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A new species of Temple Pitviper (*Tropidolaemus* Wagler, 1830) from Sulawesi, Indonesia (Squamata: Viperidae: Crotalinae)

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Abstract

The Asian Temple Pitviper *Tropidolaemus wagleri* is a widespread polytypic species complex with a complicated taxonomic history, a lengthy species synonymy list, and a geographic distribution encompassing Vietnam, Thailand, Malaysia, Singapore, Brunei, portions of Indonesia, and the Philippines. As a prelude to a comprehensive review of this species complex, we describe a new species of Temple Pitviper based on five historic museum specimens from the Indonesian island of Sulawesi. The new species can be distinguished from sympatric members of the *Tropidolaemus subannulatus* complex and other congeners on the basis of its conspicuous color pattern and scalation characters. Available collecting data suggest that the new species has a wide distribution in rainforests and lower montane wet forests of Sulawesi Utara and Sulawesi Tengah provinces.

Key words: Reptilia, Squamata, Viperidae, Crotalinae, *Tropidolaemus*, *Tropidolaemus laticinctus* sp. nov., *Tropidolaemus subannulatus*, *Tropidolaemus wagleri*, Indonesia, morphological characters, pitviper, snake, Southeast Asia, Sulawesi, venomous

Introduction

The genus *Tropidolaemus* Wagler, 1830 currently comprises two species of pitvipers from mainland and insular Asia (McDiarmid et al. 1999; Gumprecht et al. 2004). These small to medium-sized (about 35–100 cm total length) snakes are arboreal ambush predators with remarkable morphological features (Burger 1971; Hoge & Romano-Hoge 1983). Their venom contains neurotoxins called waglerins which are unique among snake venom toxins (Molles & Taylor 2002). Snakes of this genus are used in ceremonial contexts and traditionally displayed in a Buddhist temple in Pulau Pinang, Malaysia (Manthey & Grossmann 1997), and consequently often referred to as Temple Pitvipers, or Wagler's Pitvipers.

After a long period of inclusion in the complex genus *Trimeresurus* (sensu lato), *Tropidolaemus* was resurrected from synonymy and regarded as a subgenus of the latter by Brattstrom (1964) based on anatomical and external characters. On the basis of morphological characteristics Burger (1971) considered *Tropidolaemus* to be a distinct genus. This view was widely adopted in the literature (*e.g.*, Hoge & Romano-Hoge 1981, 1983; McDiarmid *et al.* 1999; Orlov *et al.* 2002; Gumprecht *et al.* 2004), and further supported by molecular studies (Kraus *et al.* 1996; Malhotra & Thorpe 2000; Parkinson 1999; Parkinson *et al.* 2002; Vidal & Lecointre 1998), which identified *Tropidolaemus* as an ancient lineage of Old World pitvipers without close relationships to the various genera now recognized from within the *Trimeresurus* complex (Malhotra & Thorpe 2004;

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Creer *et al.* 2006). Instead, most genetic studies suggested the possibility of a sister-group relationship between *Tropidolaemus* and the terrestrial Indochinese pitviper genus *Deinagkistrodon* Gloyd, 1979 (Kraus *et al.* 1996; Parkinson 1999; Parkinson *et al.* 2002; Vidal & Lecointre 1998).

Temple Pitvipers are distributed in Southeast Asia, including southern Vietnam, peninsular Thailand, Malaysia and Singapore, the Philippines, the Indonesian islands of Sumatra, Sulawesi, and Borneo including Brunei and the Malaysian states of Sabah and Sarawak, and on various smaller islands (Gumprecht *et al.* 2004; Iskandar & Colijn 2001; Leviton 1964; Manthey & Grossmann 1997). However, David and Vogel (1998) referred the holotype of a rare pitviper from southern India (*Trimeresurus huttoni* Smith, 1949) to *Tropidolaemus* based on similarity in its external phenotype, thereby greatly extending the known range of this genus. If confirmed by genetic or osteological data, this extended concept of *Tropidolaemus* will raise interesting biogeographical questions.

Temple Pitvipers are remarkably diverse in color pattern, and herpetologists in the nineteenth century described various taxa from this group (*e.g.*, Gray 1842, 1849; Peters 1872). However, all of these were considered to be conspecific, and synonymized with the species *Tropidolaemus wagleri* (F. Boie, 1827), by Boulenger (1896, as *Lachesis wagleri*). Instead of various nominal taxa, Boulenger (1896) recognized five unnamed color varieties ("A" to "E"). An attempt to revise Boulenger's view was made by Taylor (1917, 1922a, b), who described a new subspecies (*T. wagleri alboviridis* Taylor, 1917) from Negros Island in the Philippines, and recognized three additional taxa elsewhere in the Philippines: *T. w. wagleri* (restricted to Balabac and Palawan), *Tropidolaemus wagleri subannulatus* (type locality: “Philippines”; Gray, 1842), and *Tropidolaemus philippensis* (type locality: “Philippine Islands”; Gray, 1842). All these were however again synonymized with a monotypic *T. wagleri* by Leviton (1964). Boulenger's (1896) and Leviton's (1964) interpretation of *T. wagleri* as a single, widespread and morphologically variable species has been followed, although sometimes with hesitation, by most subsequent authors (e.g., David & Ineich 1999; David & Vogel 1996, 1998; Gumprecht *et al.* 2004; Hoge & Romano-Hoge 1981; McDiarmid *et al.* 1999; Orlov *et al.* 2002). A common argument against the recognition of subspecies within *T. wagleri*, or several species of *Tropidolaemus*, has been the apparent difficulty of correlating differences in color pattern with geographic populations or morphology (Leviton 1964).

Recent molecular studies on *Tropidolaemus* have allowed us to appreciate more fully the dramatic ontogenetic color change and sexual dimorphism occurring in these snakes, thus unveiling phenotypic and geographic congruence and helping define species boundaries (U. Kuch & N. Vidal, unpubl.). Following conference presentations of this work, the availability of old names for Temple Pitviper populations was highlighted in regional checklists for Southeast Asia, where various color morphs, subspecies, and species from within *T. wagleri* were provisionally recognized (Iskandar & Colijn 2001; Vogel 2006) but without accompanying data or taxonomic justification.

