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Phylogenetic Relationships of the Genus *Ptyctolaemus* (Squamata: Agamidae), with a Description of a New Species from the Chin Hills of Western Myanmar

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A new species of *Ptyctolaemus* is described from the Chin Hills, Chin State, western Myanmar. Specimens were found on the slopes of Mount Victoria between elevations of 709 m and 1,940 m in areas of secondary forest in close proximity to human habitation. The new species differs from *P. gularis*, by having a more developed nuchal crest in males, shorter limbs, larger and more heterogeneous dorsal body scales, and a shorter tail. *P. phuwuanensis* can be distinguished from *P. gularis* and the new species by the presence of femoral pores and a distinct gular region. A molecular phylogenetic analysis of *P. gularis*, *P. phuwuanensis*, the new species of *Ptyctolaemus* from Chin State, and other species in the draconine clade indicates that *P. phuwuanensis* is sister to all other draconine agamids and we recommend the recognition of the genus name *Mantheyus* for *P. phuwuanensis* in light of these results. *Ptyctolaemus* from Chin State and *P. gularis* are related but significantly different genetically and morphologically representing separate species.

Two species of *Ptyctolaemus* are currently recognized. *Ptyctolaemus gularis* (Peters, 1864) currently known from northeastern India (Boulenger 1890; Wall 1908; Smith 1935; Mathew 1995; Pawar and Birand 2001), Xizang Autonomous Region [Tibet], China (Huang 1980), Kachin State, Myanmar (Smith 1940), Sagaing Division, Myanmar (California Academy of Sciences specimens), and Chin State, Myanmar (Shreve 1940; Moody 1980), and *P. phuwuanensis* Manthey and Nabhitabhata, 1991, is known from northeastern Thailand and western central Laos (Manthey and Nabhitabhata 1991; Ananjeva and Stuart 2001). After examining specimens of *P. phuwuanensis*, Ananjeva and Stuart (2001) provided a number of characters, including the presence of femoral glands and a unique gular fold morphology that lead them to place *P. phuwuanensis* in the new genus *Mantheyus*. Hallermann and Böhme (2003) objected to the placement of *M. phuwuanensis* into a monotypic genus stating that Ananjeva and Stuart (2001) did not provide autapomorphic characters distinguishing *M. phuwuanensis* from *P. gularis* and thus did not demonstrate that *Mantheyus* represented an isolated evolutionary lineage without close relatives. Hallermann and Böhme (2003) argued that femoral glands are a plesiomorphic character and the similarity of the gular folds represented a possible synapomorphy for *P. gularis* and *M. phuwuanensis* and therefore regarded *Mantheyus* as a junior, subjective synonym.

In March 2001, while surveying Nat Mat Taung National Park and surrounding areas of the southern Chin Hills, Chin State, Myanmar, the Myanmar Herpetological Survey team collected eight individuals (seven adults and one juvenile) belonging to the genus *Ptyctolaemus*. After comparing these specimens with the holotype of *P. gularis* as well as other specimens from India and northern Myanmar, we determined that the specimens from the Chin Hills represent a new species. The external comparisons were followed by a molecular phylogenetic analysis of the genus utilizing tissue samples of *Ptyctolaemus* from Chin State, *P. gularis* from northern Myanmar, and *P. phuwuanensis* from Laos. Because the type locality of *P. gularis*, given in Peters (1864) as "Calcutta", is thought to be in error (Jerdon 1870; Zhao and Alder 1993), we analyzed the mensoral data of the Chin State specimens, the holotype of *P. gularis* and other specimens of *P. gularis* from India and northern Myanmar, using principal component analysis. This allowed us to determine which species of *Ptyctolaemus* are most similar to the holotype of *P. gularis* and should be recognized as the nominal species.

Materials and Methods

All California Academy of Sciences (CAS) specimens were hand collected, euthanized, fixed in 10% buffered formalin and later transferred to 70% ethanol. Samples of liver tissue were taken from selected specimens and stored in 95% ethanol. Latitude, longitude and elevation were recorded using a Garmin 12 Global Positioning System receiver (datum WGS 84).

Comparative material was obtained from the Institute of Systematic Zoology, Humboldt University, Berlin (ZMB); the Natural History Museum (British Museum), London; Field Museum of Natural History; Museum of Comparative Zoology, Harvard University; National Museum of Natural History, Smithsonian Institution; Myanmar Biodiversity Museum, Hlawga; and California Academy of Sciences (see material examined section). Museum symbolic codes follow Leviton et al. (1985) except for the ZMB, the Wildlife Heritage Trust, Colombo, Sri Lanka (WHT), Bombay Natural History Society (BNHS), and the, newly established, Myanmar Biodiversity Museum (MBM). The codes BNHS-AMB, MBM-JBS, MVZ-RM, WAM-ERP are followed by the field numbers for Aaron M. Bauer, Joseph B. Slowinski, J. Robert Macey, and Eric R. Pianka, respectively, for uncataloged specimens being deposited at the designated institutions.

The following measurements were obtained from all specimens of *Ptyctolaemus gularis* and *Ptyctolaemus* from Chin State examined in the study (limb lengths were taken from the right side unless noted otherwise): snout-vent length (SVL); tail length (TailL); head length (HeadL), distance from tip of snout to rear border of right angle of jaw; head width (HeadW), widest point in the temporal region, anterior to the tympanum; upper arm length (UarmL), from elbow to forelimb insertion; forearm length (ForeaL), from base of palm to elbow; hand length (HandL), from base of palm to end of fourth finger (not including the claw); thigh length (ThighL), from knee to thigh insertion; crus length (CrusL), from base of heel to knee; foot length (FootL), from heel to end of fourth toe; fourth toe length (4^{th}Toe), from base or fourth toe to toe tip (not including the claw); and ratios of TailL/SVL, HeadW/HeadL, HeadW/SVL, HeadL/SVL, UarmL/SVL, ForeaL/SVL, ThighL/SVL, and CrusL/SVL.

Data for the following meristic characters were recorded: supralabials (SupL), number of enlarged scales bordering left and right margin of upper lip (not including rostral scale); infralabials (InfL), number of enlarged scales bordering left and right margin of lower lip (not including mental scale); number of nuchal crest spines (NuchalC), enlarged mid-dorsal crest scales from posterior portion of the head to the posterior portion of the nape; number of scales around midbody (MidB); number of ventral scale rows (VentSR), scale rows between posterior margin of gular and

anterior edge of vent; and number of subdigital lamellae on the right fourth toe (SDL).

Scale counts and observations of external morphology were made using a dissecting microscope. Measurements, except for TailL, were made with digital calipers with a 0.01 mm precision and rounded to the nearest 0.1 mm. Tail lengths were measured using a measuring tape with a precision of 1 mm.

Genomic DNA was extracted from liver using the Qiagen QIAamp tissue kit. Amplification of genomic DNA was conducted using a denaturation at 94°C for 35 s, annealing at 50°C for 35 s, and extension at 70°C for 150 s with 4 s added to the extension per cycle, for 30 cycles with Life Technologies (Gibco) Taq polymerase. Negative controls were run on all amplifications to check for contamination. Amplified products were purified on 2.0% Nusieve GTG agarose gels and reamplified under the conditions described above. Reamplified double-stranded products were purified using the Qiagen Qiaquick Purification kit. Cycle-sequencing reactions were run using ABI Prism Big Dye Terminator version 3 DNA Sequencing Kit (Perkin-Elmer) with a denaturation at 95°C for 15 s, annealing at 50°C for 1 s, and extension at 60°C for 4 min for 35–40 cycles. Sequencing reactions were run on a MJ Research Basestation or ABI PRISM® 3100 Genetic Analyzer.

Amplifications of the mitochondrial ND1 gene to the COI gene from genomic DNA were done with three primer combinations. All samples were amplified with L3914 in combination with H4980. *Ptyctolaemus phuwuanensis* was amplified with L4437 in combination with H6159. *P. gularis* and the new species were amplified with L4437 in combination with H5934a. Both strands were sequenced using L3914, L4160, L4437, L4882a, L4882b, H4980, L5549b, L5638b, H5934a, and H6159.

Most primers are as described by Macey et al. (1997a) except L3914, which is erroneously reported in Macey et al. (1998a) as L3878. Additional primers used include L4160 (Kumazawa and Nishida 1993), L4882a (Schulte et al. 1998), L4882b (Macey et al. 2000), L5549b (Schulte et al. 2003), and H6159 (Weisrock et al. 2001). Primer numbers refer to the 3' end on the human mitochondrial genome (Anderson et al. 1981), where L and H denote primers whose extension produces the light and heavy strands, respectively. Voucher specimen information and GenBank accession numbers for newly reported sequences are provided in the material examined section. Aligned DNA sequences are available in TreeBASE (Study accession S1056; Matrix accession number M1800).

DNA sequences were aligned initially by eye. Positions encoding part of ND1, all of ND2, and part of COI were translated to amino acids using MacClade 4.06 (Maddison and Maddison 2003) for confirmation of alignment. Alignments of sequences encoding tRNAs were based on secondary structural models. Secondary structures of tRNAs were inferred from primary structures of the corresponding tRNA genes using these models. Unalignable regions were excluded from phylogenetic analyses using the same regions excluded by Macey et al (2000).

