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A new species of *Pseudocalotes* (Squamata: Agamidae) from the Bukit Barisan Range of Sumatra with an Estimation of its phylogeny

MICHAEL B. HARVEY¹, KYLE SHANEY², AMIR HAMIDY³, NIA KURNIAWAN⁴ & ERIC N. SMITH²

¹Department of Biological Sciences; Broward College; 3501 S.W. Davie Road; Davie, FL 33314; USA.

E-mail: mharvey@broward.edu

²The Amphibian and Reptile Diversity Research Center and Department of Biology; University of Texas at Arlington; 501 S. Nedderman Drive; Arlington, TX 76010; USA

³Laboratory of Herpetology; Museum Zoologicum Bogoriense; Research Center for Biology, Indonesian Institute of Sciences–LIPI; Jl. Raya Jakarta Bogor km 46; Cibinong, West Java, 16911; Indonesia

⁴Department of Biology; Universitas Brawijaya; Jl. Veteran; Malang, East Java, 65145; Indonesia

Abstract

We describe a new species of *Pseudocalotes* from montane forests of the central, western coast of Sumatra. The combination of 3 or 4 interoculabials, slightly enlarged and heavily keeled scales on the lower flanks, a white scapular spot, a relatively long fifth toe, bicarinate lamellae at the base of Toe III, absence of a postrictal modified scale, and three rows of paravertebrals directed dorsally and posteriorly distinguishes the new species from its congeners on Sumatra and Java. Among the new characters defined in this study, counts of subdigital lamellae within the “span of Toe V” proved particularly useful for diagnosing species of *Pseudocalotes*. Phylogenetic analysis of DNA sequences identified a monophyletic group containing the Sumatran and Javan *Pseudocalotes*. Based on the phylogeny, we define a *P. cybelidermus* Group containing *P. cybelidermus* and *P. guttalineatus* and a *P. tympanistriga* Group containing *P. tympanistriga*, *P. rhammanotus*, and the new species. Combinations of five morphological characters define each of these two clades. As currently defined, *Pseudocalotes* is polyphyletic; Javan and Sumatran species are more closely related to other draconines such as *Dendragama boulengeri* than they are to some mainland species.

Key words: Draconinae, *Pseudocalotes baliomus* new species, *Pseudocalotes dringi*, *Pseudocalotes rhammanotus*, *Pseudocalotes tympanistriga*, Sauria

Introduction

With 36 species in 13 genera, more species of agamid lizards inhabit Sumatra than Peninsular Malaysia (8 genera, 35 species), Borneo (10 genera, 32 species) or Java (5 genera, 13 species; Uetz & Hošek 2015). These numbers are even more surprising when one considers that the other landmasses have been much more thoroughly explored than Sumatra (Das 2004; L. Grismer 2011), mainly because herpetological research in Sumatra slowed to a glacial pace after World War II. Recently, Patrick & Vogel (1999) noted that herpetologists named 76 new species of Sumatran snakes before 1926, but only six species between 1926 and 1996. A similar pattern characterizes the Sumatran agamids. Researchers described 12 species before 1934, and no other agamids were described from Sumatra until Manthey & Denzer (1991) named *Gonocephalus lacunosus* from North Sumatra.

Most of the 22 species of *Pseudocalotes* Fitzinger occur on the Asian mainland. Dring (1979) reviewed the species and noted that they fall into Sundaland and Indochinese groups. Until recently, herpetologists had reported few species from the Sunda Shelf. Inger & Stuebing (1994) first reported this genus from Borneo when they described *P. saravacensis*. Elsewhere in the region, *P. tympanistriga* (Gray) occurs on Java, and *P. dringi* Hallermann & Böhme, *P. drogon* Grismer *et al.*, *P. flavigula* (Smith), *P. larutensis* Hallermann & McGuire, *P. rhaegal* Grismer *et al.*, and *P. viserion* Grismer *et al.* occur on Peninsular Malaysia (Hallermann & McGuire 2001; L. Grismer 2011; L. Grismer *et al.* 2016). Dring (1979), Hallermann & Böhme (2000), Teynié *et al.* (2010) and Werner (1900) each included Sumatra in the distribution of *P. tympanistriga*.

In 2013, we began a systematic inventory of the highland herpetofauna of Sumatra (Harvey *et al.* 2014, 2015). During our first expedition, we found three new species of *Pseudocalotes* in southern Sumatra (Harvey *et al.* 2014) and named them *P. cybelidermus*, *P. guttallineatus*, and *P. rhammanotus*. We postponed description of a fourth species from that collection until we could study the holotype and a larger sample of *P. tympanistriga*. While visiting the Naturalis Museum, Leiden, we found additional specimens of this fourth species. We take this opportunity to describe this new species and estimate its phylogenetic relationships to congeners.

Materials and methods

Teams of researchers from Broward College (BC), the Museum Zoologicum Bogoriense (MZB), the Universitas Brawijaya (UB), and the University of Texas at Arlington (UTA) conducted surveys mostly along trails and streams through montane forests, cultivated areas, and areas of secondary growth during May and June, 2013. We conducted most surveys entirely at night. We photographed specimens in life, euthanized them with benzocaine, stored either liver or muscle in 1.5 ml of cell lysis buffer for DNA extraction, fixed the lizards in 10% formalin, and transferred them to 70% ethanol for permanent storage at the MZB and UTA. Before fixing specimens, we weighed each specimen using an electronic balance. We placed each specimen on a flat surface next to a ruler and took photographs of the dorsal, lateral, and ventral sides. We deposited photos of all specimens at UTA.

To the nearest 1 mm with a straight ruler, we measured snout–vent length (SVL), body length (axilla to groin), pectoral width (axilla to axilla) and length of the tail (from the posterior lip of the vent). We measured Finger III and IV and Toes IV and V by pressing the digits to a flexible ruler and measuring from the interdigital skin to the base of the claw. To the nearest 0.1 mm with digital calipers, we measured head length, head width (at rictus), diameter of the orbit (bony edge to bony edge; not the ocular aperture as used by Harvey *et al.* 2014), shortest distance from the posterior border of orbit to the anterior margin of the auditory meatus, widest horizontal length of the auditory meatus, width of the snout (between upper margins of nostrils), greatest width and height of the rostral, length of the shank (from center of knee to preaxial base of Toe I), height of the longest nuchal crest scale (a straight-line measure from the anteriormost edge of the scale to its apex, and height of the longest dorsal crest scale (using the same technique as for nuchal crest scales). Some authors measure head length from the occiput to the tip of the snout, whereas others measure head length from the tympanum to the tip of the snout. In the description, we report both types of measurements, although we only used the second method when calculating ratios. When using the second method, we measured from the anterior border of the auditory meatus. When the two methods are compared across numerous species of Draconinae, we find these two methods to give very similar results.

We scored specimens for many traditional characters of squamation. When we took counts on both sides of a specimen (i.e., for counts of circumorbitals, canthals, supraciliaries, labials, supralabials contacted by the nasal, enlarged keeled scales between the eye and ear, and postmentals contacting the infralabials), we treat each count as a separate observation when reporting frequency data. In the description, we use a solidus (/) to separate counts from opposite sides of the same specimen and present ranges followed by mean \pm standard deviation in parentheses.

A few characters used in this study require further comment. The last supralabial is lower and more elongate than the supralabials in front of it. It overlies the rictus and extends posterior to it along a short rictal fold. The last infralabial is the scale positioned directly below the center of the last supralabial. We identified the last canthal as a scale ending directly above or extending beyond a straight vertical line at the anterior margin of the orbit. We counted circumorbitals using the method of Harvey *et al.* (2014) and transorbitals as the number of scales in a transverse line between but not including the last supraciliary scale. Our transorbital count is identical to the “Head Scales: HeadStr” character defined by Zug *et al.* (2006). Counts of subdigital lamellae include all scales from the interdigital skin to the claw, including the elongate unguis scale. As defined by Harvey *et al.*, nuchal, posttemporal, posttympanic, and postrectal modified scales are enlarged and heavily keeled to subpyramidal scales variably present in *Pseudocalotes* and other Draconinae.

Herein, we introduce new terms for several additional scales that proved to be of taxonomic importance. Most Draconinae have a specialized scale positioned at the dorso-posterior corner of the orbit. We refer to this scale as a “postciliary scale” and refer to more than one scale in this position as a “postciliary series.” Most draconines also possess a depressed area between the postciliary scale and the supraciliaries. Herein we refer to this area as a “supraciliary notch.”

The fifth toe has undergone varying degrees of reduction among draconines, but is completely lost only in *Sitana ponticeriana* Cuvier (Russell & Rewcastle 1979). In addition to measuring Toes IV and V, we assessed reduction of Toe V by defining a new meristic character: we addressed the toes and noted the position of the base of the fifth claw under the fourth toe. We then counted subdigital lamellae under Toe IV from this position to the interdigital skin. Hereafter, we refer to this count as the “number of lamellae under Toe IV within the span of the fifth toe.” Due to the diagnostic value of this character, we add it to the standardized, numbered diagnosis developed by Harvey *et al.* (2014). We then compared this new meristic character to relative toe lengths analyzed using ANCOVA. For the ANCOVA, we restricted our comparisons to species for which we had six or more specimens, used an *F*-test for equality of the regression slopes to test the assumption of parallelism, and used Levene’s test and the Shapiro-Wilk test to verify assumptions of homoscedasticity and normality before the ANCOVA. We used the PAST 3.10 statistical software program (Hammer *et al.*, 2001) for these statistical tests.