In the course of revisions of museum specimens we found that green Temple Pitvipers with narrow bands or spots are common in eastern Indonesia and the Philippines. Pending the completion of studies in progress, we will refer to these as an operational *Tropidolaemus subannulatus* complex. However, we also discovered several unusual specimens of *Tropidolaemus* whose external phenotype differs substantially from that of *T. subannulatus*. Among the most divergent of these are several Temple Pitvipers from the Indonesian island of Sulawesi. The distinctiveness of these was first noticed by Boulenger (1896: 564) who established a separate variety "E" within his concept of *Lachesis wagleri* for a specimen from "Minahasa, Celebes" (later specified as "Sonder, Minahassa" [Boulenger 1897: 227], now Sonder, Province of Sulawesi Utara, Indonesia) whose coloration was green dorsally with large brick-red, black-edged spots, and white ventrally with black spots and brick-red marblings, and a red tail tip (Boulenger 1896, 1897). A second, similarly colored specimen from "between L. Posso and Tomini Gulf, Central Celebes" (*i.e.*, between Lake Poso and Tomini Bay, Province of Sulawesi Tengah, Indonesia) was illustrated by Boulenger (1897: Pl. XV; figs. 1–5, 6A, 7A), and contrasted to three specimens from the Bone Valley (Province of Sulawesi Utara) which Boulenger referred to "the typical

form" (*i.e.*, variety "A" in Boulenger [1896]) based on their green coloration with white blue- or purple-edged transverse lines (Boulenger 1897: 227). Two additional specimens with this remarkable brick-red to brown ringed pattern were reported by Ahl (1933) and illustrated in Gumprecht *et al.* (2004). The photograph of an apparently uncollected individual from Gunung Tangkoko (Province of Sulawesi Utara, Indonesia) is contained in de Lang and Vogel (2005, 2006) and Vogel (2006). Here we present evidence supporting the recognition of this highly distinctive form as a species separate from *T. wagleri* and members of the *T. subannulatus* complex, employing the criterion of diagnosability (*sensu* de Queiroz 1998, 1999). As this conspicuous form is not represented by any of the available types and names for Temple Pitvipers, we introduce it as a new species, for which we provide a detailed description and diagnosis.

Material and methods

We examined preserved or live specimens of *Tropidolaemus* from the entire range of the genus except Vietnam. Institutional abbreviations are listed in Leviton *et al.* (1985). Terminology follows Campbell and Lamar (2004). Ventral scale counts were performed according to the method proposed by Dowling (1951). Dorsal scale rows were counted one head length behind the angle of the jaw, at midbody, and one head length before the cloaca. Measurements of the head were made with calipers to the nearest 0.1 mm. A string was used to determine the snout-vent length (from the tip of the snout to the posterior margin of the anal plate) and the tail length (from the posterior edge of the cloacal plate to the tip of the tail). The following head measurements were recorded: distance from anteroventral corner of eye to caudal border of pit (EP), distance from anterodorsal corner of eye to centre of naris (EN), horizontal distance across eye (ED), distance from tip of snout to angle of jaw (HL), height of rostral taken at midline (RH), width of rostral taken at widest point (RW). Sex was determined by direct observation of the gonads or hemipenes in most specimens; in some cases sex was determined based on sexually dimorphic characters of body and tail size and proportions in combination with sexually dimorphic color pattern characters, or by probing in live snakes. Color descriptions of the new species are based on the examination of alcohol-preserved specimens and photographs of two live specimens (de Lang & Vogel 2005, 2006; this paper). Data on the color pattern of sympatric members of the *T. subannulatus* complex and of *T. wagleri* were obtained from both live and preserved specimens. Latitudes, longitudes and elevations were either taken from specimen tags, from the online database of the Koninklijk Instituut voor de Tropen (2006), or from the Indonesia file of geographic names available from the GEOnet names server (National Geospatial-Intelligence Agency 2006).

Systematic account

***Tropidolaemus laticinctus* sp. nov.**
(figs. 1–6, 7A+B, 8A+B, 9–10, and 11A+B)

Lachesis wagleri variety E (Boulenger 1896)
Lachesis wagleri (Boulenger 1897, in part)
Trimeresurus wagleri, "bunte, rotgebänderte Form" (Ahl 1933)
Trimeresurus wagleri (Leviton 1964, in part)
Tropidolaemus wagleri (Hoge & Romano-Hoge 1981, in part)
Tropidolaemus wagleri celebensis (Iskandar & Colijn 2001, in part)
Tropidolaemus wagleri, "red form" (de Lang & Vogel 2005)
Tropidolaemus subannulatus (*celebensis* morph 2) (Vogel 2006) [Date of publication: 10 March 2006]
Tropidolaemus wagleri, "red form" (de Lang & Vogel 2006) [Date of publication: 16 December 2006]

Suggested English name: Broad-banded Temple Pitviper

FIGURE 1. Color plate of Boulenger's variety "E" of *Lachesis wagleri* showing the holotype of *Tropidolaemus laticinctus* (BMNH 96.12.9.80 from "between L. Posso and Tomini Bay, Celebes" [= between Lake Poso and Tomini Bay, Province of Sulawesi Tengah, Indonesia]). Drawing and lithography by J. Green, from Boulenger (1897: Pl. XV).

FIGURE 2. Dorsal view of male holotype of *Tropidolaemus laticinctus* (BMNH 96.12.9.80 from "between L. Posso and Tomini Bay, Celebes" [= between Lake Poso and Tomini Bay, Province of Sulawesi Tengah, Indonesia]). Photograph by Andreas Gumprecht.

FIGURE 3. Ventral view of holotype of *Tropidolaemus laticinctus* (BMNH 96.12.9.80). Photograph by Andreas Gumprecht.

FIGURE 4. Holotype of *Tropidolaemus laticinctus* (BMNH 96.12.9.80), detail of ringed color pattern on lateral body. Photograph by Andreas Gumprecht.

FIGURE 5. Holotype of *Tropidolaemus laticinctus* (BMNH 96.12.9.80), dorsal view of head. Photograph by Andreas Gumprecht.

Holotype: BMNH (= The Natural History Museum, London, United Kingdom) 96.12.9.80, subadult or adult male, "between L. Posso and Tomini Bay, Celebes" [= between Lake Poso and Tomini Bay, Province of Sulawesi Tengah, Indonesia], collected by P. & F. Sarasin (figs. 1–5, 6A, 7A).

Paratypes (4): ZMB (= Institut für systematische Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin, Berlin, Germany) 34317, adult male, "Matinan-Gebirge, Celebes" [likely foothills of Gunung Tentolo Matinan, southwest of Paleleh, Province of Sulawesi Tengah, Indonesia], ca. 100 m above sea level, collected by G. Heinrich, on 20 October 1930 (figs. 6B, 9B); ZMB 34318, adult female, "Paleleh,

Nord Celebes" [Paleleh, Province of Sulawesi Utara, Indonesia; approximately 01°02'53"N, 121°57'05"E], collected by G. Heinrich, on 15 December 1930 (fig. 8A); ZMB 47809, adult female, without collecting data, donated by Aquarium Berlin (figs. 9A, 10); NMW (= Naturhistorisches Museum Wien, Vienna, Austria) 27963:2, juvenile female, "Bua Praeng (…)lebes", obviously Celebes (specimen tag damaged) [presumably in error for Bua, Boea Poeang, or between Bua and Ponrang; all of these localities are near Palopo, Province of Sulawesi Selatan, Indonesia], donated by F. Steindachner in 1801 (figs. 7B, 8B).