Phylogenetic trees were estimated using PAUP* beta version 4.0b10 (Swofford 2002) with a heuristic search featuring TBR branch swapping and 500 random taxon additions using maximum parsimony (MP). Bootstrap resampling (Felsenstein 1985a) was applied to assess support for individual nodes using 1000 bootstrap replicates with 100 random taxon additions per replicate. Decay indices (= "branch support" of Bremer 1994) were calculated for all internal branches using TreeRot.v2c (Sorenson 1999). In our evaluation of branch support strength, we consider a bootstrap value of 95% and above as strongly supported (Felsenstein and Kishino 1993), 95–70% as moderately supported, and below 70% as poorly supported. Maximum-likelihood (ML) analyses were also performed. Simultaneous optimization of ML parameters and phylogenetic hypotheses for this data set was computationally impractical; therefore, ModelTest v3.06 (Posada and Crandall 1998) was used to find the best fitting model of sequence evolution for the tree from unweighted

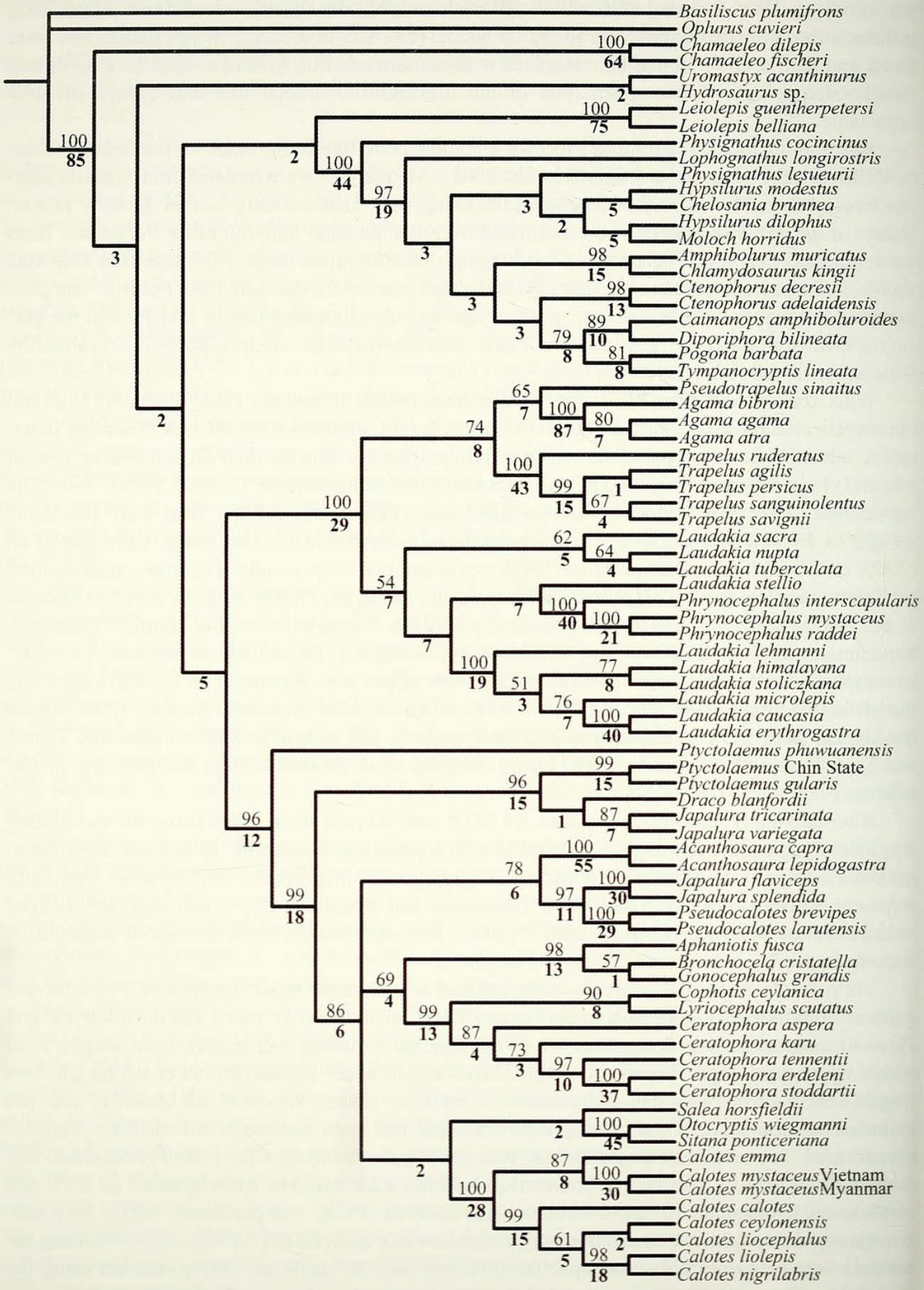
parsimony analysis. Posada and Crandall (2001) found that the starting tree did not significantly influence the estimated parameters found by ModelTest. The best fitting model parameters were fixed, and then used in 25 heuristic searches with random addition of taxa to find the overall best likelihood topology. Bootstrap analysis of the maximum-likelihood tree was computationally intractable.

Bayesian analysis was used to estimate a phylogenetic tree using many of the default values in MrBayes 3.04 (Huelsenbeck and Ronquist 2001). All analyses were initiated from random starting trees and run for 40,000,000 generations using four incrementally heated Markov chains. Values of the likelihood model were estimated from the data and initiated using flat priors. Trees were sampled every 100 generations resulting in 400,000 saved trees. To ensure that Bayesian analyses reached stationarity, the first 200,000 saved trees were discarded as "burn-in" samples. Sampled trees were used to generate a 50% majority-rule consensus tree in PAUP* and the percentage of trees having a particular clade represented that clade's posterior probability (Huelsenbeck and Ronquist 2001).

Wilcoxon signed-ranks (WSR) tests (Felsenstein 1985b; Templeton 1983) were used to examine statistical significance of the shortest tree relative to alternative hypotheses. This test determines whether the most parsimonious tree is significantly shorter than an alternative tree or whether their differences in length are statistically indistinguishable (Larson 1998). Wilcoxon signed-ranks tests were conducted as two-tailed tests (Felsenstein 1985b). Tests were conducted using PAUP* (Swofford 2002), which incorporates a correction for tied ranks. Goldman et al. (2000) criticized the application of the WSR test as applied in this study. Therefore, nonparametric Shimodaira-Hasegawa (SH) tests (Shimodaira and Hasegawa 1999), as advocated by Goldman et al. (2000), also were performed to test the shortest tree relative to the shortest alternative hypotheses using 10,000 resampling estimated log-likelihood (RELL) approximations in PAUP* to compare with the results of WSR tests. Parameter values were estimated on the ML trees using the likelihood criteria under the GTR + I + G model of sequence evolution. Buckley (2002) found the SH test to be a conservative model-based hypothesis test and, in general, to have low Type 1 and Type 2 error relative to the SOWH test (Goldman et al. 2000) and Bayesian posterior probabilities.

Alternative phylogenetic hypotheses for WSR and SH tests were tested using the most parsimonious phylogenetic topologies compatible with a particular constraint. To find the most parsimonious tree(s) compatible with a particular phylogenetic hypothesis, phylogenetic topologies were constructed using MacClade 4.06 (Maddison and Maddison 2003) and analyzed as constraints using PAUP* (Swofford 2002) with a heuristic search of 500 random addition of sequences.

Multivariate statistical analyses were applied to specimen measurements of *Ptyctolaemus gularis*, from India, northern Myanmar (Sagaing Division and Kachin State), and the holotype, and *Ptyctolaemus* from Chin State using 11 morphological variables: tail length, head length, head width, upper arm length, lower arm length, hand length, upper leg length, lower leg length, foot length, length of the four toe, and number of midbody scales. Specimen MCZ 44747 was not included because it contained missing data (the skull had been removed). All variables were ln-transformed. To examine shape differences between *P. gularis* and the Chin State *Ptyctolaemus* and remove the effects of size on morphometric variables, each variable was regressed on SVL and residuals were calculated. Principal components analysis (PCA) was performed on the variance-covariance matrix of the residuals. A discriminant function analysis (DFA) was employed using the same 11 variables to examine interspecific differentiation. All analyses were conducted using the statistical package PAST (Hammer et al. 2001). These complementary analyses were performed to


Basiliscus plumifrons
Oplurus cuvieri
Chamaeleo dilepis
Chamaeleo fischeri
Uromastyx acanthinurus
Hydrosaurus sp.
Leiolepis guentherpetersi
Leiolepis belliana
Physignathus cocincinus
Lophognathus longirostris
Physignathus lesueurii
Hypsilurus modestus
Chelosania brunnea
Hypsilurus dilophus
Moloch horridus
Amphibolurus muricatus
Chlamydosaurus kingii
Ctenophorus decresii
Ctenophorus adelaidensis
Caimanops amphiboluroides
Diporiphora bilineata
Pogona barbata
Tympanocryptis lineata
Pseudotrapelus sinaitus
Agama bibroni
Agama agama
Agama atra
Trapelus ruderatus
Trapelus agilis
Trapelus persicus
Trapelus sanguinolentus
Trapelus savignii
Laudakia sacra
Laudakia nupta
Laudakia tuberculata
Laudakia stellio
Phrynocephalus interscapularis
Phrynocephalus mystaceus
Phrynocephalus raddei
Laudakia lehmanni
Laudakia himalayana
Laudakia stoliczkana
Laudakia microlepis
Laudakia caucasia
Laudakia erythrogastra
Ptyctolaemus phuwuanensis
Ptyctolaemus Chin State
Ptyctolaemus gularis
Draco blanfordii
Japalura tricarinata
Japalura variegata
Acanthosaura capra
Acanthosaura lepidogastra
Japalura flaviceps
Japalura splendida
Pseudocalotes brevipes
Pseudocalotes larutensis
Aphaniotis fusca
Bronchocela cristatella
Gonocephalus grandis
Cophotis ceylanica
Lyriocephalus scutatus
Ceratophora aspera
Ceratophora karu
Ceratophora tennentii
Ceratophora erdeleni
Ceratophora stoddartii
Salea horsfieldii
Otocryptis wiegmanni
Sitana ponticeriana
Calotes emma
Calotes mystaceus Vietnam
Calotes mystaceus Myanmar
Calotes calotes
Calotes ceylonensis
Calotes liocephalus
Calotes liolepis
Calotes nigrilabris

determine whether morphological variation provided a basis for detectable structure between the two forms, and to identify with which group the holotype, and thus the name belong.