To visualize some structures such as subdigital keels on very small specimens, we applied the reversible stain Methylene Blue in 70% ethanol. We compared the new species to specimens of *Pseudocalotes* (Appendix I) and descriptions of species not available for study. Herein, we use the institutional abbreviations of Sabaj Pérez (2013).

We extracted genomic DNA from liver or muscle samples from 26 specimens representing *Dendragama boulengeri* Doria, *Gonocephalus sp.*, *Bronchocela jubata* Duméril and Bibron, *B. cristatella* (Kuhl), *Calotes versicolor* (Daudin), and nine species of *Pseudocalotes* (Appendix 2). We then sequenced a fragment of the NADH dehydrogenase subunit 4 gene (ND4), using the forward primer “ND4” (CACCTATGACTAC CAAAAGCTCATGTAGAAGC) and reverse primer “LEU” (CATTACTTTTA CTTGGATTTGCACCA). The ND4 thermal cycle profile consisted of an initial denaturation at 94° C for three minutes, followed by 30 cycles of denaturation at 94° C for 30 seconds, a 50° C annealing phase for 45 seconds and a 72° C extension for one minute, followed by a 72° C extension for seven minutes and a holding phase at 4° C. We cleaned the products of amplification using Sera-Mag Speedbeads (Fisher Scientific, Pittsburgh, PA, USA), following the procedure outlined by Rohland & Reich (2012). We supplemented this dataset with two additional ND4 sequence for *Calotes versicolor* and *Pogona vitticeps* (Ahl) downloaded from GenBank (Appendix 2).

We aligned all sequences using the Geneious aligner implemented within Geneious v. 6.1.8 (Kearse *et al.* 2012). ND4 sequences range in length from 616 to 934 bp. We selected the most likely model of evolution for each codon position using Bayesian information criteria implemented in PartitionFinder (Lanfear *et al.* 2012). We partitioned codon positions using GTR+ Γ . We conducted maximum likelihood analyses using raxmlGUI (Silvestro & Ingo 2012). We utilized the thorough bootstrapping setting, sampling over 10 runs of 10,000 repetitions. We carried out Bayesian phylogenetic analysis using MrBayes v3.2.1 (Ronquist & Huelsenbeck 2003). We used four independent runs (nruns=4) and four chains (three heated chains and one cold chain) for 10 million generations, sampling every 100 generations. We discarded the first 25% of samples as burn-in. We confirmed adequate mixing and assessed the appropriate amount of burn-in and convergence by inspecting the trace files in the program TRACER v1.6 (Rambaut *et al.* 2014). We conducted UPGMA analyses and calculated uncorrected pairwise distances using Mega 5.1 (Tamura *et al.* 2011).

We interpret our phylogeny as the most likely hypothesis of interspecific relationships, given the data and included taxa. Simulations and investigations of known phylogenies have shown that bootstrap values above 50% underestimate phylogenetic accuracy under a variety of conditions, whereas values below 50% may overestimate accuracy (Hillis & Bull 1993). As Hillis and Bull (1993, p. 192) caution, bias of these estimates differ from “branch to branch and study to study” due to numerous factors including numbers of characters and taxa, number of iterations, rates of change, tree topology, and method of phylogenetic inference. In spite of their shortcomings, we interpret bootstrap proportions as relative rankings of degree of support for various nodes in our phylogeny (Hillis & Bull 1993). Bayesian posterior probabilities provide less conservative estimates of accuracy than bootstrap proportions, so that they will usually be higher than bootstrap values (Alfaro & Holder 2006). We interpret posterior probabilities as unbiased estimates of phylogenetic accuracy provided that the model of character evolution is correct (Huelsenbeck & Rannala 2004).

Systematics

Pseudocalotes baliomus sp.nov.

(Fig. 1–4)

Holotype. An adult male (MZB 9813; collector's tag ENS 14429) from forest west of the mountain crest next to the road from Tapan to Sungai Penuh, Sumatera Barat Department, Sumatra, Indonesia, 2.04294°S, 101.31129°E (WGS 84 geodetic system), 1181 m, collected by Elijah Wostl and Eric N. Smith on 23 June 2013.

Paratypes. An adult male (RMNH 3013a) and female (RMNH 3013b) from “Sumatra” Indonesia, collected by Salomon Müller. The paratypes lack any locality data other than “Sumatra.”

Diagnosis. A species of *Pseudocalotes* reaching at least 218 mm (68 mm SVL) and distinguished from congeners by the following combination of characters: (1) interoculabials 3 or 4; (2) canthals 6 or 7; (3) enlarged, heavily keeled to subpyramidal posttemporal and posttympanic scales present; postrictal modified scale absent; (4) gulars relatively small, homogenous, no sharp transition to small scales on gular pouch; (5) antehumeral fold poorly developed; (6) dorsolateral row of widely spaced heavily keeled scales present; (7) scales on lower flanks heterogenous with heavily keeled scales interspersed with smaller feebly keeled scales; (8) 53–55 scales around midbody; (9) dorsal crest of denticulate scales extending to base of tail; all projecting scales of crest separated by medial contact between scales of paravertebral series; (10) ventrals smaller than dorsals; (11) subdigital lamellae at base of Toe III bicarinate with preaxial and postaxial keels well developed; (12) 7 or 8 lamellae under Toe IV within the span of the fifth toe; (13) dorsum green, banded; distinctive white scapular spot; (14) ventral body yellow-green, immaculate; (15) gular pouch yellow-green immaculate; (16) tongue pale blue, throat black.

Comparisons. *Pseudocalotes baliomus* most closely resembles *P. rhammanotus* and *P. tympanistriga* (characters in parentheses, Table 1). Unlike these species, *P. baliomus* has three or four interoculabials (two except for one specimen of *P. tympanistriga* with three interoculabials), enlarged scales on the lower flanks (absent), and a distinctive white scapular spot including an enlarged, heavily keeled scale (absent). In addition to these characters, unlike *P. rhammanotus*, *P. baliomus* has 28–30 subdigital lamellae under the fourth toe (24) and 7 or 8 lamellae (vs. 2) under Toe IV within the span of the fifth toe.

TABLE 1. Occurrence of selected diagnostic characters among Sumatran and Javan *Pseudocalotes*.

	<i>P. baliomus</i> <i>n</i> = 3	<i>P. rhammanotus</i> <i>n</i> = 1	<i>P. tympanistriga</i> <i>n</i> = 16	<i>P. cybelidermus</i> <i>n</i> = 8	<i>P. guttalineatus</i> <i>n</i> = 8
Interoculabials	3 (67%) 4 (33%)	2 (100%)	2 (94%) 3 (6%)	2 (100%)	2 (100%)
Paravertebral rows directed upward	3	2	3	4 or 5	3
Pectoral gap	3–7	7	0–4	4–7	5–8
Lamellae under Toe IV	28–30 (29 ± 1)	24	25–32 (28 ± 2)	24–30 (28 ± 2)	27–32 (29 ± 2)
Span of lamellae within Toe V	7 or 8	2	5–8	2	4–7
Enlarged scales on lower flanks	Present	Absent	Absent	Present	Absent
Antehumeral fold	Absent	Present	Absent	Absent	Absent
Postrictal modified scale	Absent	Absent	Absent	Present	Present
Ventrals smaller than dorsals	Yes	Yes	Yes	No	Yes
Lamellae modified at base of Toe III	No	No	No	Yes	Yes

With its bright green coloration and enlarged scales on the lower flanks, *Pseudocalotes baliomus* might be confused with the superficially similar Sumatran congeners *P. cybelidermus* and *P. guttalineatus*. Unlike these species, *P. baliomus* has 3 or 4 interoculabials (two), bicarinate lamellae at the base of the third toe (preaxial keel noticeably enlarged relative to postaxial keel; postaxial keel absent or vestigial), and a cream to bluish white buccal epithelium and tongue (bright yellow to orange). The new species lacks a postrictal modified scale (present). In addition to these characters, unlike *P. cybelidermus*, *P. baliomus* has three paravertebral rows directed upward and backward (4 or 5), ventrals smaller than dorsals at midbody (larger), and 7 or 8 lamellae (vs. 2) on Toe IV within

the span of the fifth toe. For those three characters, *P. baliomus* and *P. guttalineatus* resemble one another. However, unlike *P. guttalineatus*, *P. baliomus* has enlarged scales on its lower flanks (absent).