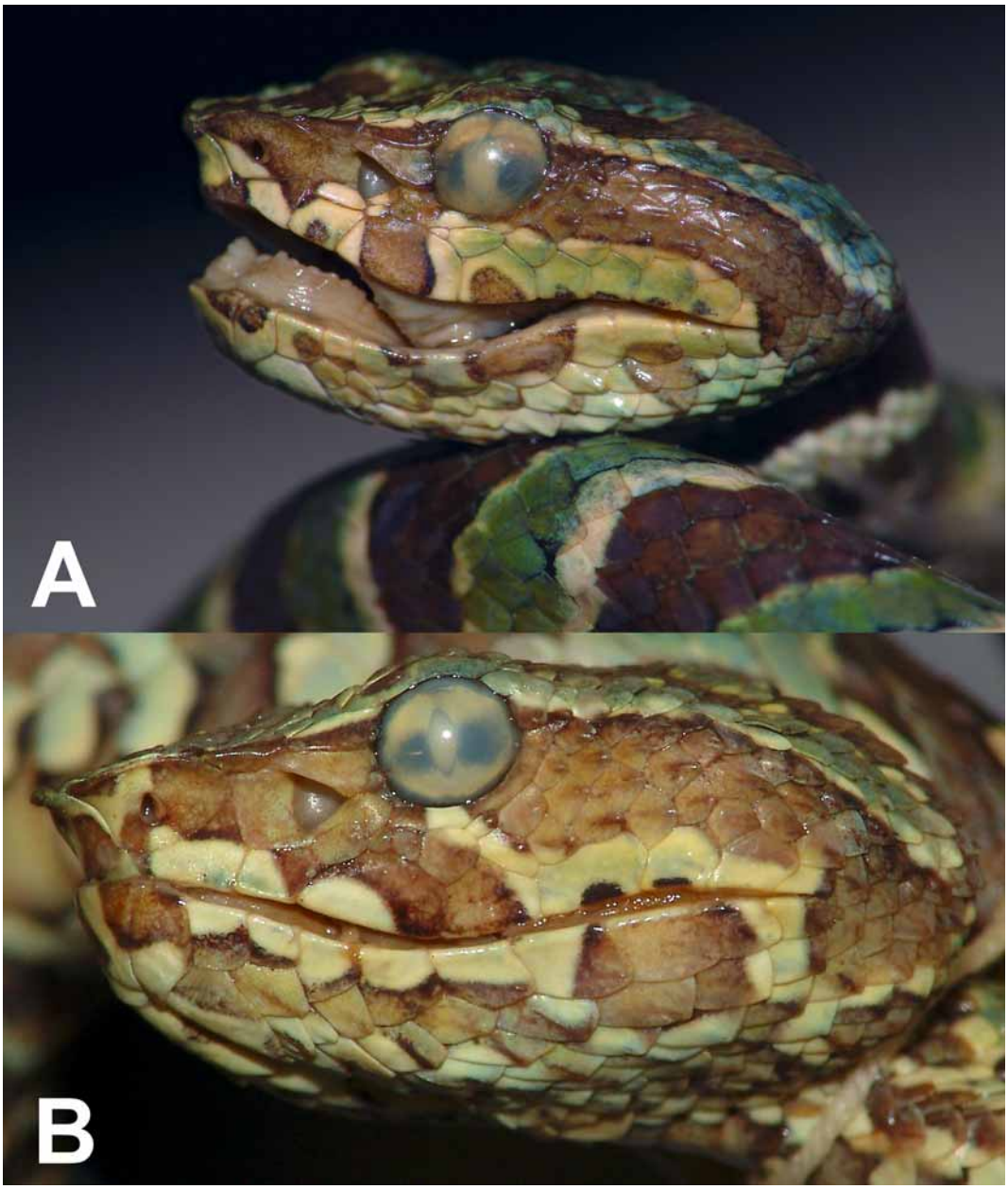

FIGURE 6. *Tropidolaemus laticinctus*, lateral view of left side of heads. A: Holotype (BMNH 96.12.9.80). B: Adult male paratype (ZMB 34317; "Matinan-Gebirge, Celebes"). Photographs by Andreas Gumprecht.

Diagnosis: A species of *Tropidolaemus*, an Asian pitviper genus characterized by strongly keeled gular scales, a splenial that is separate from the angular (Burger 1971), and a unique dorsal scale microdermatoglyphic pattern of rounded cells that are strongly covered with longitudinal parallel lines and comb-like ridges (Hoge & Romano-Hoge 1983; striocristate pattern subtype sensu Price 1982, verified in ZMB 47809). *Tropidolaemus laticinctus* differs from all congeners by the following combination of characters: lack of pronounced sexual or ontogenetic differences in color pattern; presence of ornate head pattern with brown dorsal

markings on green ground that are bordered by cream scales and are largest on the posterior head; wide brown pre- and postocular stripe that extends to lower side of head beyond angle of jaw; ornate labial pattern consisting of brown spots bordered by white or black, on green to cream ground color; conspicuous large brown spot extending from anteroventral corner of eye and posteroventral margin of pit to lower margin of supralabials; lower side of head with similar pattern as dorsal side of head, or mottled with numerous brown and black spots and streaks; dorsal body pattern consisting of broad brick-red to brown rings that may be incomplete dorsally or laterally and are about as wide as or wider than the cream to white interspaces; anterodorsal part of light interspaces of body pattern containing wide green bands; brown rings across belly connected midventrally to form midventral stripe (if brown rings incomplete ventrally, venter heavily spotted, with chessboard-like pattern); base of tail with whitish and brown rings, tip of tail lighter reddish brown with no or only indistinct bands.

Tropidolaemus wagleri differs from *T. laticinctus* in having distinct sexual differences in color pattern, in females undergoing a dramatic ontogenetic color change from a bright green ground color to a largely black and yellow coloration with or without green components, in lacking an extensively patterned venter, and in lacking an ornate labial pattern. Juvenile females of *T. wagleri* further differ from *T. laticinctus* in having a dorsal pattern of very narrow red and white bands on bright green ground color and in lacking a dorsal head pattern; male *T. wagleri* of all ages differ from *T. laticinctus* in having a dorsal pattern of tiny red and white spots and in lacking a dorsal head pattern. Members of the *T. subannulatus* complex (including the types of *Trimesurus* [sic] *philippensis* Gray, 1842, *Trimesurus* [sic] *subannulatus* Gray, 1842, and *Trigonocephalus wagleri* var. *celebensis* Gray, 1849) differ from *T. laticinctus* in lacking a well-defined ornate head pattern with light-bordered dorsal markings and in lacking an ornate labial pattern, in lacking a ventral pattern of brown rings and/or midventral stripe, and in having a dorsal pattern of narrow bands or spots (vs. broad brick-red to brown rings). Both sexes of sympatric members of the *T. subannulatus* complex differ from *T. laticinctus* in having a uniform or near-uniform green dorsal head color (fig. 8C, vs. ornate brown head pattern), a narrower bluish (vs. wide brown) pre- and postocular stripe and largely patternless labial region (fig. 7C, vs. ornate labial pattern), the presence (vs. absence) of well-defined, black-edged ocelli on outer posterior margins of ventral scales (fig. 7C), and an otherwise uniform green to bluish green venter (vs. heavily patterned venter with brown rings and midventral stripe). Sympatric members of the *T. subannulatus* complex further differ from *T. laticinctus* in having narrow white and bluish or reddish bands or spots on uniform green ground color (fig. 11C, vs. broad brick-red to brown rings), and in having a tail pattern consisting of narrow bluish bands and wide green interspaces at the base and nearly equidistant, distinct narrow black and white bands on brownish to greyish ground towards the tail tip (fig. 11C, vs. well-defined, approximately equidistant light and brown rings on base of tail, and light reddish brown tail tip with no or only indistinct bands). Adult females of sympatric members of the *T. subannulatus* complex also differ from the adult female *T. laticinctus* illustrated by de Lang & Vogel (2005, 2006) in having a yellow to golden (figs. 7C, 11C; vs. reddish) eye color.