Results

The three new mitochondrial DNA sequences range in size from 1706–1721 bases and were aligned with 30 draconine ingroup and 45 acrodont and iguanid outgroup sequences from Macey et al. (1997a–b, 1998b, 2000) and Schulte et al. (2002) for a total of 1972 aligned positions. Sequences reported here were inferred to be authentic mitochondrial DNA, based on the criteria of Macey et al. (1997a). All sequences show strong strand bias against guanine on the light strand, a characteristic of the mitochondrial genome but not the nuclear genome and there were no stop codons after translation to amino acids using MacClade. In the phylogenetic analysis of 1434 unambiguous sites in 78 aligned sequences, 1147 (946 ingroup only) were variable and 1051 (795 ingroup only) are phylogenetically informative (parsimony criterion). Of the 1972 aligned positions, 538 positions were judged unsuitable for phylogenetic analysis because of questionable alignment.

Analysis of DNA sequence data produced three overall most-parsimonious trees each 12,777 steps in length (Fig. 1). Phylogenetic relationships were overall congruent with the hypothesis of Macey et al. (2000). The clade containing *Ptyctolaemus phuwuanensis* and all previously sampled members of Draconinae is recovered with strong support (96% bootstrap, decay index 12). The sister taxon relationship between *P. phuwuanensis* and the remaining draconine taxa also is recovered with strong support (99% bootstrap, decay index 18). The remaining taxa form two clades, one containing species in the genera *Ptyctolaemus, Draco,* and *Japalura* that is strongly supported (96% bootstrap, decay index 15) and the other forming a weakly supported group (86% bootstrap, decay index 6) with all other taxa sampled. The monophyly of the clade comprised of *Ptyctolaemus gularis* and the Chin State *Ptyctolaemus* is well supported with a bootstrap of 99% and decay index of 15. Topological differences between the parsimony tree presented here and in Macey et al. (2000) within Draconinae and among outgroups are restricted to weakly supported nodes in both trees. In addition, all strongly supported relationships recovered in our analysis are consistent with the phylogeny of Macey et al. (2000).

Hierarchical likelihood-ratio tests, as implemented in ModelTest, find that the most complex model (GTR + I + G) best explains the DNA sequence data and topology of the overall most-parsimonious tree. Model parameters are as follows: $\alpha = 0.5902$; proportion of invariant sites = 0.1382; substitution rates R(a) = 0.268, R(b) = 3.355, R(c) = 0.315, R(d) = 0.238, and R(e) = 1.000; and estimated base frequencies A = 0.418, C = 0.325, G = 0.063, and T = 0.193. A single optimal tree is found using maximum likelihood (Fig. 2) with a negative log likelihood of 51384.41. All groupings that received strong heuristic support (> 95% bootstrap, decay index > 10) from parsimony analyses occurred in the tree recovered by ML analyses.

Results from Bayesian analyses were congruent with those of ML and MP for all strongly supported nodes under MP, however, due to recent critiques regarding the interpretation of posterior probability values as overestimates of a node credibility (Buckley 2002; Suzuki et al. 2002) and by request of a reviewer these results are not presented.

Both MP and ML analyses recovered *Ptyctolaemus* as a nonmonophyletic group as recognized by Ananjeva and Stuart (2001). The WSR tests applied to the molecular data showed that the short-

← FIGURE 1. Phylogenetic relationships among agamid lizards based on maximum parsimony analysis of molecular data (length = 9047 steps). Bootstrap values are presented above branches and decay indices are shown in bold below branches on the phylogram.

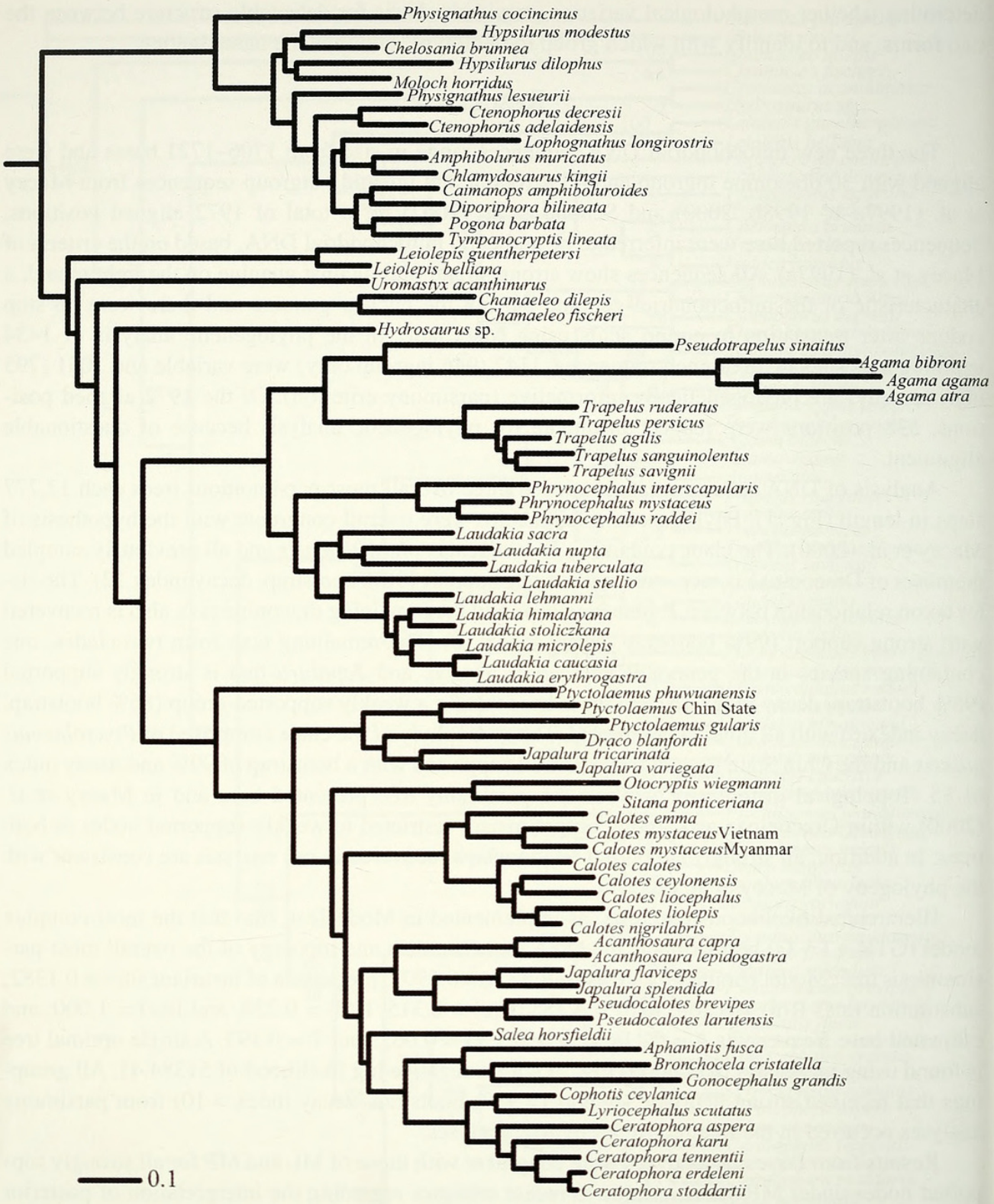


FIGURE 2. Phylogenetic relationships among agamid lizards based on maximum likelihood analysis using GTR + I + G model (mean -log-likelihood = 51384.41). Outgroups are identical to those presented in figure 1 and are not presented. The above tree is a phylogram.

est alternative tree showing *Ptyctolaemus* constrained to be monophyletic is significantly longer than the three overall shortest trees (n = 114; Ts = 4485; P < 0.001*). The SH test applied to the molecular data also rejected the alternative hypotheses of *Ptyctolaemus* monophyly (D ln L = 70.13; P < 0.001*) in favor of the overall shortest tree. We also tested the monophyly of the agamid clade Draconinae. The WSR tests applied to the molecular data showed that the three overall most parsimonious alternative trees showing Draconinae nonmonophyletic were not significantly longer than the three overall shortest trees (n = 110–142; Ts = 3386–5500; P < 0.253–0.324). The SH test did reject the alternative hypothesis of draconine nonmonophyly (D ln L = 24.4–25.06, P < 0.023–0.03*) in favor of the overall shortest trees showing monophyly.