Most congeners not present on Sumatra have greatly enlarged, serrate preaxial keels at the base of Toe III (Dring 1979; Hallermann & Böhme 2000; Hallermann *et al.* 2010; Harvey *et al.* 2014), and this character immediately distinguishes them from *Pseudocalotes baliomus*. Bicarinate lamellae at the base of Toe III have been reported for *P. dringi*, *P. khaonanensis*, *P. saravacensis*, and *P. viserion*. Harvey *et al.* (2014) recoded this character for *P. flavigula* noting that it has an intermediate condition similar to that of *P. cybelidermus* and *P. guttalineatus*. With 53–55 scales at midbody, *P. baliomus* has substantially fewer midbody scale rows than either *P. khaonanensis* (72–75, Chan-Ard, Cota & Laoteow 2008) or *P. saravacensis* (68, Inger & Stuebing 1994); it has substantially more scales around midbody than *P. viserion* (35–38, L. Grismer *et al.*, 2016). We directly compared the new species to the holotype and paratype of *P. dringi*. Unlike *P. dringi*, *P. baliomus* has keeled gulars (smooth), 6–8 loreals separating the last canthal from the supralabials (3–5), 3 or 4 interoculars (two), 34–39 interrials (27–28), a dorsolateral series of enlarged scales (absent), a posttympanic modified scale (absent), and enlarged scales on the lower flanks (absent). As for *P. flavigula*, *P. dringi* has enlarged preaxial keels and vestigial or absent postaxial keels at the base of the third toe.

Pseudocalotes baliomus can be distinguished from other agamids on Sumatra by its clearly visible tympanum, relatively wide gap between the dorsal and nuchal crests, heterogenous dorsal squamation, tail not prehensile and about twice as long as SVL, keeled subdigital lamellae, dorsals larger than ventrals, absence of large spines in the nuchal and postorbital regions, relatively narrow head, absence of a rostral appendage, and other characters of external morphology described in the differential diagnosis of Hallermann & Böhme (2000; see also Mahony 2010 and Harvey *et al.* 2014).



FIGURE 1. Adult male holotype of *Pseudocalotes baliomus* (MZB 9813, SVL 68 mm) from forest along road from Tapan to Sungai Penuh, Sumatera Barat Department, Sumatra, Indonesia, 1181 m. Photo by E. N. Smith.

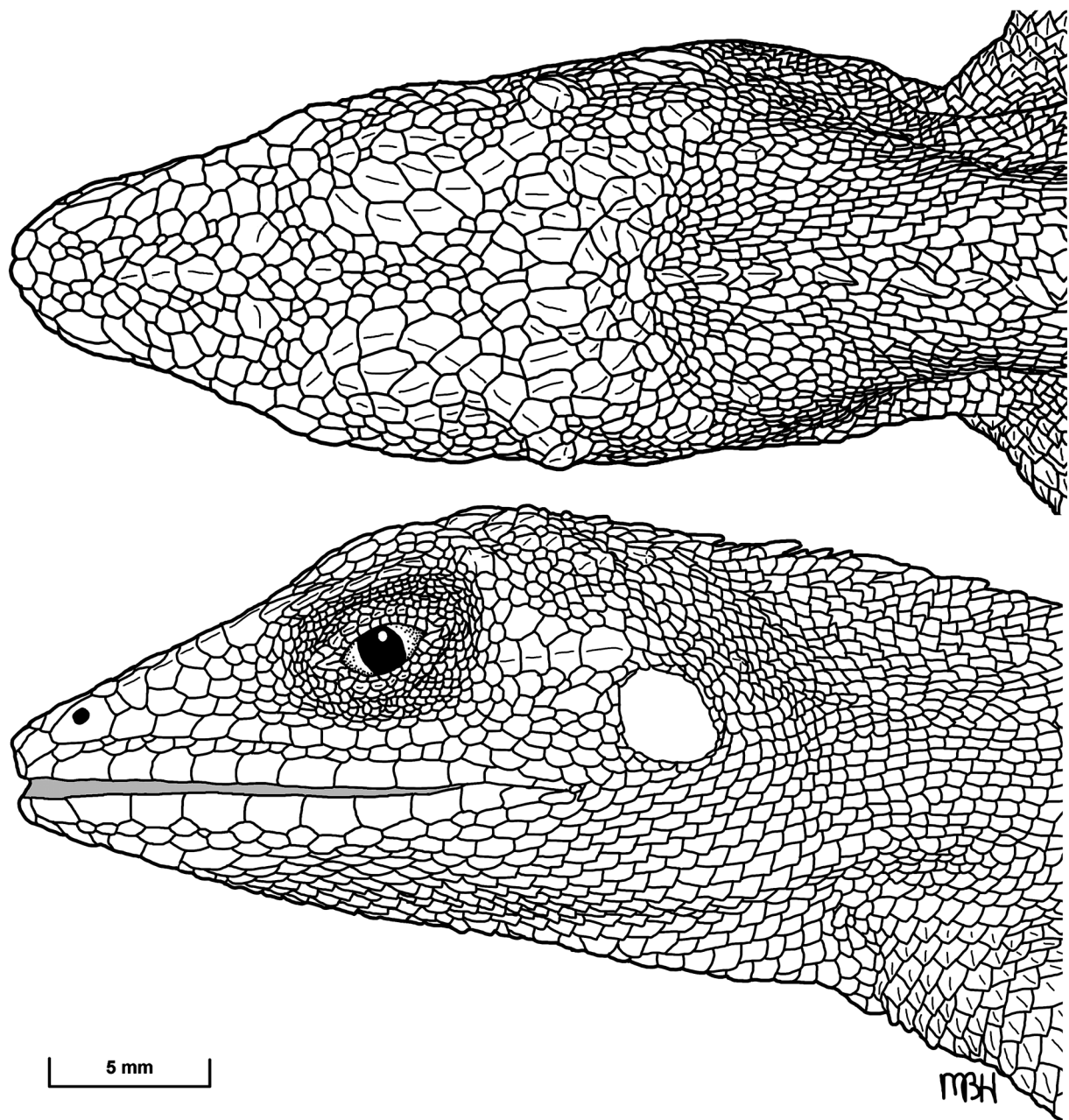


FIGURE 2. Head scalation of *Pseudocalotes baliomus* (Holotype, MZB 9813).

Description. We describe the holotype and provide data for the male then female paratypes in brackets. Adult male 218 mm (SVL 68 mm) [190 (62), 181 (55)] in length; SVL 31.2% [32.6, 30.4] and tail 68.8% [67.4, 69.7] of total length; tail 2.21X [2.06, 2.29] as long as SVL; distance from axilla to groin accounting for 47.1% [51.6, 49.1] of SVL; head 55.4% [60.0, 57.4] as wide as long, accounting for 26.2% [26.7, 27.3] of SVL; snout subacuminate in dorsal view and in profile, sloping upward at about 20° to horizontal (Fig. 2); dorsal head scales imbricate, keeled; rostral not visible from above, its height 32.4% [42.6, 29.9] of its width, broadly contacting first supralabials and five [5, 6] small postrostrals; postrostral series separating nasal from rostral on both sides (100%, $n = 3$); five scales forming Y-shaped arrangement of enlarged, heavily keeled scales on snout; two scales forming each “arm” of Y with posterior-most of these two scales enlarged, heavily keeled obliquely, and positioned just anterior to orbital border; scales of frontal region keeled, much smaller than medial supraoculars; interparietal narrow, keeled,

subrectangular, depressed to same position as frontal scales, flanked on either side by raised parietal series of large swollen and keeled scales; parietal eye not visible; area in front of nuchal crest distinctly depressed, lower than interparietal and flanked on either side by large, keeled scales overlying raised supratemporal region (presumably covering a raised portion of the skull or a particularly thick origin of one of the jaw muscles).