In characters of scalation, the specimens of the available small series of *T. laticinctus* (N=5) differ from the examined *T. subannulatus* complex members from Sulawesi (N=16) in having a slightly convex anterior margin of the mental scale (vs. centrally concave when viewed from the same angle, or indented at the level of the tongue), and in having higher ventral scale counts (139–146 vs. 134–139, respectively). The females of *T. laticinctus* (N=3) also differ from the majority of examined *T. subannulatus* complex females from Sulawesi (11 of 13) in having a higher number of dorsal scale rows at midbody (25 vs. 23, respectively).

Description of holotype: A small pitviper with a subtriangular head that is very distinct from the neck, and a prehensile tail. Rostral overall trapezoidal, lower margin of rostral 2 × wider than upper margin, higher than wide, almost vertical along suture with first supralabial on right side, only slightly concave along supralabial suture on left side; dorsal margin of rostral rounded, projecting anteriorly, forming part of very sharply upturned canthus rostralis; nasal very large, undivided, dorsal margin of nasal projecting dorsally and laterally, forming major part of canthus rostralis; internal naris subelliptical, upper part turned slightly more

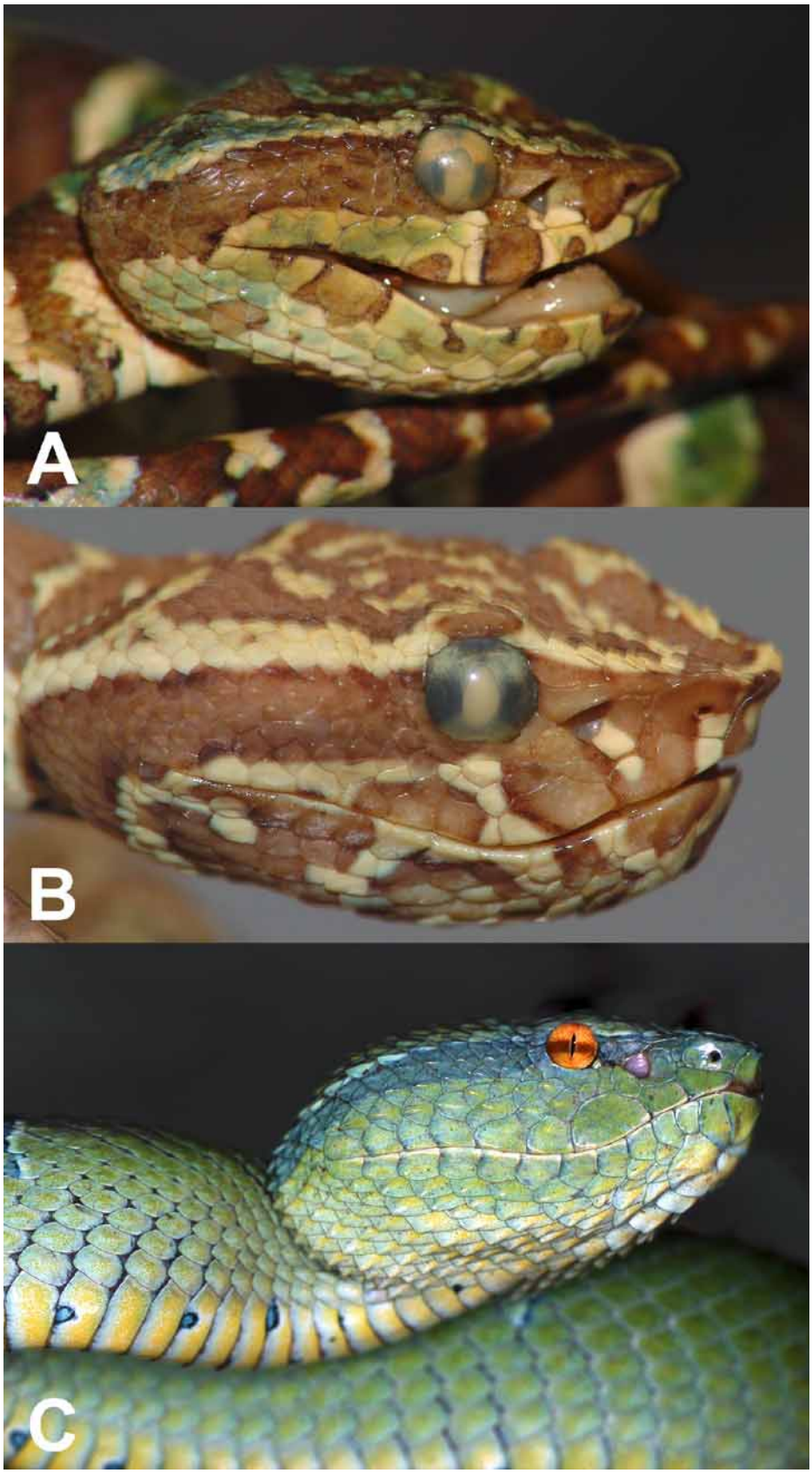

FIGURE 7. A: Holotype of *Tropidolaemus laticinctus* (BMNH 96.12.9.80); B: juvenile female paratype of *T. laticinctus* (NMW 27963:2), lateral view of right head sides. C: Adult female member of the *Tropidolaemus subannulatus* complex from northern Sulawesi; lateral view of head showing bluish pre- and postocular stripe, largely patternless labial region, and presence of distinct black-edged blue ocelli on outer posterior margins of ventral scales. Photographs by Andreas Gumprecht.