Results of principal components analyses (PCA) using size-adjusted morphometric variables are presented in Table 1. The first two axes represent 80.9% of the variation. The first PC axis loads highest for tail length, hind limb measurements, and upper arm length. The highest loading for PC axis 2 is for midbody scale row number. PC axes 1 and 2 are plotted in Fig. 3. According to the PCA, *P. gularis* differs morphometrically from the Chin State *Ptyctolaemus* with no overlap.

According to discriminant function analysis (DFA), the two *Ptyctolaemus* species have almost no overlap in body shape. The classification procedure correctly classified 96.8% of specimens under their own species. All individuals of the Chin State *Ptyctolaemus* were classified correctly and one specimen of *P. gularis* (CAS 226687), the smallest specimen measured, was misclassified. Hotelling's T^2 test conducts a t-test on the canonical variates of the DFA. This test was highly significant with P < 0.0004* and correctly placed the type (ZMB 5004) of *Ptyctolaemus gularis* with other specimens identified as this species.

TABLE 1. Loadings and percentage of explained variance for the first two principal component axes based on size-adjusted morphometric variables. Analysis applied to 11 morphometric variables.

Variable	*PC 1*	*PC 2*
TailL	0.857	0.104
HeadL	0.499	0.305
HeadW	0.607	0.135
UarmL	0.931	-0.169
ForeaL	0.685	0.008
HandL	0.757	-0.282
ThighL	0.933	0.125
CrusL	0.958	0.057
FootL	0.91	-0.286
4thToe	0.888	-0.324
MidB	0.783	0.512
Eigenvalue	0.074	0.006
% of total variance	74.58	6.35

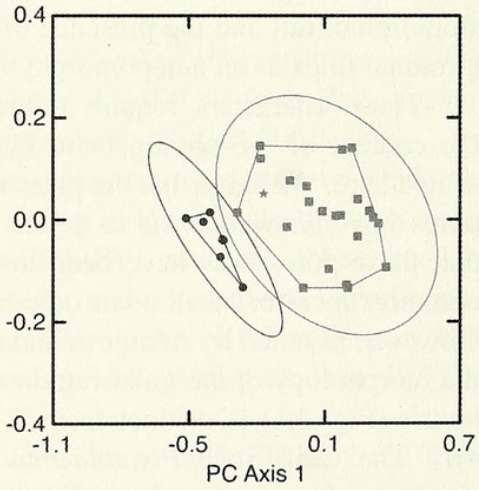


FIGURE 3. Position of adult *Ptyctolaemus* from Chin State and *P. gularis* specimens in morphospace based on the first two principal component axes from size-corrected body measurements. The first factor correlates with tail length, head width, all limb lengths, and midbody scale number. The second factor correlates with midbody scale number. Squares denote *P. gularis* specimens, circles denote *Ptyctolaemus* from Chin State specimens and the star indicates the type specimen of *P. gularis*. Ninety-five percent confidence ellipses and convex hulls are presented around specimens of each species.

DISCUSSION

Analysis of DNA sequence recovers *Ptyctolaemus phuwuanensis* as the sister taxon to all other sampled species of draconine agamids. Results of statistical hypothesis tests applied to these mtDNA sequences strongly reject the hypothesis that *Ptyctolaemus,* as circumscribed by Hallerman and Böhme (2003), is monophyletic. As such, *P. phuwuanensis* represents a distinct evolutionary line without close relatives. The uncorrected pair-

wise percent sequence divergence between *P. gularis* and the Chin State *Ptyctolaemus* is 21.16%. This level of sequence divergence is greater than the maximum uncorrected sequence divergences between sampled species with *Acanthocercus* (13.12%), *Calotes* (20.31%), and *Ceratophora* (16.48%). Pairwise sequence divergence between *P. phuwuanensis* and the other species of *Ptyctolaemus* ranges from 30.14–30.57% providing genetic evidence that this taxon is quite different from the former two species.

Honda et al. (2000a) using mitochondrial DNA recovered a monophyletic Draconinae containing a clade of *P. phuwuanensis* as the sister taxon to *Draco*. However, in another phylogenetic study of the Draconinae, Honda et al. (2000b), also found *P. phuwuanensis* sister to all other draconine genera included in the analysis. In both analyses, the position of *P. phuwuanensis* was weakly supported using bootstrap analyses and *P. gularis* was not sampled.

Hallerman and Böhme (2003) recommended that *Mantheyus phuwuanensis* be a junior, subjective synonym of *Ptyctolaemus*. They suggested there was insufficient evidence for nonmonophyly of species within *Ptyctolaemus*, interpreting the femoral pores present in *P. phuwuanensis* as a plesiomorphic trait and the presence of parallel, longitudinal folds as an autapomorphy of the genus.

These characters require reinterpretation in the context of the phylogenetic hypotheses presented here. We agree that the presence of femoral pores in *P. phuwuanensis* is a plesiomorphy and that these pores may have been lost once in the common ancestor of all other draconine agamids. However, as noted by Ananjeva and Stuart (2001), the morphology of the gular region in *P. phuwuanensis* (Fig. 4A) is distinct from *P. gularis* (Fig. 4B). The Chin State *Ptyctolaemus* (Fig. 4C) is similar to *P. gularis* and equally distinct from *P. phuwuanensis*. *Ptyctolaemus phuwuanensis* has a well defined gular sac surrounded by a "U"-shaped fold; this fold is encompassed by a second "U"-shaped fold. In addition, a transverse gular fold is formed by the posterior portion of the outer fold being connected on either side to the oblique folds in front of the shoulders and continuing dorsally and posteriorly from the shoulder. The gular folds of *P. gularis* and the Chin State *Ptyctolaemus* are formed by the collapsing of the gular pouch and surrounding skin in an accordian-like fashion, causing a pleating of the gular skin. The gular

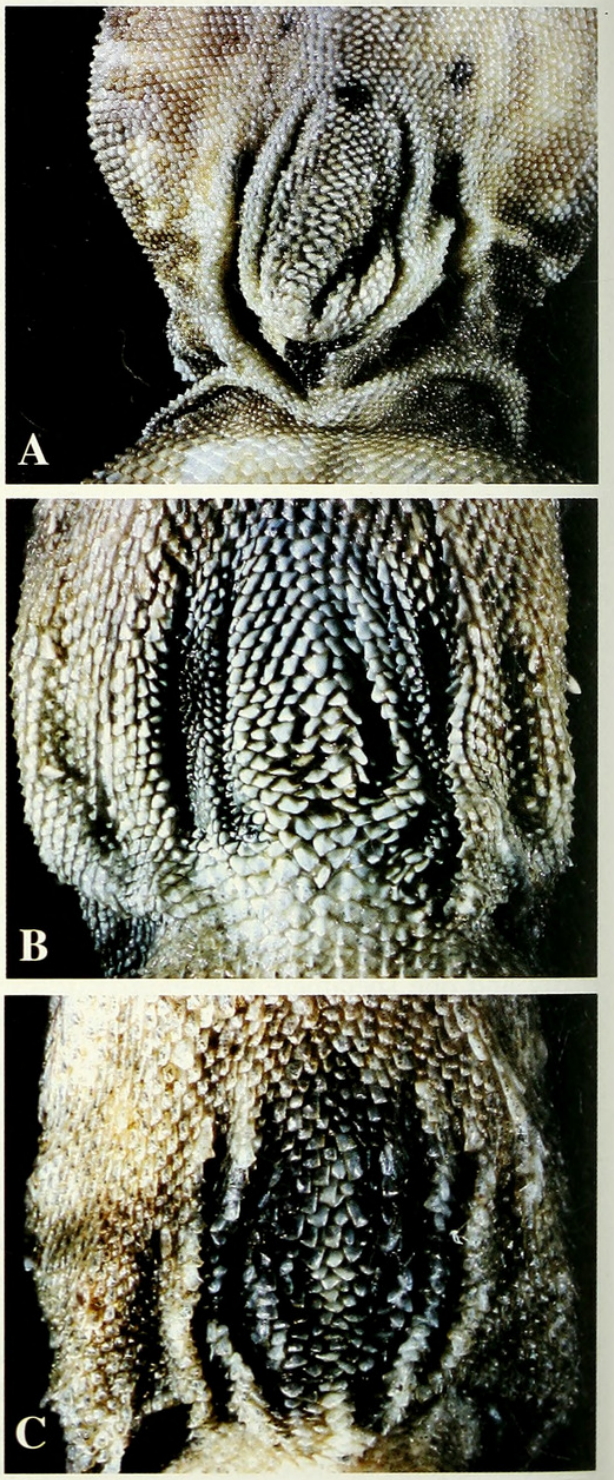


FIGURE 4. View of gular region of (A) *P. phuwuanensis*, FMNH 262582; (B) *P. gularis*, CAS 225592; and (C) *Ptyctolaemus* from Chin State, CAS 227489.

folds of *P. gularis* and of the Chin State *Ptyctolaemus* have longitudinal gular pleating curving medially at the posterior end. Thus, the parallel, longitudinal folds do not appear to be a homologous, shared derived trait for this genus and represent two independent alterations of the gular region. This is not surprising, given that the gular region of iguanian lizards has been modified numerous times independently in chamaeleons, *Anolis,* corytophanines, amphibolurine agamids, *Polychrus,* and within the Draconinae (common ancestor of *Sitana* and *Otocryptis*). Therefore, we recommend *P. phuwuanensis* be removed from synonymy and placed in the genus *Mantheyus* in accordance with Ananjeva and Stuart (2001).