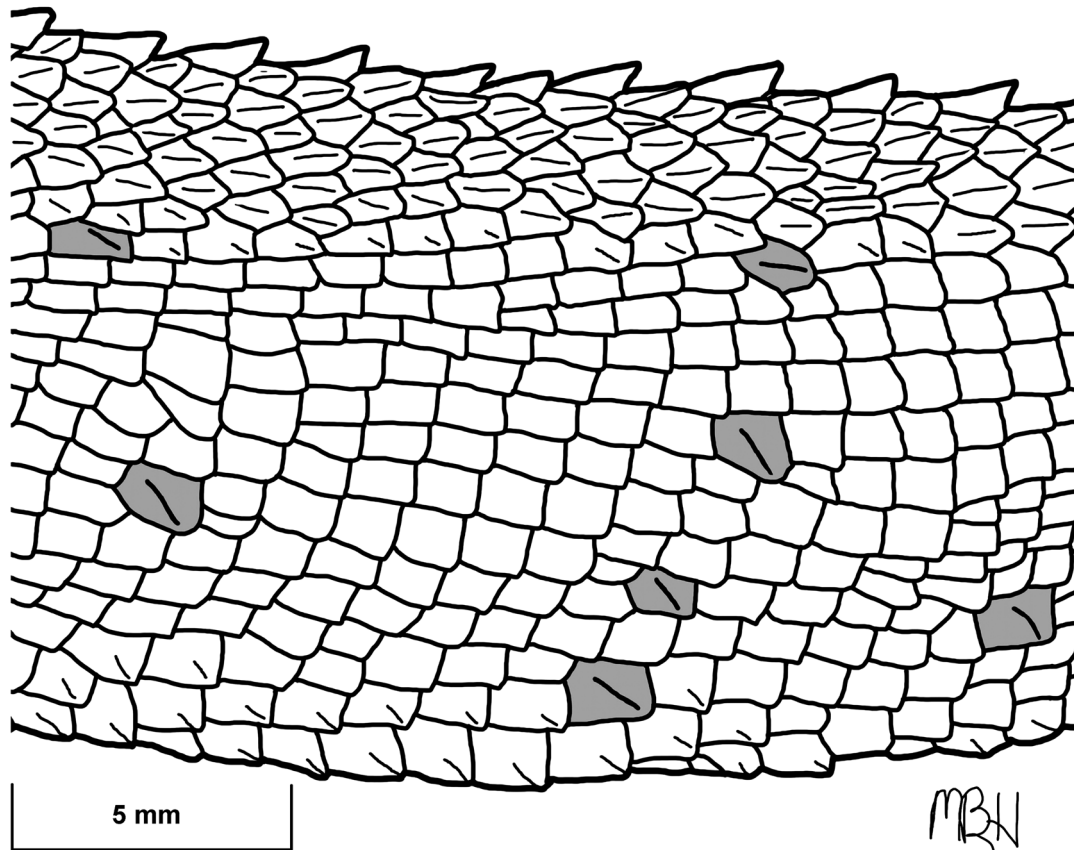


FIGURE 3. Left flank of *Pseudocalotes baliomus* (Holotype, MZB9813), showing distribution and morphology of enlarged, heavily keeled scales (shaded gray) of dorsolateral series and lower flanks.

Supranasal scale single, elongate; circumorbital scales 10/10, distinctly enlarged, roughly pentagonal or hexagonal, contacting canthal series laterally; transorbitals 20 [16, 13]; canthals keeled, 6/6 [6/7, 7/7]; first canthal divided along canthus; supraciliaries 7/8 [7/7, 6/6]; anterior supraciliaries elongate with their posterior edges imbricating onto medial side of next scale back; direction of imbrication abruptly changing two supraciliaries in front of ciliary notch where anterior edge imbricates onto medial side of scale in front of it; supraciliary notch present, with 3/2 small scales separating supraciliaries from postciliary scale; postciliary scale enlarged, rounded, single, positioned at dorso-posterior corner of orbit; small angulate scales of temporal region ending posteriorly in 2/2 larger scales with noticeably higher keels, the last positioned at posterior margin of skull; 1/1 [100%, $n = 6$] subpyramidal posttemporal scale on neck separated from last enlarged temporal by 2/3 [3/3, 2/2] small scales.

Nasal trapezoidal, separated from supralabials by continuous row of lorilabials [contacting supralabials 1 and 2/1 and 2, 1/1]; nostril large, oval, directed laterally, positioned at dorsal edge in center of nasal with its upper margin slightly raised and contributing to canthus; loreal region slightly sloping; scales of loreal region smooth, 7/7 [6/6, 8/7] scales in vertical row between last canthal and supralabials, 6/6 [7/7, 7/6] scales in horizontal row from anterior border of orbit to nasal; orbit 32.3% [30.5, 34.8] of head length; palpebrals granular; second row of palpebrals above eye containing 12/12 [12, 15] scales between ocular angles, central four of these largest and more heavily keeled; on both sides, large subocular scale row separated from supralabials by continuous row of

lorilabials (= 3/3 interoculabial [3/3, 4/4]); horizontal row of 4/4 [4/5, 5/5] enlarged, keeled scales between orbit and anterior margin of auditory meatus; external auditory meatus oval, shallow, its length 43.7% [37.7, 41.7] of orbital diameter and 14.1% [11.5, 14.5] of head length, its distance from orbit 22.0% [20.2, 21.0] of head length; tympanic membrane clearly visible, opaque throughout, protruding where it attaches to extracolumella; scales surrounding meatus small, granular; post-tympanic modified scale subpyramidal separated from meatus by five scales; postrictal modified scale absent.

Supralabials smooth, 11/9 [8/9, 9/9]; rictal fold short, bordered dorsally and ventrally by two elongate scales behind supralabial and infralabial series; infralabials smooth, 10/10 [8/9, 10/10], first 2/2 [3/damage, 1/3] contacting postmentals, thereafter, sublabial scales separating enlarged postmentals from infralabials; first pair of postmentals separated medially by 2 [0, 1] gulars; gulars keeled, 41 [41, 42] from posterior tip of mental to preaxial margin of arm, arrayed as 35 [34, 39] interriotal scales between last right and left infralabials; gular pouch moderately developed, longitudinal; gular fold in front of arms; scales in gular fold not differentiated (i.e., equal in size and shape to scale behind and in front of fold); scales in center of gular pouch same size as gulars lateral to it, weakly keeled, lacking mucrons.

Nuchal crest consisting of 10 [10, 11] elongate scales, all separated from one another by medial contact of paravertebrals and/or small scales of similar size and shape to the paravertebrals; longest nuchal crest scales 75% [112, 103] of length of longest scales of dorsal crest, smaller than tympanum, their length 51.8% [96.8, 52.1] of length of tympanum; dorsal crest prominent, denticulate, extending onto base of tail, consisting of transversely narrow scales (though still with the lateral portions of the scales flat against the back) with heavy keels and projecting tips, 41 [39, 37, count excludes paravertebral scales between most vertebrales] vertebral scales to posterior margin of thigh; all scales of dorsal crest separated from one another by medial contact between small scales of paravertebral series or individual flat keeled scales similar to paravertebrals; largest scales of dorsal crest smaller than tympanum, their lengths 68.9% [86.8, 50.7] of length of tympanum; scales of dorsal crest separated from nuchal crest by pectoral gap of 7 [4, 3] low, keeled dorsals; paravertebral series same size as adjacent dorsals; dorsals larger than ventrals; on neck, dorsals much smaller than those between limbs; upper 11 rows of dorsals in center of neck pointed dorsally and posteriorly, two rows below them pointed posteriorly, and remaining rows pointed downward and posteriorly; upper rows of dorsal reorienting at level of scapula so that all point posteriorly rather than upward; behind scapula, upper 3 rows of dorsals pointing upward and backward, scale row below them pointing backward, and lower scales pointing backward and downward; scales above and in front of arm slightly smaller at location of poorly developed antehumeral skin fold; crossing antehumeral fold, scales not undergoing any reorientation of keels.

Scales of flanks feebly keeled; dorsolateral row of widely spaced, heavily keeled scales present; first scale of series on neck positioned half way between upper margin of auditory meatus and scapula, second scale of series in center of white scapular blotch, positioned 10/9 scale rows below vertebrales of pectoral gap, remaining scales of series in 5–7th row of dorsals below dorsal crest (heavily keeled scales form a broken line, but number of scales separating them from dorsal crest changes along body); dorsolateral keeled scales 6/5 between limbs, separated from one another by 4–10 scales; scales of lower flanks heterogenous, larger heavily keeled scales interspersed among smaller feebly keeled scales; keels of larger modified scales on lower flanks directed more ventrally than keels of adjacent smaller scales; scales around midbody 53 [55, 54]; ventrals heavily keeled, without sharp transition from scales on flanks, noticeably smaller in front of axilla, 57 [66, 62] from preaxial edge of arm to vent; scales around vent unspecialized; scales around base of tail (counted five subcaudals behind vent) 19 reducing to 6, then 4, then 2 at tip; throughout most of length of tail, scales surrounding tail subequal, only at base vertebral row enlarged relative to scales on side and ventral surface of tail.

Scales of brachium, antebrachium, thigh, and shank imbricate, keeled; 2/2 scales in middle of postaxial border of antebrachium modified, their keels more prominent than surrounding scales and blade-like toward distal tip of scales; 1/1 similar scale with pointed blade-like keel positioned slightly postaxial to middorsal in center of thigh; this modified scale of thigh also larger than all other scales on dorsal surface of thigh and with its large keel pointing slightly more distal than the scales proximal and distal to it; keels of modified scales on antebrachium and thigh white; palmar scales tiny, keeled with spinose mucrons; palmar subdigital lamellae multicarinate with spinose mucrons at base of fingers, bicarinate distally, 26 [22, 24] under Finger IV; terminal phalanges of fingers lacking unicarinate lamellae; Finger III same length as Finger IV (same length, 91.3% shorter); Finger IV 66.7% [63.6, 72.7] as long as Toe IV; plantar scales heavily keeled, mucronate, imbricate, those proximal to Toes III and IV

noticeably larger than other plantar scales; pedal subdigital lamellae bicarinate except under Toe IV where 2/2 lamellae under most proximal phalanx divided to form unicarinate scales; pre- and postaxial keels of bicarinate lamellae similar under all digits; preaxial and postaxial keels of subdigital lamellae at base of Toe III subequal; subdigital lamellae 30 [28, 30] under Toe IV; single subdigital and single supradigital unguis lamellae contacting one another on all fingers and toes; unguis lamellae much longer than other subdigital lamellae; supradigital scales proximal to supradigital unguis lamellae 4 on all fingers and toes; in relative length, Finger III = IV > II > V > I and Toe IV > III > V > II > I; Toe V 70.8% [68.2, damaged] as long as Toe IV; when adpressed, 8 [7, damaged] lamellae under Toe IV within span of fifth toe; leg relatively long; shank 20.1% [18.0, 22.8] of SVL.