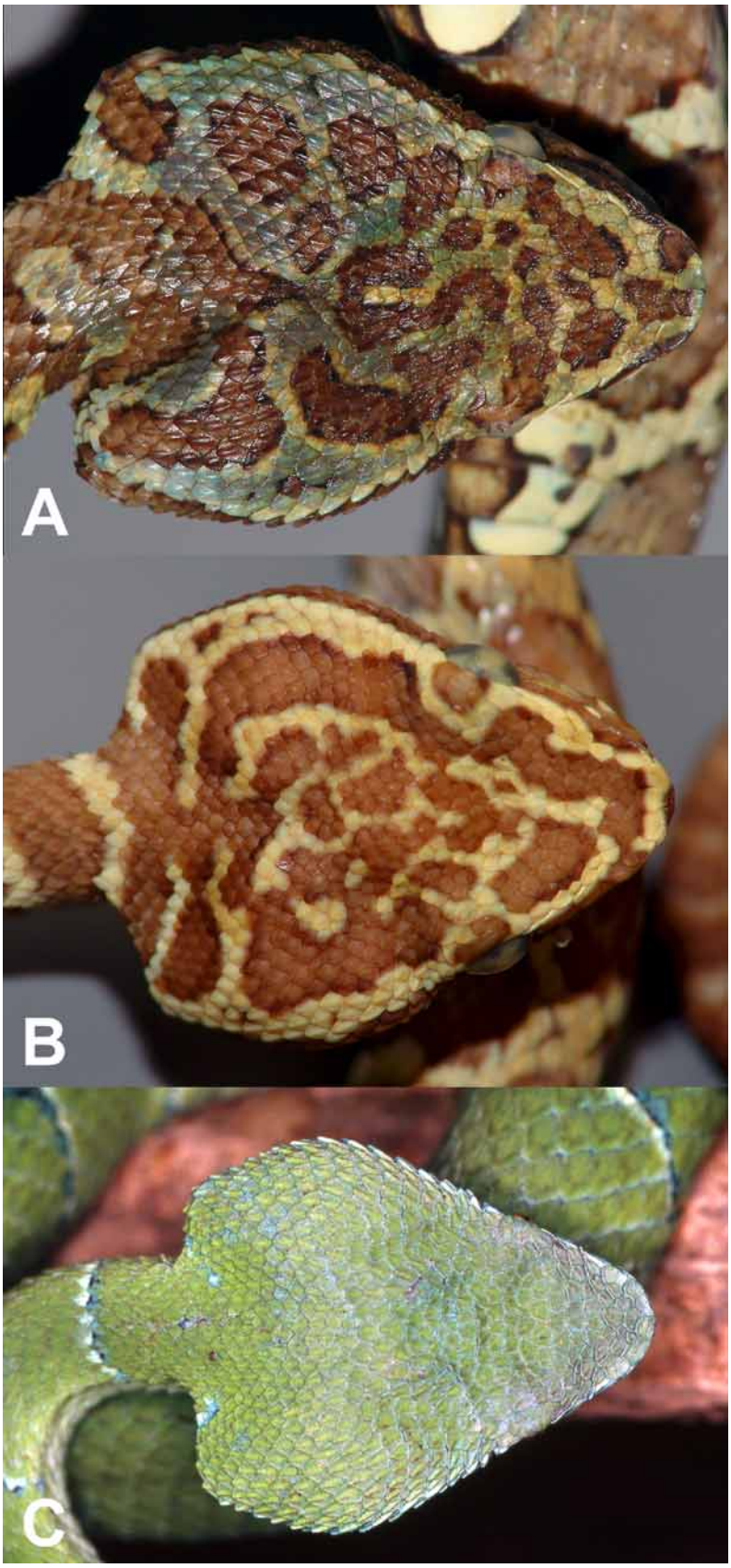

FIGURE 8. Adult female paratype of *Tropidolaemus laticinctus* (ZMB 34318) from "Paleleh, Nord Celebes" (Paleleh, Province of Sulawesi Tengah, Indonesia); B: juvenile female paratype of *T. laticinctus* (NMW 27963:2) from "Bua Praeng, [Ce]lebes"; dorsal view of heads. C: Adult female member of the *Tropidolaemus subannulatus* complex from northern Sulawesi, dorsal view of head showing lack of distinct color pattern. Photographs by Andreas Gumprecht.

FIGURE 9. A: Adult female paratype of *Tropidolaemus laticinctus* (ZMB 47809); B: adult male paratype of *T. laticinctus* (ZMB 34317; "Matinan-Gebirge, Celebes"); ventral view of heads. Photographs by Andreas Gumprecht.

anteriorly, twice as high as wide; external nare with posteroventral extension pointing toward supralacunal-postlacunal suture; posteroventral margin of external nare terminating at level of end of first half of nasal; loreals absent, nasal borders upper half (right side) to almost upper two-thirds (left side) of anterior margin of prelacunal; prefoveals 1/1, tiny, at junction of nasal, prelacunal and first supralabial; subfoveals 2/2, anterior one elongate, projecting towards anteroventral margin of orbit, bordering posteroventral corner of prelacunal, posterodorsal corner of second supralabial, anterodorsal corner of third supralabial, anteroventral half of postlacunal, and posterior subfoveal; posterior subfoveal drop-like in shape, wider posteriorly, directed towards lower margin of orbit, bordering posterior margin of anterior subfoveal, posterior part of first half of third supralabial, posteroventral half of postlacunal, anterior margin of sublacunal, lower margin of preocular; two-thirds of posterior subfoveal extending beyond posterior corner of pit; prelacunal separated from second supralabial on both sides; postfoveals 1/1, tiny, anterior and lower portions partly covered by sublacunal and posterior subfoveal, excluded from orbit by posteroventral extension of supralacunal. Prelacunal moderately large, wider in lower part, higher than wide; on both sides bordered anteriorly in upper two-thirds by nasal, in lower one-third by first supralabial; anterior two-thirds of upper margin of prelacunal bordered by posterior half of third canthal; posterior one-third deep inside pit, covered by supralacunal; lower margin of prelacunal bordered by upper margin of second supralabial; lower posterior extension of prelacunal ending at level of upper posterior corner of second supralabial, bordered posteriorly by 1/1 subfoveals. Sublacunal small and short; shorter than lower margin of prelacunal, about as wide as height of posterior margin of nasal, slightly wider than lower margin of supralacunal; anterior end narrow, covered by lower posterior extension of prelacunal; extending in straight line up to contact with supralacunal; about 2 × wider posteriorly than anteriorly; lower anterior margin bordered by subfoveal that also contacts upper posterior part of second supralabial, upper anterior corner of third supralabial, lower/anterior postfoveal, and lower posterior corner of prelacunal;