Species description

***Ptyctolaemus collicristatus* Schulte and Vindum, sp. nov.**

Ptyctolaemus gularis, Shreve 1940, Proc. New England Zool. Club 18:24.
Ptyctolaemus gularis, Moody 1980, Ph.D. Dissertation, Univ. Michigan, Ann Arbor, p. 308.

Diagnosis and camparisons.—The only clear character that distinguishes the genus *Ptyctolaemus* from other genera of the subfamily Draconinae (sensu Macey et al. 2000) or Group V agamids (sensu Moody 1980) of mainland southeast Asia is that the males of *P. gularis* have longitudinal gular folds on either side of the midline with the posterior portion of the folds curving medially on each side of the throat. However, these folds are only evident when the gular pouch is in a relaxed position (as in preserved specimens). The folds are formed when the gular pouch is relaxed in an accordion-like fashion, the folds become more pronounced because the scales within the folds are darkly pigmented.

The only other species with gular folds is *Mantheyus phuwuanensis*, however it has rounded "U"-shaped folds encompassing the gular sac. *M. phuwuanensis* also differs from *Ptyctolaemus* and all other draconines by the presence of femoral pores (Ananjeva and Stuart 2001).

The new species can be distinguished from *P. gularis* by having a more prominent nuchal crest (Fig. 5) comprised of larger, flattened, triangular, scales, consisting of fewer scales in adult males (15–16 versus 17–30 scales); a shorter tail, with an average TailL:SVL ratio of 1.99 versus 2.24 (Fig. 6); stouter and shorter limbs (Fig. 6); and more heterogeneity among dorsal and lateral scales.

Holotype.— CAS 227489 (Figs. 5–10), from Myanmar, Chin State, Min Dat District, Min Dat Township, 21°22′20.1″N, 93°58′34.6″E, 1,482 m, collected by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun, 7 April 2001.

Description of holotype.— Adult male with a SVL of 91.3 mm; TailL 182 mm (see Table 2 and 3 for additional measurements and meristic characters and Table 4 for body proportions).

Rostral scale 2.9 times as wide as high, about 1.4 times higher than touching upper labials, bordered behind by two supralabials and six postrostrals, medial two postrostrals being largest; supraciliary edge sharp; canthus rostralis moderately sharp, less so toward nostral; nasals extending slightly beyond vertical plane of canthus rostralis; scales on snout irregular in shape and size, slightly imbricate; series of seven, enlarged, keeled scales form an inverted 'Y'-shaped pattern on middle of snout, first three anterior scales on midline, pointing posteriorly, posterior to third scale are two scales on either side directed diagonally toward superciliary ridge; inner border of supraocular region with a semicircular series of slightly larger, feebly keeled scales, at closest point one head scale separates left and right series; scales within semicircular series smaller and feebly keeled; most upper head scales with one hair receptor on posterior end of scale keel; small, slightly conical, postorbital scale; slightly circular group of enlarged, keeled, scales on either side of occiput; seven supralabials on left and 9 on right; orbit 6.0 mm in horizontal diameter; distance

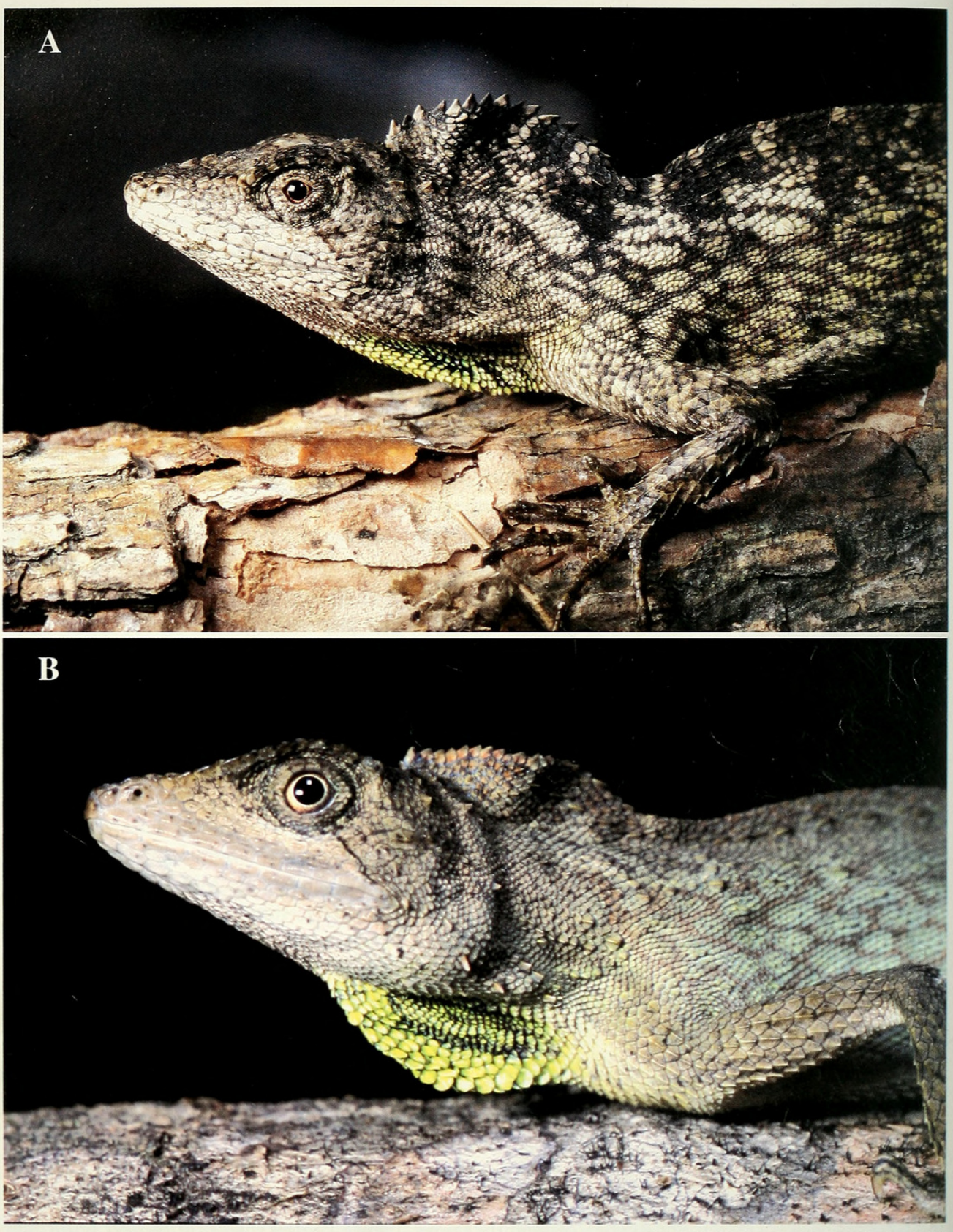


FIGURE 5. (A) View of anterior portion of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489, and (B) *P. gularis*, CAS 221433. Photographed by Hla Tun and Dong Lin, respectively.