Scale surfaces covered in macrohoneycomb; scale organs lenticular, single and positioned subterminally atop keel on body, more numerous and also concentrated on keels on head; bristled sense organs single, positioned below distal tip of keel, on digital scales and at least some scales of ventral surface (distribution difficult to determine since stratum corneum missing from most scales of body); callous glands, pigmented generation glands (sensu Maderson & Chiu 1970; Harvey *et al.* 2012), and femoral and preloacal pores absent.

Measurements in mm of holotype followed by male then female paratype in brackets: snout–vent length 68 [62, 55]; length of tail 150 [128, 126]; length of body 32 [32, 27]; pectoral width 9.4 [6.5, 5.7]; length of head from occiput to rostral 16.5 [16.1, 15.0]; length of head from auditory meatus to rostral 17.8 [16.6, 15.0]; width of head 9.9 [9.9, 8.6]; diameter of orbit 5.8 [5.0, 5.2]; distance from orbit to tympanum 3.9 [3.4, 3.2]; length of auditory meatus 2.5 [1.9, 2.2]; height of largest scale of nuchal crest 1.3 [1.8, 1.1]; height of largest scale of dorsal crest 1.7 [1.7, 1.1]; width of snout 3.8 [3.7, 3.4]; width of rostral 2.1 [2.0, 1.9]; height of rostral 0.7 [0.8, 0.6]; length of shank 13.7 [11.2, 12.5]; length of Finger IV 8 [7, 8]; length of Finger III 8 [7, 7.3]; length of Toe IV 12 [11, 11]; length of Toe V 8.5 [7.5, toe damaged].

Coloration in life: dorsum bright green (Fig. 1) with six transverse vertebral bands from pectoral gap to area between legs; each vertebral band narrow, 1 or 2 paravertebrals long and extending laterally to cover four or fewer paravertebral rows; tail with 11 greenish brown bands separated by longer light green interspaces; caudal bands becoming progressively darker and less green distally; limbs faintly banded; 3/3 bands crossing brachium, 2/2 crossing antebrachium, 5/5 crossing Finger IV, 3/3 crossing thigh, 3/3 crossing shank, 3/3 crossing foot proximal to digits, and 4/4 crossing Toe IV; bands on limbs consisting of green scales surrounded by black skin; interspaces on limbs slightly paler shade of green than that of bands; specialized heavily keeled scales on postaxial antebrachium and mid-dorsal thigh with bright yellow keels.

Sides of head nearly immaculate green; yellow-green ring around eye (= palpebrals closest to ocular aperture bright yellow-green); yellow-green subocular stripe overlapping enlarged subocular row and curving upward to contact last enlarged keeled scale in front of tympanum; tympanic membrane uniform bright green; 2/2 distinctive white blotches overlapping scapula; upper scapular blotch largest and covering 9/8 scales including one enlarged, more heavily keeled scale in center of blotch; lower scapular blotch covering 1/3 scales, also including an enlarged, more heavily keeled scale; first scale of dorsal crest also white, located above large scapular blotch; venter yellow-green, brightest on throat; palms pinkish, immaculate; soles pinkish but crossed by 4/4 distinctive black bands.

Roof of mouth and throat black (Fig. 4); tongue and ventral buccal epithelium pale blue; iris bronze, sharply contrasting with pale gold ciliary ring.

In preservative, the green pigmentation of the holotype has faded to bluish gray. As in other Sumatran congeners (Harvey *et al.* 2014), the lower flanks darkened somewhat following fixation. The paratypes (RMNH 3013a,b) have faded to a dull gray with age. However, they have the same distinctive scapular spots as the holotype. In all three specimens, enlarged scales of the dorsolateral series and lower flanks are either entirely more pale than adjacent scales (perhaps yellow-green or white in life; RMNH 3013a) or have a paler center and keel than adjacent scales (holotype).

Etymology. The new name *baliomus* is a masculine adjective derived from the Greek adjective *balius* meaning spotted and Greek noun *omos* meaning shoulder. The new name refers to the diagnostic white blotches on the shoulder of *Pseudocalotes baliomus*.

Standard English Common Name. Spot-Shouldered False Garden Lizard.

Distribution and Natural History. Since the paratypes lack definite locality data, this species is known only from the type locality. Although the RMNH catalogue contains no other information about the paratypes, the collector S. Müller worked along the west coast of Sumatra near Padang from 1833–1835 (Fransen *et al.* 1997). The type locality (Fig. 5) lies within a transitional zone between the West Coast and Kerinci zoogeographic regions

of Whitten *et al.* (1987) in one of the wettest regions of Sumatra. At the time of capture, the male holotype was approximately 3.5 m aboveground sleeping on thin branches of a small tree near a creek and a couple of meters from the edge of the road (E. Wostl, personal communication). On that night, the air was cold and relatively dry. There had been no recent rain.



FIGURE 4. Morphology of the head and pigmentation of the buccal epithelium of *Pseudocalotes baliomus* (Holotype, MZB 9813, head length 17.8 mm). Photos by E. N. Smith.

Phylogeny. Bayesian and Maximum Likelihood analyses recovered nearly identical topologies for the Javan and Sumatran species of *Pseudocalotes*, with only the placement of *P. baliomus* and *P. rhammanotus* varying slightly (Fig. 6). Our Bayesian analysis recovered *P. baliomus* as sister to a *P. rhammanotus* + *P. tympanistriga* clade, whereas the placement of *P. rhammanotus* and *P. baliomus* was reversed in our Maximum Likelihood analysis. The Sumatran and Javan *Pseudocalotes* form two clades. One contains *P. cybelidermus* and *P. guttalineatus*, and the other contains *P. baliomus*, *P. tympanistriga*, and *P. rhammanotus*. We identified two clades of *P. tympanistriga* on Java, one represented by our samples from Cibodas, West Java, and the other by specimens from several mountains in the vicinity of Bandung.

The distribution of some morphological characters is concordant with the molecular phylogeny, whereas that of others is not. On Sumatra and Java, we recognize a *Pseudocalotes tympanistriga* Group containing *P. baliomus*, *P. rhammanotus*, and *P. tympanistriga*, and a *P. cybelidermus* Group containing *P. cybelidermus* and *P. guttalineatus*. Referring to Table 1 in Harvey *et al.* (2014) and results published here, characters that define the *P. tympanistriga* Group include (1) bicarinate lamellae at the base of Toe III with subequal keels, (2) 30–42 gulars, (3) relatively small gulars without sharp a transition to smaller scales on the gular pouch, (4) postrictal modified scale absent, and (5) buccal epithelium and tongue cream to pale blue. Characters that define the *P. cybelidermus* Group include (1) asymmetric keels at the base of the third toe with preaxial keels larger than postaxial keels; (2) 17–31 gulars; (3) noticeably larger gulars laterally with a sharp transition to smaller scales on the pouch; (4) postrictal modified scale present; and (5) buccal epithelium and tongue yellow to orange. Distribution of two characters is not consistent with the molecular phylogeny. Few lamellae within the span of the fifth toe characterize *P. cybelidermus* and *P. rhammanotus*, whereas enlarged, heavily keeled scales on the lower flanks characterizes *P. baliomus* and *P. cybelidermus*.

Among species pairs of Javan and Sumatran *Pseudocalotes*, ND4 sequences have diverged 7.4–18.3% (Table 2). Sequences have diverged 9.1–11.3% between *Pseudocalotes baliomus* and *P. tympanistriga* and 8.9% between *P. baliomus* and *P. rhammanotus*. Interestingly, these levels of divergence are comparable to those between *P. cybelidermus* and *P. guttalineatus* (9.4%), the only insular species known to occur in microsympatry. The two clades of *P. tympanistriga* have diverged by 7.0–7.5%.