posteriorly, sublacunal bordering 2/2 postfoveals. Supralacunal large, anterodorsal projection bordering posterolateral margin of third canthal, remaining dorsal margin of supralacunal covered by fourth canthal which also forms upper preocular; posterior margin of supralacunal almost vertical, but rounded in lower posterior corner, here covering upper anterior end of small, rounded lower preocular; lower margin anteriorly bordering sublacunal, posteriorly bordering upper postfoveal; lower anterior margin forming posterodorsal border of pit, extending upwards in an angle of approximately 45° from above posterior one-third of sublacunal to start of posterolateral one-fourth of third canthal and posterior one-fourth of dorsal margin of prelacunal; lower anterior margin of supralacunal straight to slightly concave in upper part bordering pit. Preoculars 3/3, formed by entire posterior margin of small keeled scale that is completely fused to the posteriormost (fourth) canthal (upper preocular, bordering one-fourth of anterior margin of orbit), posterior margin of supralacunal (middle preocular, bordering half of anterior margin of orbit), and a small lower preocular; lower preocular touching the eye, forming only one-fourth of anterior margin of orbit; lower preocular located between supralacunal and subocular, separated from third supralabial by subocular and one small interoculabial. Suboculars 1/1, long and narrow; extending from before anterior margin of lower preocular to level of posteriormost point of orbit, about as wide anteriorly as posteriorly, smooth anteriorly, slightly rugose posteriorly, upper posterior margin covered by lower of two postoculars. Postoculars weakly keeled; upper postocular slightly larger, participating in orbit with about half of length of scale, about as much as lower postocular. Anterior end of left subocular in contact with central part of upper margin of third supralabial, posterior one-third of dorsal margin of third supralabial separated from subocular by one tiny triangular and one larger keeled interoculabial; right subocular separated from third supralabial; interoculabials 3/3, one row of scales between subocular and supralabials: one scale each between subocular and suture of third/fourth and fourth/fifth supralabial; 2/2 scales (in diagonal view) between posterior part of subocular and corner of sixth supralabials, the lowermost covered anteriorly by posterodorsal margin of fifth supralabial, posteriorly covering anterodorsal margin of sixth supralabial, both weakly keeled; 3/3 scales between posterior part of subocular and corner of seventh supralabials. Upper lip curved; highest parts located at rostro-mental contact and the corners of the mouth; lowest parts at suture of third/fourth supralabials, corresponding approximately to level of fourth/fifth infralabials. Supralabials 9/10; first supralabial extending up to one-third of height of prelacunal, separate from nasal; second supralabial about as large as first, separate from prelacunal; third supralabial largest, more than 2 × size of first supralabial, about 2 × wider than high; fourth supralabial second largest, about as high as wide; supralabials 5–9/5–10 much smaller than fourth, but larger than dorsally adjacent scales; ninth/tenth supralabials smallest. Internasals 1/1, small, about as wide as long; laterally covering anteromedian ends of first canthals. Canthals 4/4, first pair widest, second shortest, third and fourth elongate and narrow, smooth but some with uneven scale surface; first pair approximately 2 × longer than wide, entirely on top of head, bordered laterally by two intercanthals; second canthals ca. 1½ × longer than wide, bordered by three intercanthals; third canthals about 2 × longer than wide, bordered by two intercanthals; fourth canthals approximately 2 × longer than wide, bordered by two intercanthals and the supraocular; outer margins of third and fourth canthals turned to side of head; posteror tip of fourth canthal on both sides fused to tiny keeled scale adjacent to anterolateral margin of supraoculars. Canthus rostralis sharply pronounced, projecting anteriorly and anterolaterally; nasals, first and second canthals and internasals contributing more to canthus rostralis than third and fourth canthals. Anterior and lateral intercanthals only weakly keeled, central intercanthals more distinctly keeled, mostly narrower than internasals but often longer; three intercanthals between first pair of canthals immediately posterior to internasals, the middle one directly posterior to the internasal suture being very small; increasing posteriorly to 5, 6, 7, 8 and 9–10 intercanthals, the latter between the fourth canthals. Supraoculars small, elongate and narrow, with uneven scale surface and poorly defined margins due to obvious fusion with at least two adjacent scales each, on either side with 1–2 indistinct keels; supraoculars about 1½–2 × longer and 2 × wider than fourth canthals; bordered by 8/8 scales including the fourth canthals with posteriorly fused scale and postoculars. Intersupraoculars keeled, minimum number 9 (between anterior ends

FIGURE 10. Adult female paratype of *Tropidolaemus laticinctus* (ZMB 47809). A: dorsal view; B: ventral view. Photographs by Andreas Gumprecht.

of supraoculars), maximum number 13 (between posterior ends), 11 between middle of supraoculars. Posterior head scales weakly to strongly keeled; approximately 32 interrictals. Scales on lower head (especially mental, chinshields, also anterior infralabials and supralabials) with numerous tiny tubercular structures (presumably mechanoreceptors). Mental large, anterior margin of convex appearance, slightly concave on both sides, wider than long; bordered by first infralabials; posterior tip of mental separating first infralabials,

extending between anterior end of chinshield suture. Infralabials 9/10; first infralabials 2 × higher than wide in upper part, in contact with mental, second infralabials, and chinshields; second infralabials small, rectangular, wider than high; on left side, third infralabial wider and ca. 1½ × higher than second infralabials; on right side, third infralabial small, 2 × higher than wide; infralabials 4/5+6 largest, infralabials 5–9/7–10 of similar size and shape, gradually becoming smaller posteriorly; on left side, ninth infralabial smallest (about ½ × smaller than second infralabial); on right side, tenth infralabial second smallest, being slightly larger than third infralabial. One pair of chinshields, wide, with pointed posterior extension left and right of distinct mental groove, about 2 × longer than wide at longest part; bordered by mental, infralabials 1–2, two sublabials, and first gular; chinshields followed by seven pairs of smooth to very slightly keeled gulars, the anterior of which are wider than long, followed posteriorly by one preventral that is mostly covered by laterally adjacent scales; 6–7 rows of sublabials between last infralabial and posteriormost gular; 146 ventrals; anal plate undivided; 52 subcaudals, all divided, plus a terminal scale equal in length to two terminal subcaudals; dorsal body scales arranged in 21/21/17 rows, only slightly keeled, most keels only on posterior half of scale, extending to terminus of scale; paraventrals smooth over most of body, slightly wider than adjacent dorsals; dorsal scales on tail and parasubcaudals without keels. Measurements of holotype (in millimeters): SVL 350, TL 66, EP 1.2, EN 5.8, ED 3.5, HL 20.9, RH 2.69, RW 2.63.

FIGURE 11. A+B: Live *Tropidolaemus laticinctus* from the western side of Dumoga Bone National Park, about 30 km northeast of Gorontalo, Sulawesi Utara, Indonesia. Photographs by Tommy Ahnby. C: Live adult female member of the *Tropidolaemus subannulatus* complex from northern Sulawesi showing narrow white and bluish bands and spots on uniform green ground color, and tail tip with distinct pattern of nearly equidistant, narrow black and white bands on brownish to greyish ground. Photograph by Andreas Gumprecht.

Coloration of holotype (in preservative; figs. 1–5, 6A, 7A): Top of head with ornate head pattern composed of brown, green and cream elements; in dorsal view, outer margins of internasals and first canthals