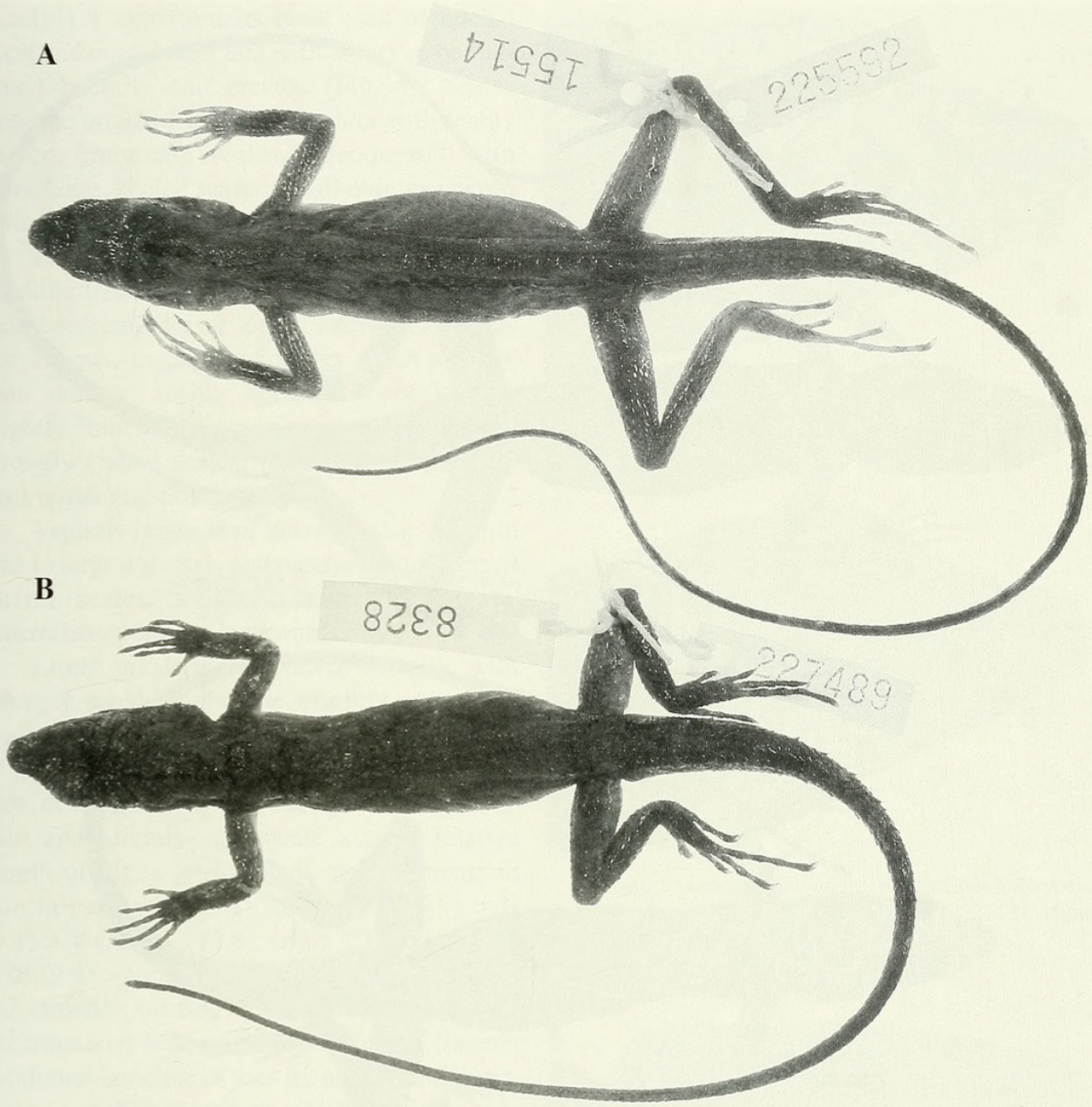


FIGURE 6. Dorsal views of (A) *Ptyctolaemus gularis*, CAS 225592, and (B) holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Dong Lin.

from anterior edge of orbit to nostril 6.7 mm, and 10.6 mm to tip of rostral scale; tympanum concealed, covered with smooth, slightly imbricate scales, scales equal in size to adjacent scales; two enlarged scales posterior and horizontal to orbit, keeled and elevated; temporal area with three enlarged, slightly conical, scales, first between circular group of scales adjacent to occiput and horizontal enlarged scales posterior to orbit, second and third horizontal and posterior to first, on right side scales one and two are separated by three scales and second and third separated by one scale, on left, first and second scale are separated by four scales, and scales two and three are touching.

Mental scale triangular, wider than long, slightly narrower than rostral; mental followed by an infralabial on either side and two rectangular shaped postmentals which contact first infralabials and length of mental except for posterior tip of mental where postmentals are separated by one small gular scale medially; posterior to postmentals are three chin shields on each side that run par-

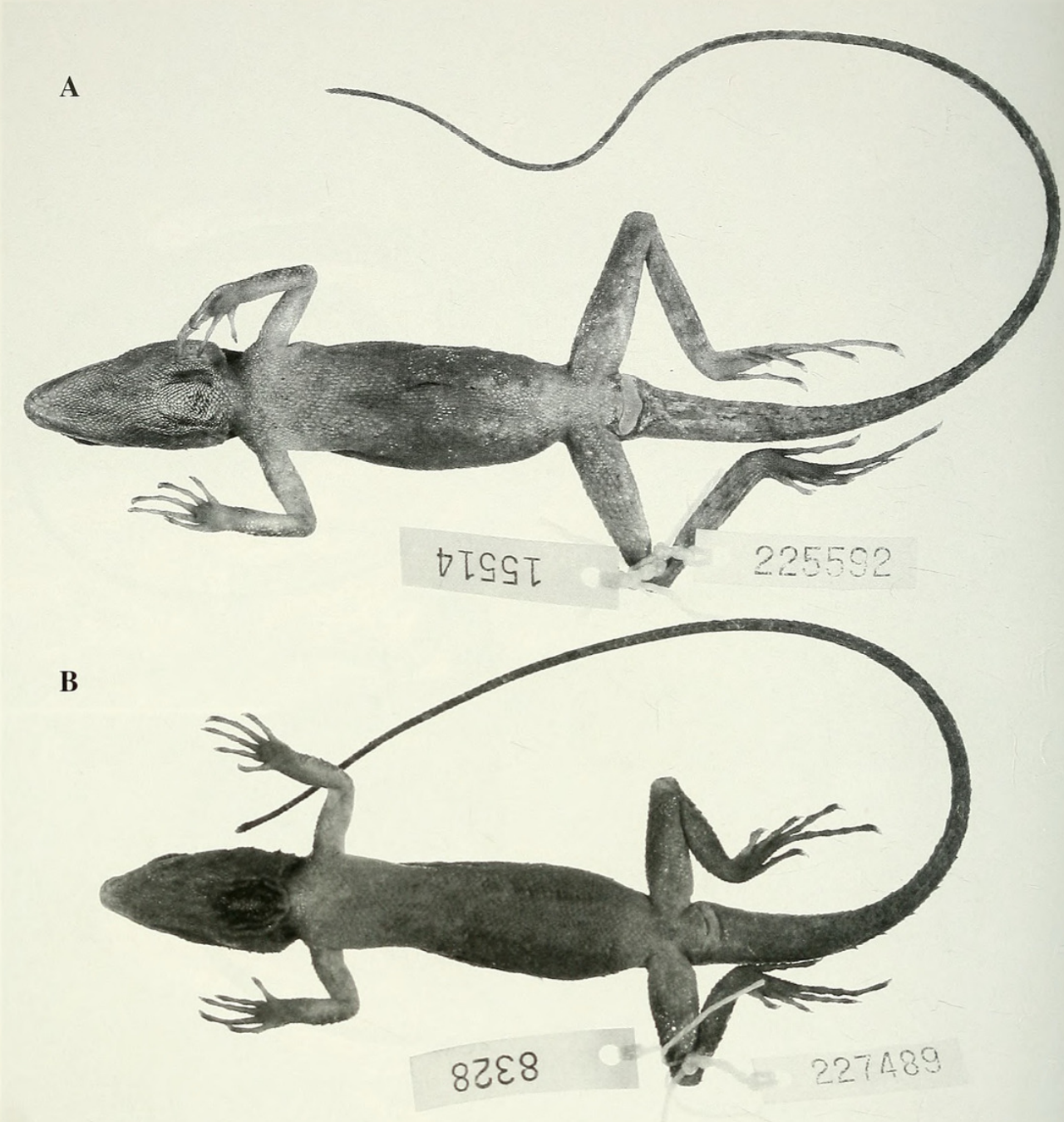


FIGURE 7. Ventral views of (A) *Ptyctolaemus gularis*, CAS 225592, and (B) holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Dong Lin.

allel to infralabials, anterior portion of first chin shield touching first infralabial, remaining portion of first chin shield and following two chin shields are separated from infralabials by one scale row; eight infralabials on either side. Gular scales anterior to gular pouch small (smaller than ventral scales), rounded, imbricate and slightly mucronate, most terminating with hair-bearing receptors; scales of gular pouch slightly triangular and smooth, becoming larger toward center, most with hair-receptors on tip; three distinct raised gular folds on either side of midline; folds curve toward midline posteriorly.

Nuchal crest composed of 16 erect, compressed, triangular scales, each scale notched on posterior side below apex, notch contains one hair-bearing receptor; longest nuchal scale extends ver-

tically 1.4 mm from its base; skin of nuchal crest and dorsal crest lax, with ability to be flattened laterally and erected (Fig. 5). Scales between angle of jaw and shoulder with feebly keeled, imbricate scales, interspersed with three large, keeled scales; small oblique curved fold in front of shoulder; axial scales granular.

Dorsal scales strongly keeled, imbricate, pointing backwards; mid-dorsal scales smaller than bordering dorsal scales; lateral scales heterogeneous, majority of scales much smaller than dorsals, feebly keeled or not keeled, slightly imbricate, interspersed with enlarged strongly keeled scales; lateral scales pointing backwards and down.

Ventrals larger than lateral scales, equal in size to largest dorsals and enlarged interspersed lateral scales, strongly keeled, imbricate, mucronate, pointing backwards.

Limbs moderate, covered dorsally with strongly keeled, imbricate, slightly mucronate scales; ventral surface of forelimbs with smaller feebly keeled, imbricate, scales; ventral surface of hind limbs with feebly keeled, imbricate and slightly mucronate scales; relative length of digits (right hand; measurements in mm in parentheses): IV (8.5) > III (7.9) > II (6.1) > V (5.2) > I (3.8); (right foot): IV (13.3) > III (9.4) > V (9.0) > II (6.6) > I (4.2); subdigital lamellae on fingers bicarinate with a few tricarinate on base of third and fourth fingers; subdigital lamellae of toes tricarinate and bicarinate: I and II bicarinate, III bicarinate, base with enlarged and rounded keels along leading edge, IV and V tricarinate becoming bicarinate distally; 21 and 22 subdigital lamellae under third and fourth fingers, respectively, and 22 and 28 under third and fourth toes, respectively.

Tail slightly compressed laterally, covered with homogenous, strongly keeled, imbricate, mucronate scales.