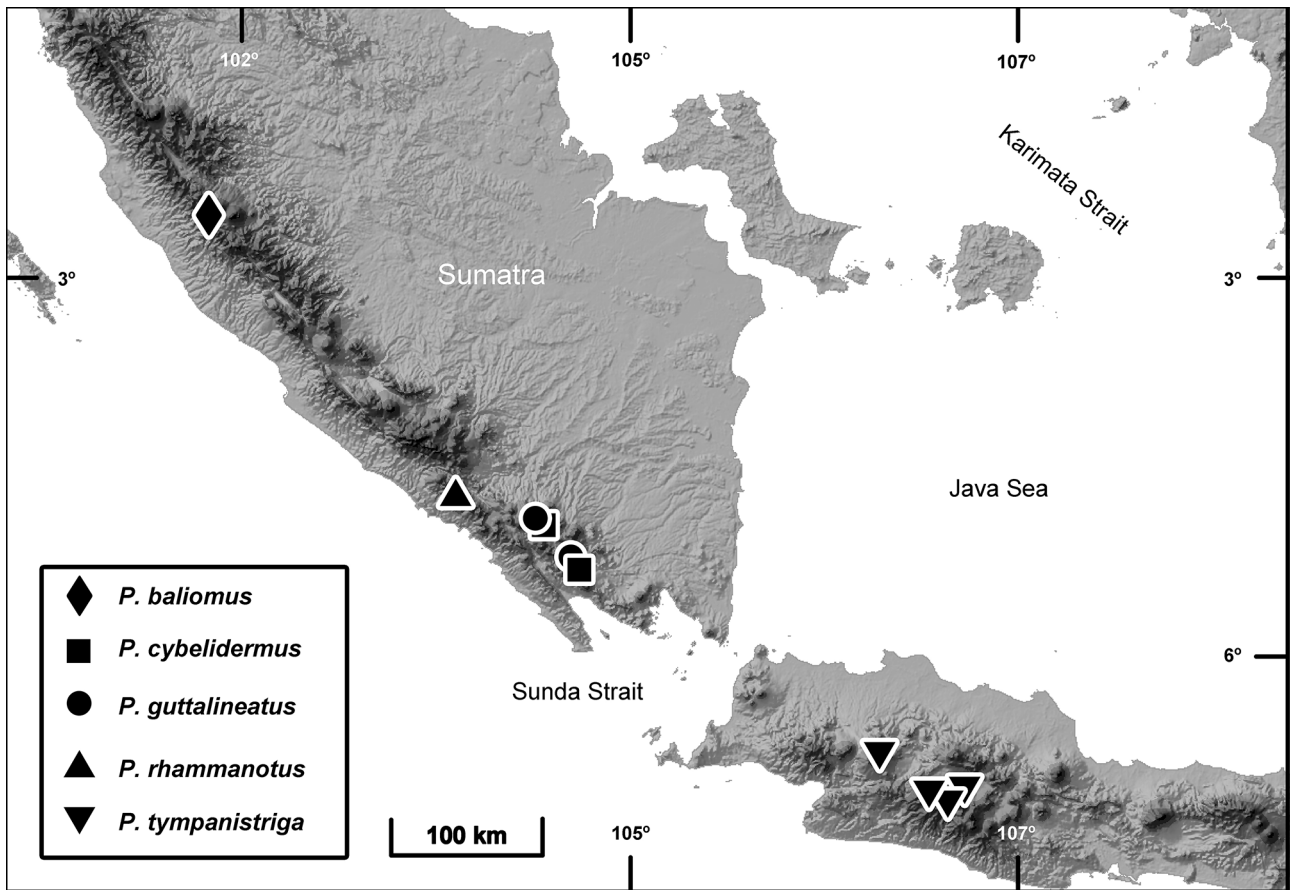


FIGURE 5. Known distribution of Javan and Sumatran species of *Pseudocalotes*.

TABLE 2. Uncorrected pairwise genetic distances for ND4 sequences between species pairs of Javan and Sumatran *Pseudocalotes* and *Dendragama boulengeri*

	<i>P. rhammanotus</i> (n = 1)	<i>P. tympani-</i> <i>striga</i> Cibodas (n = 2)	<i>P. tympani-</i> <i>striga</i> Bandung (n = 2)	<i>P. cybelidermus</i> (n = 2)	<i>P. guttalineatus</i> (n = 2)	<i>Dendragama</i> <i>boulengeri</i> (n = 1)
<i>baliomus</i>	8.9	11.1–11.3	9.1–9.6	15.4	17.5	21.2
<i>rhammanotus</i>		10.1–10.3	7.4–7.9	15.2	15.9	21.1
<i>tympanistriga</i> (Cibodas)		0.0	7.0–7.5	16.4–16.6	18.2–18.3	20.7–20.9
<i>tympanistriga</i> (Bandung)			0.0	16.1–16.6	17.0–17.5	21.2–21.7
<i>cybelidermus</i>				0.0	9.4	20.7
<i>guttalineatus</i>					0.0	20.5–20.7

Neither Bayesian nor Maximum Likelihood analyses recovered a monophyletic *Pseudocalotes*. Instead, the nine species in our study belong to unrelated mainland and insular clades. Javan and Sumatran *Pseudocalotes* are more closely related to *Dendragama* than they are to mainland Asian *Pseudocalotes*. The Bayesian and Maximum Likelihood analyses differed in placement of the clade of mainland *Pseudocalotes*. The Bayesian Analysis placed the mainland species as sister to a clade containing *Bronchocelela*, *Gonocephalus*, *Dendragama*, and the Javan and Sumatran species (Fig. 6). Maximum Likelihood analysis recovered the mainland species as sister to *Dendragama* + the clade of insular species, albeit with low support (bootstrap value 25). Whereas most internal nodes in our Bayesian tree have high posterior probabilities (Fig. 6), internal nodes among genera and the mainland and insular clades of *Pseudocalotes* had bootstrap values of 25–62 in the Maximum Likelihood tree. Pairwise genetic distances

between mainland and insular *Pseudocalotes* ranged from 21–26% and are comparable to divergence among pairs of draconine genera such as *Dendragama* and *Bronchocela* (25%), *Dendragama* and *Gonocephalus* (26%), and *Calotes* and *Bronchocela* (23–26%).

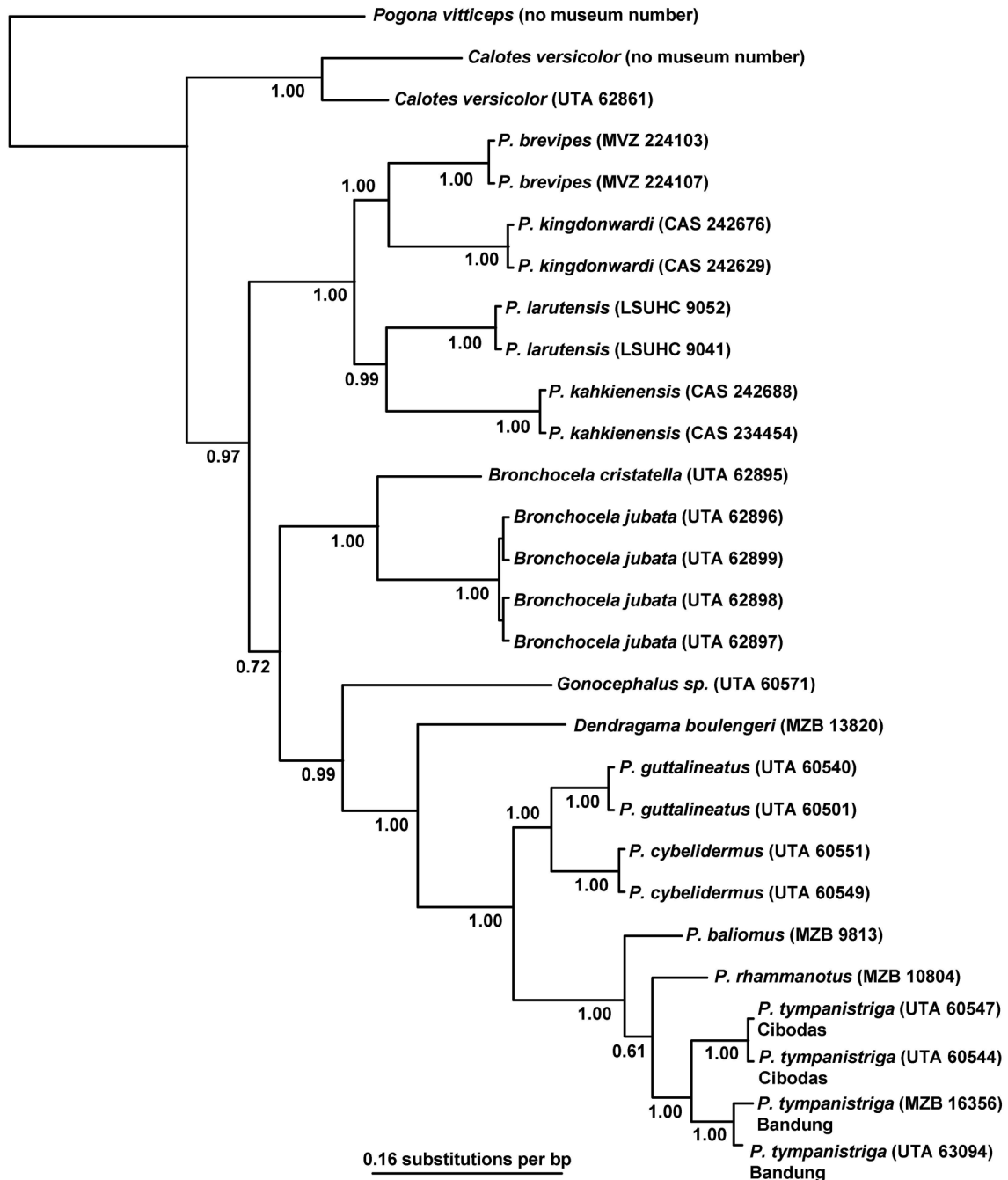


FIGURE 6. Phylogeny of *Pseudocalotes* based on Bayesian analysis of ND4 sequence data. Posterior probabilities appear below internodes.