greenish cream, central portions as well as anteromedian parts of first intercanthals brown; posterior part of resulting brown spot on right side connected to larger brown spot centered in anterior canthal region, covering an area of approximately ten intercanthals; two brown spots of similar size and shape in posterior intercanthal region, left one separate from anterior intercanthal spot and left supraocular but with small V-shaped central extension, right one broadly fused to anterior intercanthal spot and just contacting anteromedian margin of right supraocular; two smaller, irregularly shaped brown spots in anterior intersupraocular region; supraoculars centrally with brown area that is continuous (left) or near continuous (right) to large L-shaped (left) and inversely L-shaped (right) brown blotch; posteromedian extensions of these latter blotches pointing toward each other but not in contact in occipital region, thereby framing a fronto-parietal area that contains a roughly trapezoidal brown mark with central green spot; another brown spot involving about ten scales posterior to where short legs of L-shaped blotches point toward each other; right (inversely) L-shaped blotch posteriorly fused to large brown interrictal mark that is concave anteromedially and posterolaterally, convex anterolaterally, has a posteromedian extension pointing toward the neck, and at its outer posterior margins connects to brown pattern elements on the posterior sides of the head; brown spots on top of head in various parts with indistinct darker to blackish outer margins, in addition to more distinct, narrow cream to greenish cream borders that set off the brown head pattern from much of the intervening light green (top of snout) to dark green (posterior head) areas. Rostral pale greenish yellow with brown upper and lower margins and small brownish central suffusion; anteroventral corner of nasal pale greenish yellow up to anteroventral margin of naris, rest of nasal brown; first pair of supralabials brown along sutures with rostral and brown part of nasal and prelacunal, pale greenish yellow elsewhere; second supralabial pale yellow with greenish hue centered near posterodorsal corner, and irregularly dark-edged brown spot in lower central part of scale; lower part of prelacunal cream, upper part greenish, finely dusted with brown; posterior two canthals with cream inner and brown outer margins; all scales bordering anterior orbit, including entire supralacunal, brown mixed with green pigment; posterior half of sublacunal brown mixed with green, anterior half cream; subfoveal cream; postfoveals brown mixed with green; third supralabial with wide central brown area extending down from brown preocular area, set off from cream anterior and posterior margins of third supralabial by narrow dark brown to black margins; anteriormost tip of subocular brown (part of brown preocular area), then cream up to about level of center of eye, and brown posteriorly; lower postocular brown, upper postocular cream with brown lower corner; from fourth supralabial posteriorly, ground color of supralabials and margins of adjacent scales pale yellowish green; anterior margin of fourth supralabial and anterior one-third of interoculabial between third and fourth supralabial and subocular cream; fourth supralabial with dorsally rounded brown spot on lower central margin; fifth to eighth supralabials with brown or black lower central margins; color of eye golden, with extensive black pigment anterior and posterior to vertically elliptical pupil, indicative of a continuation of the brown pre-and postocular stripe; wide brown postocular stripe extending from posterior orbit to beyond angle of jaw, covering 3–4.5 scales in width, upper and lower margin delimited by black pigment only on a few scales; upper margin of postocular stripe bordered by narrow cream line extending from upper postocular to beyond angle of jaw. Mental and first infralabials greenish yellow, with indistinct brown spots on both upper mental-infralabial sutures and lower (posterior) end of mental; ground color of infralabials from cream and greenish yellow anteriorly to pale yellowish green posteriorly, with variable degrees of brown dusting and spots; posterior part of second infralabial dusted with brown; third infralabial with poorly defined small brown streak in upper central part; fourth infralabial with brown spot in lower anterior corner and narrow diagonal extension to upper posterior corner; brown posterior margin of fifth and brown anterior margin of seventh supralabial forming dark-edged light brown infralabial spot together with brown-dusted sixth infralabial; upper posterior corner of seventh and upper anterior corner of eighth infralabial also with brown spot; posterior half of posteriormost supralabial and posterior one-third of posteriormost infralabial forming part of dark brown margin of postocular stripe; ground color of scales on lower side of head cream to yellowish green; chinshields each with small black central spot and posterolateral black-edged brown spot that continues

posteriorly as a poorly defined brown pattern element on adjacent scales; numerous gulars and other scales with small brown or black spots or streaks or dusted with brown or black pigment.

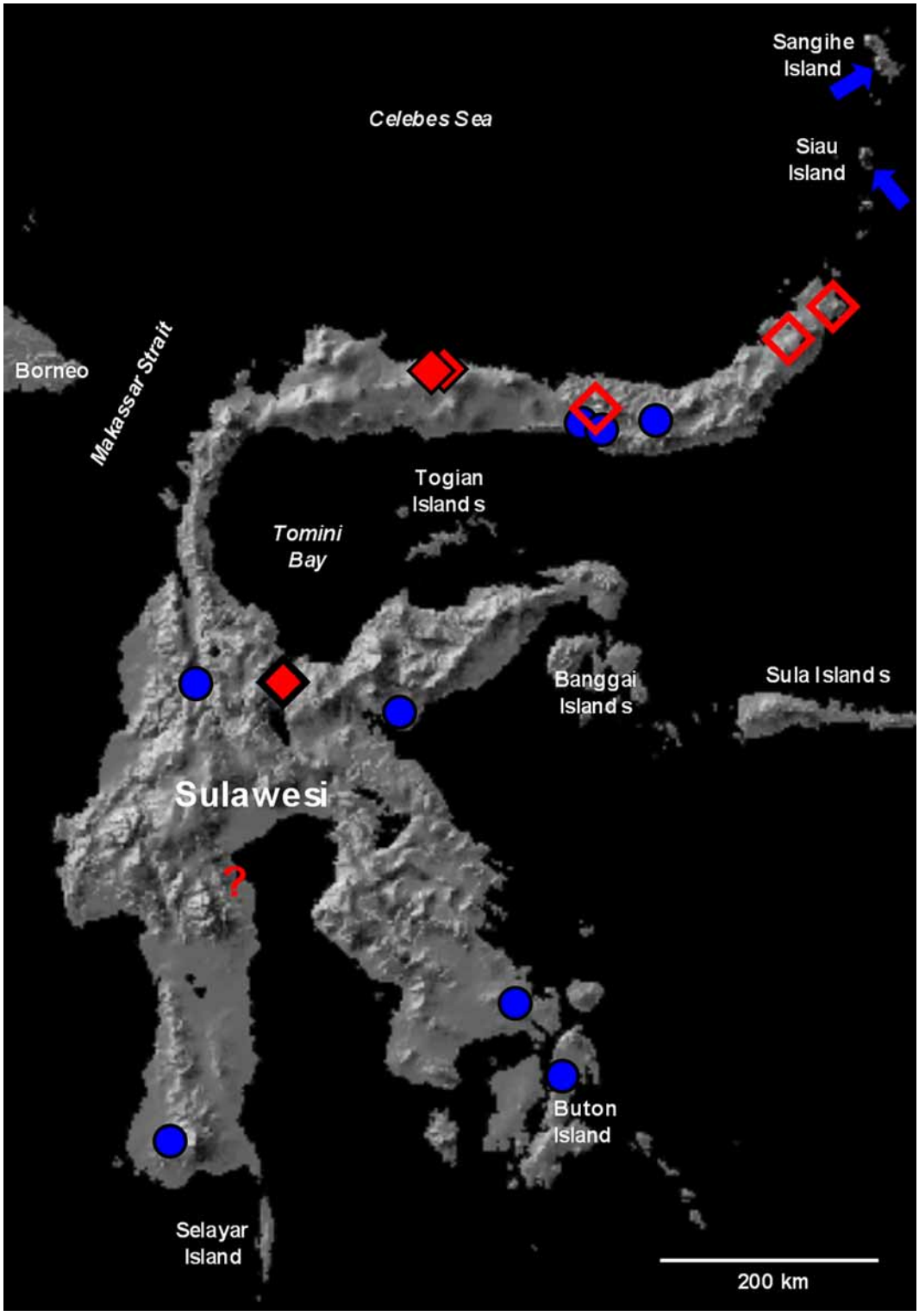

FIGURE 12. Relief map of Sulawesi, Indonesia, showing selected localities of *Tropidolaemus laticinctus* (rhomboids; filled: examined specimens; unfilled: photographs and literature records; area of the type locality marked by rhomboid with thick black line) and *Tropidolaemus subannulatus* complex members (dots). Arrows designate localities of *T. subannulatus* complex members in the Siau and Sangihe Islands. An additional collecting locality of *T. laticinctus* ("Bua Praeng", presumably in error for Bua, Boea Poeang, or between Bua and Ponrang; all of these near Palopo, Province of Sulawesi Selatan) could not be reliably placed and is indicated by a question mark.