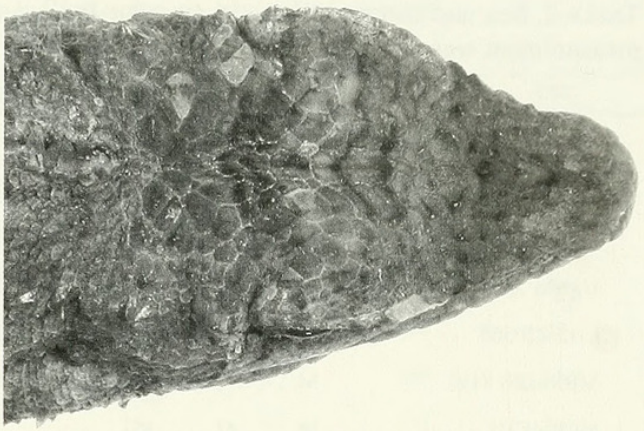


FIGURE 8. Dorsal view of the head of the holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Alan E. Leviton.

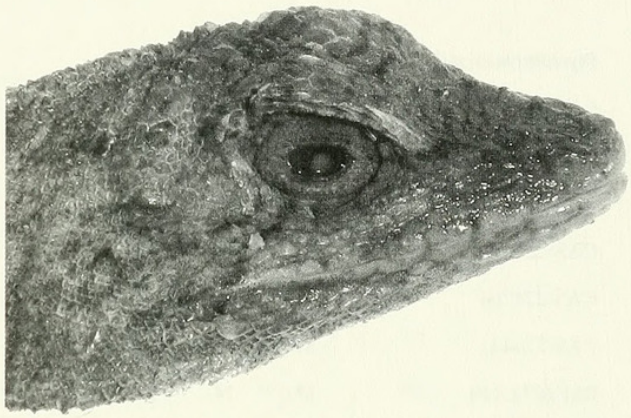


FIGURE 9. Lateral view of the head of the holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Alan E. Leviton.

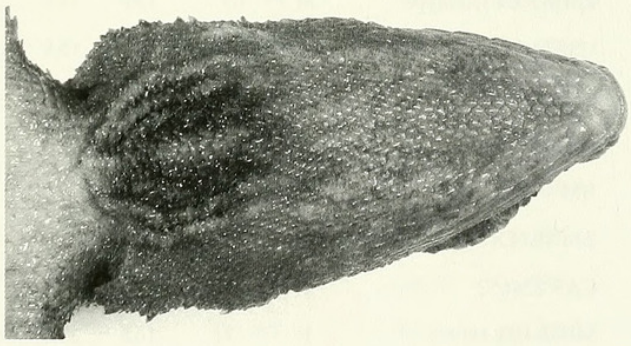


FIGURE 10. Ventral view of the head of the holotype of *Ptyctolaemus collicristatus*, sp. nov., CAS 227489. Photographed by Alan E. Leviton.

COLORATION IN ALCOHOL. Dorsum has a dull, grayish brown appearance. Snout a uniform gray brown; two faint, irregular, light brown bars bordered by darker brown bars, extending perpendicular to head axis, between anterior and posterior superciliary scales; two brown parallel stripes radiating posteriorly and diagonally from eye, anterior, stripe reaching jaw angle, posterior stripe shorter; gular scales anterior to gular pouch light

TABLE 2. Sex and mensural data (in mm) for *Ptyctolaemus collicristatus* sp. nov. and *P. gularis* (* indicates measurement was taken from left side).

	Sex	SVL	TailL	HeadL	HeadW	UarmL	ForeaL	HandL	ThighL	CrusL	FootL	4thToe
Ptyctolaemus collicristatus												
CAS 227489 Holotype	M	91.3	182	24.7	13.2	11.9	12.4	11.8	19.7	16.4	22.7	13.3
CAS 219991	M	82.8	174	22.9	11.9	10.3	13.2	11.4	19.5	16.2	21.7	13.4
USNM 559811	M	79.7	157	21.5	11.9	10.7	11	12.1	17.6	15.4	22.5	12.5
CAS 220560	M	78.4	167	22.1	11.5	10.9	11.9	12.2	18	16.7	21.3	13.5
MBM-JBS 8195	M	77.3	137	21.5	11.5	9.7	10.9	11.3	18.3	15.5	22.7	13.3
MCZ 44747	M	47	83			6.5	7.2	6.6	11.3	9.7	13.9	7.5
CAS 220561	F	81.3	171	22.3	11.8	10	11.4	10.7	17.7	15.3	20.2	11.8
MBM-JBS 8312	F	71.1	148	19.9	10.9	9.1	9.9	10.4	16	14.2	19.6	11.8
Ptyctolaemus gularis												
CAS 225592	M	87.4	213	25.3	13.7	15	14.1	15.6	27.2	24.8	27.4	16.5
BM 1974.847	M	81.5	198	25	12	12.7	12.2	13.5	25.3	21.8	27.8	16.7
CAS 224733	M	79.8	209	23.9	12.6	13.4	13.3	13.6	22.9	21.1	26.4	14.6
CAS 226690	M	79.6	191	22.6	12.9	12.7	12.8	12.9	22.4	20.9	23.5	13.6
CAS 224704	M	76.5	188	23	12	12.3	12.6	12.6	20.1	19.5	25.2	14.3
CAS 224431	M	78	183	23.8	12.1	12.9	12	13.2	22.1	18.6	24.8	14.1
BM 1974.849	M	74	181	22.4	11.9	11.4	11.6	11	23.4	20.4	23	14.5
CAS 221433	M	73.2	177	21	11.8	118	12	12.8	21.1	19.3	25.5*	14.8*
FMNH 42675	M	72.5	181	22.1	11.5	12.7	13	11.7	22.7	21.8	24.8	14.1
BM 1946.8.1.14	M	70.7	161	22.2	11.3	11.5	12.3	10.3	20.3	18.4	23.1	13
ZMB 5004 Holotype	M	65.7	153	18.6	10.9	9.1	10.1	10.4	17.8	14.6	18.9	11.8
USNM 123425	M	56.1	124	15.9	9.2	7.6	7.6	9	15.4	13.8	17.4	9.8
CAS 226687	M	45.1	100	12.7	7.5	6.6	7.8	8.2	13.1	11.5	14	8.9
MBM-JBS 17893	F	77.9	201	22.1	12.5	11.9	11.9	12.6	24	20.6	26.1	15.8
BM 1974.846	F	75	177	20.9	10.9	10.3	10.1	10	19.4	18.7	20.9	11.8
BM 1974.848	F	72.1	170	18.2	11.1	11.4	10.7	11.4	20.9	20	24	14.2
CAS 224652	F	71.4	169	20.5	11.9	10.6	11.2	11.2	19.6	18.2	21.9	12.5
MBM-JBS 18089	F	71	162	22.3	11.8	10	11.6	10	20.2	17.5	21.1	12.5
CAS 226688	F	70.2	184	20.2	11.4	11.1	12.6	11.5	21.2	19.1	22.7	14.4
CAS 226689	F	66.9	157	18.8	11.1	9.8	10.4	10.8	18.4	16.6	20	12.2
CAS 221297	F	62.1	144	18.4	10.1	10.7	9.1	12	18.6	17.8	22.2	13.5
CAS 221296	F	61.7	162	18.7	10.2	11.2	12.1	11.2	19.4	18.4	23.2	13.7
CAS 221515	F	58	143	18.2	10.2	8.9	9.6	9.7	15.3	16.2	19.3	11.7
CAS 226691	F	48.8	125	12.5	8.7	8.6	8.3	8.5	14.2	13.5	16.9	10.8

TABLE 3. Sex and meristic characters for *Ptyctolaemus collicristatus* sp. nov. and *P. gularis*.

	SEX	MidB	VentSR	NuchalC	SupL (L/R)	InfL (L/R)	SDL
Ptyctolaemus collicristatus							
CAS 227489 Holotype	M	82	77	16	7/9	8/8	28
CAS 219991	M	78	64	15	8/8	8/7	28
USNM 559811	M	87	80	15	8/9	8/8	29
CAS 220560	M	76	84	15	8/7	8/8	34
MBM-JBS 8195	M	83	75	15	8/7	8/8	30
MCZ 44747	M	75	74	15	7/7	8/8	28
CAS 220561	F	76	74	15	9/8	8/9	30
MBM-JBS 8312	F	85	81	15	10/8	9/9	30
Ptyctolaemus gularis							
CAS 225592	M	111	81	30	8/8	9/8	34
BM 1974.847	M	106	77	20	9/9	9/9	38
CAS 224733	M	104	75	22	8/8	7/8	32
CAS 226690	M	111	73	18	8/8	8/7	31
CAS 224704	M	102	74	24	8/9	8/9	31
CAS 224431	M	101	72	21	8/8	7/7	36
BM 1974.849	M	108	73	19	9/9	9/9	37
CAS 221433	M	89	66	21	8/8	7/8	30*
FMNH 42675	M	96	80	22	9/8	9/9	30
BM 1946.8.1.14	M	91	78	24	7/8	8/8	33
ZMB 5004 Holotype	M	90	76	24	7/8	9/8	34
USNM 123425	M	81	75	18	8/9	9/9	30
CAS 226687	M	100	68	17	8/7	8/8	31
MBM-JBS 17893	F	96	67	18	9/10	10/9	35
BM 1974.846	F	90	79	16	8/8	8/8	30
BM 1974.848	F	89	75	17	8/9	8/8	34
CAS 224652	F	96	72	14	7/8	7/8	30
MBM-JBS 18089	F	88	75	15	8/8	8/8	33
CAS 226688	F	102	70	20	8/8	9/9	35
CAS 226689	F	86	84	15	7/7	8/8	30
CAS 221297	F	92	70	14	7/7	7/9	33
CAS 221296	F	94	73	15	7/7	8/7	34
CAS 221515	F	94	76	16	8/9	8/9	32
CAS 226691	F	81	71	15	8/8	8/8	34

TABLE 4. Sex and body proportions for *Ptyctolaemus collicristatus* sp. nov. and *P. gularis*.