New morphological characters

In our earlier study, (Harvey *et al.* 2014), we defined several new characters and discussed their variation among species of *Pseudocalotes*. However, we did not report span of the fifth toe, transorbitals, or number of loreals between the orbit and nasal. Counts of loreals and transorbitals broadly overlap among species of *Pseudocalotes*, although counts of loreals in *P. kingdomwardi* (Smith) average lower than counts for its congeners (Table 3). On the other hand, span of the fifth toe is a particularly useful character, and we urge investigators to score this character in future descriptions of draconine agamids. Only two lamellae lie within the span of the fifth toe under Toe IV of *P. cybelidermus* and *P. rhammanotus*, whereas all other congeners have four or more lamellae within the span of the fifth toe. *Pseudocalotes dringi*, *P. flavigula* (Smith), *P. kakhienensis* (Anderson), and *P. kingdomwardi* have the highest counts of lamellae within the span, whereas other mainland congeners have counts comparable to those of *P. baliomus*, *P. guttalineatus*, and *P. tympanistriga* (Table 3).

TABLE 3. New characters defined in this study and their distribution among selected species of *Pseudocalotes*. Means \pm standard deviation follow ranges in parentheses.

	Ratio of Length of Toe V/IV	Span of Fifth Toe	Transorbitals	Loreals from Orbit to Nasal
<i>P. baliomus</i>	0.68–0.70 ($n = 2$)	7 or 8 ($n = 2$)	13–20 ($n = 3$)	6 or 7 ($n = 3$)
<i>P. tympanistriga</i>	0.63–0.8 (0.70 ± 0.05 , $n = 14$)	5–8 (6 ± 1 , $n = 15$)	13–19 (16 ± 2 , $n = 14$)	5–8 (7 ± 1 , $n = 16$)
<i>P. rhammanotus</i>	-	2 ($n = 1$)	13 ($n = 1$)	7 ($n = 1$)
<i>P. cybelidermus</i>	0.58–0.66 (0.62 ± 0.3 , $n = 8$)	2 (100%, $n = 8$)	13–17 (15 ± 1 , $n = 8$)	5–7 (6 ± 1 , $n = 8$)
<i>P. guttalineatus</i>	0.65–0.78 (0.70 ± 0.04 , $n = 8$)	4–7 (6 ± 1 , $n = 8$)	14–17 (16 ± 1 , $n = 8$)	5 or 6 (5 ± 1 , $n = 8$)
<i>P. brevipes</i>	0.66–0.84 (0.74 ± 0.06 , $n = 9$)	5–7 (6 ± 1 , $n = 10$)	12–18 (15 ± 2 , $n = 10$)	6–8 (7 ± 1 , $n = 10$)
<i>P. microlepis</i>	0.63–0.69 ($n = 3$)	5 or 6 ($n = 3$)	12–14 ($n = 3$)	5–7 ($n = 3$)
<i>P. poilani</i>	0.86 ($n = 1$)	7 ($n = 1$)	15–16 ($n = 2$)	5–7 ($n = 2$)
<i>P. floweri</i>	0.82–0.86 ($n = 2$)	5–7 ($n = 2$)	13–18 ($n = 2$)	5 or 6 ($n = 2$)
<i>P. dringi</i>	0.72 ($n = 1$)	8–10 ($n = 2$)	13–14 ($n = 2$)	5 ($n = 2$)
<i>P. flavigula</i>	0.74–0.80 ($n = 2$)	11–12 ($n = 2$)	14–15 ($n = 2$)	4 ($n = 2$)
<i>P. kakhienensis</i>	0.79–0.85 (0.82 ± 0.03 , $n = 6$)	10–13 (12 ± 1 , $n = 6$)	14–16 (14 ± 1 , $n = 6$)	5–7 (6 ± 1 , $n = 6$)
<i>P. kingdomwardi</i>	0.72–0.87 (0.77 ± 0.04 , $n = 11$)	8–9 (9 ± 0 , $n = 11$)	11–14 (12 ± 1 , $n = 12$)	3–5 (4 ± 1 , $n = 12$)

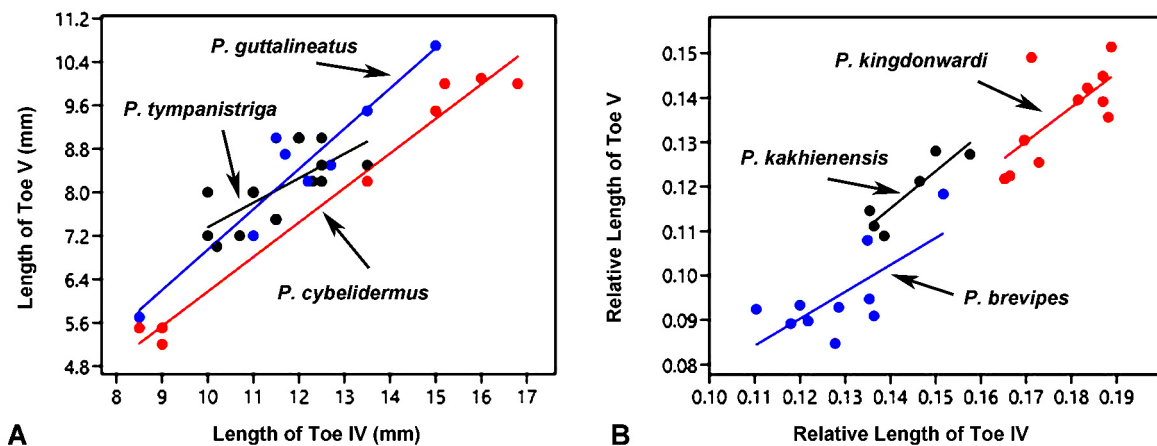


FIGURE 7. Relationship of lengths of Toes IV and V in species of *Pseudocalotes* from the Sunda Shelf (A) and from mainland Southeast Asia (B). Figure B shows relative toe lengths calculated by dividing length of the toe by SVL.

Different sizes of subdigital lamellae, different lengths of the sole, and/or relative lengths of the fifth toe could all influence this character. Nonetheless, relative lengths of the fourth and fifth toe reflect the same interspecific differences as span of the fifth toe. Our data for *Pseudocalotes cybelidermus* failed the normality test and samples did not have homogenous variances if this species was included. Nonetheless, the pattern is clear: *P. cybelidermus* has a shorter toe than *P. guttalineatus* or *P. tympanistriga* (Fig. 7). Treating length of Toe IV as a covariate, *P. brevipes* has a relatively shorter fifth toe than *P. kakhienensis* ($F_{10,6} = 5.304, P = 0.038$) and *P. kingdomwardi* ($F_{10,11} = 7.452, P = 0.014$). Thus, meristic and mensural methods of characterizing relative size of the fourth and fifth toes provide the same information. We find the meristic approach easier to apply, especially in older specimens with brittle digits that may be damaged while being measured.

Discussion

Museum collections contain modest samples of many Sumatran agamids, yet several species such as *Harpesaurus beccarii* Doria, *Phoxophrys tuberculata* Hubrecht, and *Thaumatohynchus brooksi* Parker appear to be truly rare or, at least, rarely encountered by herpetologists (Böhme 1989; Inger 1960). Both *Pseudocalotes baliomus* and *P. rhammanotus* could be added to this list of rare Sumatran agamids. Our field parties have spent hundreds of man-hours searching montane forests throughout Sumatra. Yet in four years of intensive collecting, we have found only single specimens of each species.

Research into the phylogeny of *Pseudocalotes* has just begun. Several earlier studies found *Pseudocalotes* to be monophyletic (Schulte *et al.* 2004; Zug *et al.* 2006; J. Grismer *et al.* 2016), but they only included two or three mainland species. On the issue of monophyly, a larger study of eight species by L. Grismer *et al.* (2016) obtained equivocal results: their Bayesian analysis supported monophyly, but their Maximum Likelihood analysis did not, and none of the deeper nodes in their tree was strongly supported.

In our study, we used phylogenetic analysis and comparisons of genetic distances as tools to identify a cryptic species of *Pseudocalotes* and to examine morphological character evolution among Sumatran and Javan congeners. Incidental to these primary goals, we uncovered unequivocal evidence of polyphyly. Genetic divergence between insular and mainland species of *Pseudocalotes* equals or exceeds divergences between pairs of draconine genera. Earlier studies failed to find evidence for polyphyly, because they did not include any of the insular *Pseudocalotes*. However, we caution that our study only includes nine of the 22 species in this genus and is based on a single gene.