Dorsal body pattern consisting of 35 brick-red to brown rings that are 2.5–4 dorsal scales long midvertebrally; ventrally, most of these rings are slightly directed toward the head; several rings laterally divided, juxtaposed, or incomplete dorsally or laterally (ring 1 split on right side; 2 split on left; 2+3 dorsally almost fused, 3 on right side separated from ventral part; 4 split on left; 5 split on right; 7 split on left; 8 incomplete on right; 13+30 dorsally almost interrupted, juxtaposed; 15 ventrally incomplete; 31+33 laterally divided on both sides; 34 with anterior dorsal extension pointing toward 33; 35 present only on right side, dorsally pointing toward 34); brown rings about as wide as or wider than interspaces; anterodorsal part of light interspaces of body pattern containing wide green bands; posterodorsal part of light interspaces with narrow cream bands; laterally, green color of light interspaces gradually fading towards venter; ventrolaterally, interspaces mostly cream to white, on outer edges of ventrals with small dark (brown or black-edged brown) spots of variable number (usually 1–3), size, and shape; brown rings across belly connected midventrally to form midventral stripe; midventral stripe almost continuous along body, only four times interrupted at levels of first to sixth brown rings; midventral stripe about as wide as ventral part of brown rings, approximately as wide as 1–3 ventrals, with lateral extensions; midventral stripe and ventral part of brown rings tan to light brown, mostly black-edged; posterior margins of most ventrals at midventral stripe darker brown or black; ventral ground color cream to light tan; base of tail with ten distinct brown rings; rings 2+3 on tail dorsally fused; rings 4+5 in contact dorsally; all other rings on tail separated by cream interspaces; green color on tail confined to dorsal parts of basal light interspaces; tip of tail light reddish brown with no rings or bands.

Variation: The number of ventral scales varies between 139 and 146 (males: 146; females: 139–140 ventrals); the number of subcaudals ranges from 49–52 (males: 50–52; females: 49-51), all of which are divided. Supralabials 9–11 (males: 9–10; females: 10–11); interoculabials 3–4 (males: 3; females: 3–4); postoculars 2–3 (males: 2; females: 2–3), of which the lower 1–2 may be fused to the subocular; infralabials 9–11 (males: 9–10; females: 10–11), the first pair of which may or may not be in contact posterior to the mental; 4–7 gulars (males: 4–7; females: 7) between chinshield and first (pre-)ventral, arranged in pairs or (posteriorly) in rows of three; preventrals 0–2 (males: 1–2; females: 0–2); intersupraoculars 9–13 (males: 9–10; females: 10–13); scales bordering intersupraoculars 8–9 (males: 8–9; females: 8–9); canthals 3–4 (males: 3–4; females: 3–4); intercanthals 3–7 (males: 3–6; females: 5–7) between first canthals, 9–12 (males: 9–11; females: 11–12) between posterior canthals; internasals 2, in contact, or separated by scale of approximately equal size, or anteromedian part of each internasal divided to form two separate scales; prefoveals 0–4 (males: 0–1; females: 2–4); dorsal scale rows 25/21/19 in males, 23–25/25/19 in females. Variation in color pattern includes about 30–42 dark brick-red to brown rings or bands on the body (males: 31–35; adult females: 30–38; juvenile female: ca. 40–42) which may be disintegrated, incomplete or juxtaposed vertebrally or laterally, interrupted laterally on one or both sides, and cover 2–5 dorsal scales in length midvertebrally; brown rings or bands bordered especially anteriorly, but sometimes also posteriorly, by narrow cream to white (fig. 11A+B) areas, or without distinct light borders (fig. 10A); some with narrow black borders along brown rings or bands (*e.g.*, fig. 10A); 7–11 distinct brown rings or bands on basal part of tail (males: 10–11; adult females: 7–8; juvenile female: 11); light interspaces between brown rings or bands covering 1–3 dorsal scales in length midvertebrally; light interspaces very narrow in the juvenile specimen (NMW 27963:2), cream to tan after more than 200 years in preservative (possibly green in life); light interspaces of the other specimens dorsally with wider green anterior part that may be nearly as wide as the brown rings, and with or without narrow cream to white posterior part that borders the following brown ring; laterally, green color of light interspaces gradually fading towards venter; ventrolaterally, interspaces mostly cream to white, on outer edges of ventrals with small dark (brown or black-edged brown) spots of variable number (usually 1–3), size, and shape that may be connected to a brown midventral stripe; dorsal scales of green areas of many light interspaces also with brown, black-edged brown, or black spots and streaks that may laterally extend up to the midvertebral region; green color on tail confined to dorsal parts of basal light interspaces; ventral ground color light tan to cream or dirty white; brown rings on venter connected to midventral stripe that may be incomplete and juxtaposed on

anterior body (fig. 3), or disintegrated in chessboard-like pattern of dark grey mottling especially on lateral parts of ventrals in the absence of a distinct midventral stripe (fig. 10B); midventral stripe about as wide as ventral part of brown rings, approximately as wide as 1–3 ventrals, often with multiple lateral extensions; midventral stripe and ventral part of brown rings tan to light brown, mostly black-edged; posterior margins of ventrals in midventral stripe often also darker brown or black.

Distribution and habitat: *Tropidolaemus laticinctus* is so far known only from the Indonesian Provinces of Sulawesi Utara and Sulawesi Tengah in northern Sulawesi island (fig. 12). Available information on collecting localities place this species in lowland to lower montane rainforest. The vertical distribution of the new species extends from near sea level (Paleleh) and about 100 m (Matinan Mts.) to at least 550 m above sea level (1800 feet, at Sonder, Sulawesi Utara; Boulenger [1897]). A specimen in Dumoga Bone National Park (Sulawesi Utara) was observed close to a small river (T. Ahnby, personal communication; fig. 11A+B).

Etymology: The specific epithet, the Latin adjective *laticinctus*, meaning broad-ringed or broad-banded, alludes to the color pattern on the body of the new species, which consists of comparatively broad brick-red to brown rings, and readily distinguishes it from sympatric congeners (with very narrow blue or red spots or bands on an otherwise solid bright green dorsum), as well as from any other known member of the genus *Tropidolaemus*.

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Appendix 1. Selected additional specimens examined

Tropidolaemus subannulatus complex: No locality: ZMB 63864. PHILIPPINES: "Philippine Islands": BMNH 1946.1.17.67; "Philippines": 1946.1.19.32, BMNH 1946.1.19.33. INDONESIA: "Celebes": BMNH 49.3.2.39; "Sulawesi": SMF 86850–86856, ZFMK 68525, ZFMK 76337, ZFMK 76338; "Siau Langi Ins." (likely SULAWESI UTARA PROVINCE: Sangihe Islands: Siau Island): ZMB 7427; SULAWESI SELATAN PROVINCE, Bantimurung: SMF 75739, SMF 77910; SULAWESI TENGAH PROVINCE, Kabupaten Donggala, Kulani, Torro, 600 m: BMNH 1980.936; Moronali Nature Reserve, Ranu River: BMNH 1980.1718; [SULAWESI UTARA PROVINCE], "N. Celebes, Bone Valley", 650–1000 feet (*fide* Boulenger 1897): BMNH 96.12.9.79; Sangihe Islands, Tamako, Tankoko National Park: ZFMK 73918; SULAWESI UTARA PROVINCE: Kabupaten Gorontalo: Kecamatan Suawa: Desa Lombongo: Dusun Dua: Kampung Lompongo: TNHC 59994.