yunnanese amphibians and reptiles, Yang and Rao (2008) list 12 specimens in the section on *Pareas macularius*. A black-and-white picture shows a snake with cross-bands of bicolored dorsal scales. These specimens all had 15 rows of dorsals, of which 7-9 rows were keeled-scaled. Of 11 of these specimens, the number of ventral shields (153-165) is within the range of *P. macularius*, however, the 175 ventral shields of one specimen (79II0081) are beyond this range. This specimen also showed an exceptional long tail and a number of pairs of subcaudal shields (72) far beyond the range of *P. macularius*. The specimen is misidentified as *P. macularius*, and possibly represents the recently described snail-eater *Pareas nigriceps* Guo and Deng, 2009.

- In Nguyen *et al.* (2009), Figure 502 shows a snake that is definitely identified correctly as *P. macularius*. A W-shaped collar speckled brown (Type II) and an IBB are distinct, but the resolution of the picture is insufficient to see distinct keels on the dorsal scales. However, Figure 505 shows a similar snake that was misidentified as *P. margaritophorus*. The specimen shows a white, gothic W-shaped collar, with two black dots enclosed, and a rather small but distinct IBB is present on the last supralabial. Evidently, it should be identified as *P. macularius*. The resolution of the picture was too low to see distinct dorsal keels, that would have confirmed that *P. macularius* is the correct identification.

- In *Snakes of Thailand and Southeast Asia* (Das, 2012), *P. margaritophorus* is illustrated with a picture of a juvenile *P. macularius* from Vietnam. The snake in the picture has a whitish, W-shaped nuchal collar that is sparsely speckled (type II), a distinct IBB, and
distinct keels on many dorsal scales. The picture was taken in northern Vietnam (Vogel, pers. com.). *P. macularius* is not treated in the work and Das had apparently accepted Huang’s synonymy, as in an earlier work (Das, 2010), both species were described and illustrated correctly.

- QSMI-0235 from southern Thailand was labeled *P. margaritophorus*. The presence of a W-shaped collar with fine speckles (Type II), a distinct IBB, keeled dorsal scales, and a high number of ventral shields (163) show that it should be identified as *P. macularius*.

- QSMI-1318 from northern Thailand was (initially) misidentified as *Pareas margaritophorus*. Rows of keeled dorsals, a densely speckled W-shaped collar (Type II), distinct IBBs and many large, dark blotches on the belly, identify it as *P. macularius*.

- CAS 235218, 245296, 245377, 255359 from western Myanmar had been identified as *P. macularius*. However, the dorsal side, with rows of keeled scales, is nearly completely black and shows no cross-bands of bicolored spots. A speckled, W-shaped nuchal collar cannot be distinguished. On the belly there are rows of squarish, black blotches. The 7th (last) supralabial does not show a distinct IBB, but is heavily mottled with black (in one completely black). It is clear that these snakes represent neither *P. macularius*, nor *P. margaritophorus*, but they represent another species of snail-eater.

- CAS 241270 from Myanmar’s Kachin State was misidentified as *P. margaritophorus*, as it exhibited the same set of characters as the four CAS-specimens mentioned above.

- BM 1926.3.17.9 from Myanmar was labeled “*Amblycephalus macularius*” but exhibited the same set of characteristics as the four CAS-specimens mentioned above. Its color, however, was much lighter (probably due to ninety years of preservation). Also, this specimen cannot be identified as *P. macularius* (neither as *P. margaritophorus*).