As tissues from the rare species of *Pseudocalotes* slowly accumulate and morphological study identifies new characters, we anticipate much more inclusive phylogenetic analyses of *Pseudocalotes* in the near future. The limited phylogenies in our study and those of L. Grismer *et al.* (2016) provide tantalizing glimpses of the group's evolutionary history, and we hope that our study stimulates more research into the phylogeny of these secretive montane agamids.

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APPENDIX 1. Specimens examined.

- Pseudocalotes brevipes* (10): **LAO PDR.** XE KONG; Kaleum District, Xe Sap National Biodiversity Conservation Area, near 16° 04'10"N, 106° 58'45"E, 1200–1300 m (FMNH 258703). **VIETNAM.** VINH PHU; Tam Dao, Vinh Yen District (MVZ 224103–224106; 226486, 226487, 226489, 226490, 226494).
- Pseudocalotes cybelidermus* (15): **INDONESIA.** LAMPUNG: Montane forest above Ngarip, Lampung, Sumatra, Indonesia, 5.28°S, 104.56° E, 1376–1521 m (MZB 9766, 9769, 9800, UTA 60537–60539, 60552–60555 paratypes). **SUMATERA SELATAN:** Montane forest at Maura Dua, Remanan Jaya, Gunung Pesagi (locally known as Masagi), 4.91°S, 104.13°E, 1474–1643 m (MZB 9767 holotype; MZB 9650, 9760, 9799, UTA 60549–60551 paratypes).
- Pseudocalotes dringi*: **MALAYSIA.** PAHANG: “Gunung Tahan, 6500–7200 ft (1981–2194 m) elevation” (BMNH 1906.2.28.10 holotype). **TERENGGANU:** “Summit Ridge, 4000 ft (1219 m) elevation, Gunung Lawit, Terengganu, W-Malaysia” (BMNH 1974.4929 paratype).
- Pseudocalotes flavigula* (1): **MALAYSIA.** PAHANG; Gunnong Brinchang, Cameron Highlands, 1524–1829 m (FMNH 143903); “Cameron Highlands between 5,000 and 6,000 feet” (BMNH 1946.8.11.14 holotype).
- Pseudocalotes floweri* (2): **CAMBODIA.** KOH KONG; Cardamom Highlands Plateau. 0349359 Easting, 1325813 Northing, 1200 m (FMNH 270127). **THAILAND.** No other data (FMNH 114514), “Chantaboon” = Chantaburin (BMNH 1946.8.11.25 lectotype).
- Pseudocalotes guttelineatus* (16): **INDONESIA.** LAMPUNG: Montane forest above Ngarip, 5.28°S, 104.56° E, 1341–1521 m (MZB 9796 holotype; MZB 9652, 9765, 9792–9795, 9801, UTA 60536, 60540–60543, 60554 paratypes). **SUMATERA SELATAN:** Maura Dua, Remanan Jaya, Gunung Pesagi (locally known as Masagi), 4.91°S, 104.13°E, 1574–1643 m (UTA 60500–60501, paratypes).
- Pseudocalotes kakhienensis* (6): **CHINA.** YUNAN; Nujiang Prefecture, small village S of Gongshan, 27° 42' 13.7016" N, 98° 42' 10.1982" E, ca 1451 m (CAS 214907, 214940, 214949), Fugong County, Shiwuli, 27° 09' 22.5" N, 98° 47' 57.4" E (CAS 234454–234455), Gongshan County, vicinity of village S of Gongshan, 27° 42' 13.1" N, 98° 42' 10.6" E, 1437 m (CAS 242105).
- Pseudocalotes kingdonwardi* (11): **BURMA.** “Adung Valley, 7000ft, Burma-Tibet border” (BMNH 1946.8.11.17 holotype). **CHINA.** YUNAN; Nujiang Prefecture, Gongshan County; road between Kongdang and Bapo in Dulong Valley, 27° 49' 33.9" N, 98° 19' 31.7" E, 1478 m (CAS 241965), ca 5 km N (by Dulong River) of Kongdang (CAS 241992, 241994, 241997), Dulong Valley, E of Kongdang (CAS 242015), Dulong Valley, 2 km N of Kongdang, W side of Dulong River (CAS 242020), Dulong Valley, road from Bapo N toward Kongdang, 27° 45' 29.9" N, 98° 20' 52.8" E, 1357 m (CAS 242628), Dulong Valley, Kongdang, 27° 50' 28.4" N, 98° 19' 45.4" E, 1450 m (CAS 242653), Dulong Valley, Kongdang, 27° 52' 07.7" N, 98° 20' 09.4" E, 1451 m (CAS 242674), Dulong Valley, Kongdang, 27° 51' 44.0" N, 98° 20' 04.3" E (CAS 242675), Dulong Valley, Kongdang, 27° 52' 07.2" N, 98° 20' 09.8" E, 1450 m (CAS 242676).
- Pseudocalotes microlepis* (2): **LAO PDR.** Phong Saly (FMNH 14499). **VIETNAM.** BAC THAI; Ba Be Lake National Park, cave area, ca. 1.5 km E of guest house, 22° 24' 1" N, 105° 37' 54" E. **THAILAND.** “Plapoo Tenasserim” (BMNH 1946.8.11.21).
- Pseudocalotes poilani* (2): **LAO PDR.** CHAMPASAK; Pakxong District, Dong Hua Sao National Biodiversity Conservation Area, near Ban Nongluang Village, near 15° 04'70"N, 106° 12'03"E, 1100 m (FMNH 258704), Pakxong District, Dong Hua Sao National Biodiversity Conservation Area, Bolaven Plateau, near 15° 03'55"N, 106° 13'03"E, 1200 m (FMNH 258710).
- Pseudocalotes rhammanotus* (1). **INDONESIA.** LAMPUNG: montane forest along the ridge of a mountain south of Danau Ranau (= Lake Ranau), 4.9394° S, 103.85292° E, 1237 m (MZB 10804, holotype).
- Pseudocalotes tympanistriga* (16): **INDONESIA.** JAWA BARAT. Cibodas Botanical Garden, 6.74181° S, 107.0061° E (UTA R 60544–60548); Gunung Tilu, 7.15601° S, 107.52309° E, 1389–1647 m (UTA R 63094–63096); road from S coast of Java to Gunung Patuha, 7.24716° S, 107.35696° E, 1156 m (UTA R 63097); road from S coast of Java to Gunung Patuha, 7.24711° S, 107.35722° E, 1183 m (UTA R 63098–63099); Gunung Puntang. Gibbon Research Center, 7.11828° S, 107.60493° E, 1393–1468 m (UTA R 63100–63101); Gunung Waringin, 7.15603° S, 107.49647° E, 1583–1607 m (UTA 63102–63103). NO OTHER DATA: “Java” (ZMB 689 holotype).

APPENDIX 2. Individuals included in phylogenetic analyses. NA: no museum number provided by GenBank for sequence.

Species	Museum Number	Gene	GenBank ID
<i>D. boulengeri</i>	MZB 13820	ND4	KY576742
<i>P. guttalineatus</i>	UTA 60540	ND4	KT180141
<i>P. guttalineatus</i>	UTA 60501	ND4	KT180142
<i>P. cybelidermus</i>	UTA 60551	ND4	KT180139
<i>P. cybelidermus</i>	UTA 60549	ND4	KT180140
<i>P. tympanistriga clade 1</i>	UTA 60544	ND4	KT180143
<i>P. tympanistriga clade 1</i>	UTA 60547	ND4	KT180145
<i>P. tympanistriga clade 2</i>	UTA 63094	ND4	KY884008
<i>P. tympanistriga clade 2</i>	MZB 16356	ND4	KY884009
<i>P. baliomus</i>	MZB 9813	ND4	KT211019
<i>P. rhammanotus</i>	MZB 10804	ND4	KT180147
<i>P. brevipes</i>	MVZ 224103	ND4	KY884010
<i>P. brevipes</i>	MVZ 224107	ND4	KY884011
<i>P. larutensis</i>	LSUHC 9041	ND4	KY884012
<i>P. larutensis</i>	LSUHC 9052	ND4	KY884013
<i>P. kahkienensis</i>	CAS234454	ND4	KY884004
<i>P. kahkienensis</i>	CAS242688	ND4	KY884006
<i>P. kingdomwardi</i>	CAS242629	ND4	KY884005
<i>P. kingdomwardi</i>	CAS242676	ND4	KY884007
<i>B. cristatella</i>	UTA R 62895	ND4	KT180148
<i>B. jubata</i>	UTA R 62896	ND4	KT180152
<i>B. jubata</i>	UTA R 62897	ND4	KT180151
<i>B. jubata</i>	UTA R 62898	ND4	KT180150
<i>B. jubata</i>	UTA R 62899	ND4	KT180146
<i>C. versicolor</i>	UTA R 62861	ND4	KT180149
<i>C. versicolor</i>	NA	ND4	NC009683
<i>Gonocephalus sp.</i>	UTA R 60571	ND4	KT180144
<i>Pogona vitticeps</i>	NA	ND4	AB166795