	SEX	SVL:TailL	HeadW:HeadL	HeadL:SVL	HeadW:SVL	UarmL:SVL	ForeaL:SVL	ThighL:SVL	CrusL:SVL
Ptyctolaemus collicristatus									
CAS 227489 Holotype	M	1.99	0.54	0.27	0.14	0.13	0.14	0.23	0.18
CAS 219991	M	2.1	0.52	0.28	0.14	0.12	0.16	0.24	0.2
USNM 559811	M	1.97	0.55	0.27	0.15	0.13	0.14	0.22	0.19
CAS 220560	M	2.13	0.52	0.28	0.15	0.14	0.15	0.23	0.21
MBM-JBS 8195	M	1.77	0.54	0.28	0.15	0.13	0.14	0.24	0.2
MCZ 44747	M	1.77				0.14	0.15	0.24	0.21
CAS 220561	F	2.1	0.53	0.27	0.14	0.12	0.14	0.22	0.19
MBM-JBS 8312	F	2.08	0.55	0.28	0.15	0.13	0.14	0.24	0.2
Ptyctolaemus gularis									
CAS 225592	M	2.44	0.54	0.29	0.16	0.17	0.16	0.31	0.28
BM 1974.847	M	2.43	0.48	0.31	0.15	0.16	0.15	0.31	0.27
CAS 224733	M	2.62	0.53	0.3	0.16	0.17	0.17	0.29	0.26
CAS 226690	M	2.4	0.57	0.28	0.16	0.16	0.16	0.28	0.26
CAS 224704	M	2.46	0.52	0.3	0.16	0.16	0.17	0.26	0.25
CAS 224431	M	2.35	0.51	0.31	0.16	0.17	0.15	0.28	0.24
BM 1974.849	M	2.45	0.53	0.3	0.16	0.15	0.16	0.32	0.28
CAS 221433	M	2.42	0.56	0.29	0.16	0.16	0.16	0.29	0.26
FMNH 42675	M	2.5	0.52	0.3	0.16	0.18	0.18	0.31	0.3
BM 1946.8.1.14	M	2.28	0.51	0.31	0.16	0.16	0.17	0.29	0.26
ZMB 5004 Holotype	M	2.33	0.58	0.28	0.17	0.14	0.15	0.27	0.22
USNM 123425	M	2.21	0.57	0.28	0.16	0.14	0.14	0.28	0.25
CAS 226687	M	2.22	0.59	0.28	0.17	0.15	0.17	0.29	0.26
MBM-JBS 17893	F	2.58	0.56	0.28	0.16	0.15	0.15	0.31	0.27
BM 1974.846	F	2.36	0.52	0.28	0.14	0.14	0.13	0.26	0.25
BM 1974.848	F	2.36	0.61	0.25	0.15	0.16	0.15	0.29	0.28
CAS 224652	F	2.37	0.58	0.29	0.17	0.15	0.16	0.27	0.25
MBM-JBS 18089	F	2.28	0.53	0.31	0.17	0.14	0.16	0.28	0.25
CAS 226688	F	2.62	0.56	0.29	0.16	0.16	0.18	0.3	0.27
CAS 226689	F	2.35	0.59	0.28	0.17	0.15	0.16	0.28	0.25
CAS 221297	F	2.32	0.55	0.3	0.16	0.17	0.15	0.3	0.29
CAS 221296	F	2.63	0.54	0.3	0.16	0.18	0.2	0.31	0.3
CAS 221515	F	2.47	0.56	0.31	0.17	0.15	0.17	0.26	0.28
CAS 226691	F	2.56	0.69	0.26	0.18	0.18	0.17	0.29	0.28

brown (darker than ventrals); scales in center of gular pouch lighter than anterior gular scales; scales between gular folds gray or with dark brown spotting, giving appearance of fold recesses being dark brown or black. Dorsal portion of body with a base color of grayish brown; dorsal crest scales chocolate brown; lateral scales gray brown with black spotting; enlarged interspersed lateral scales with dark brown on trailing edge, less so ventrally. Dorsal portion of limbs are brown, more so than body (dorsal); posterior portion of thighs lighter brown; ventral surface of limbs, hands, feet, cream colored (lighter than gular scales anterior to gular pouch). Dorsal portion of tail like body; ventral basal third of tail light brown becoming darker brown toward tip.

COLOR IN LIFE (Fig. 5). Based on color transparency (Fuji Provia 100 AF film) of anterior portion of body. Head a uniform pale grayish brown; iris yellow-brown; two parallel brown stripes radiating diagonally from eye, darker anterior stripe reaching posterior margin of jaw, posterior stripe about half the length of anterior stripe; gular pouch bright yellow medially with greenish-yellow and dark brown laterally. Dorsal portion of body mottled or forming irregular dark brown saddles on pale grayish brown; flanks with a base color of grayish brown anteriorly becoming a yellowish brown posteriorly; brown reticulations on flanks from above shoulder continuing posteriorly. Forelimbs mottled with light and dark brown.

VARIATION.— Body measurements, meristic characters and body proportions for holotype and paratypes of *Ptyctolaemus collicristatus* sp. nov. are presented in Tables 2–4, respectively. Coloration is determined from alcohol preserved specimens. Paratypes are similar to holotype in most respects except as noted below.

CAS 219991 (adult male); four equal-sized postrostrals; series of four enlarged, keeled scales form an inverted 'Y'-shaped pattern on middle of snout, first two anterior scales on midline, pointing posteriorly, posterior to second scale is one scale on either side directed diagonally toward superciliary ridge; temporal area with two enlarged, slightly conical, scales, first between circular group of scales adjacent to occiput and horizontal enlarged scales posterior to orbit, second horizontal and posterior to first, separated by three or four scales. Three chin shields posterior to postmentals on each side that run parallel to infralabials, first two chin shields separated from infralabials by one scale row, third separated by two scales. Nuchal crest composed of 15 erect, compressed, triangular scales, longest nuchal scale extends vertically 0.75 mm from its base. Midventral incision from tissue removal.

Dorsal body appears dull, grayish brown. Snout a uniform gray brown; barring on head similar to holotype except posterior bar reduced to dark brown mottling in parietal area; lateral scales gray brown with black spotting on trailing edge of most scales.

CAS 220560 (adult male); five postrostral scales with medial scale being largest; 'Y'-shaped pattern on snout comprised of six enlarged scales, three medial to each other followed by one diagonal scale on left and two on right side. Postmental is followed by five enlarged chin shields on either side; gular folds indistinct, probably from being extended and flattened during formalin fixation. Nuchal crest pronounced, largest nuchal crest scale 1.3 mm. Midventral incision from tissue removal.

Overall body coloration similar to holotype; only anterior stripe radiating from eye distinct; dorsum interspersed with dark brown scales, vague pattern of four saddles.

CAS 220561 (adult female); five postrostral scales with medial being largest; 'Y'-shaped pattern on snout consists of five enlarged keeled scales, three along midline and posterior two, smaller and less pronounced, pointing diagonally toward superciliary ridge. Postmentals separated by two scales posterior to mental; three enlarged chin shields on left side, two on right; gular pouch indistinct, two gular folds on either side of midline. Nuchal crest low, largest scale 0.56 mm. Midventral incision from tissue removal.

Superoculars light with perpendicular dark bars on anterior and posterior edge; two brown stripes radiating from eye, anterior stripe reaching below angle of jaw by 7 scales, posterior strip reaching four scales behind orbit; area between orbit and upper labials light tan; gular pouch uniform cream colored with a few light brown scales, scales in folds cream colored; flanks with a reticulated pattern of dark brown on light brown; ventral coloration uniform light tan or cream colored except for posterior portion of tail being darker.

USNM 559811 (adult male); 'Y'-shaped pattern on snout consists of seven raised scales, three along midline and two scales on either side of third scale pointing diagonally toward superciliary ridges, anterior scale of diagonal scales smaller than posterior; five postrostral scales. Postmentals separated by two scales medially; four enlarged chin shields on left side and three on right; two gular folds on either side of midline. Largest nuchal crest scale 0.73 mm. Midventral incision from tissue removal.

Overall appearance is light brown gray. Upper head coloration uniform, head without barring over superciliary scales; dorsal scales of body darker brown than lateral scales; gular pouch with dark brown and gray scales in folds; ventral coloration uniform cream colored.

MBM-JBS 8195 (adult male); five postrostral scales with medial scale being largest; 'Y'-shaped pattern on snout comprised of five enlarged scales, three medially followed by one diagonal scale on each side. Postmentals touching, followed by three enlarged chin shields on either side; gular pouch with two folds. Largest nuchal crest scale 1.1 mm.

Only one faint gray bar across anterior superoculars is present.

MBM-JBS 8312 (adult female); six postrostral scales, distal and medial scales largest; 'Y'-shaped pattern on snout comprised of seven enlarged scales, three medially followed by two diagonal scales on each side. Three enlarged chin shields present on either side; three indistinct gular folds on each side.

Head has faint barring, posterior edge of anterior bar dark, posterior bar darkest in parietal area. Body is mostly light gray with dorsal scales darker than lateral scales.

MCZ 44747 (subadult male); 'Y'-shaped pattern on snout comprised of five enlarged scales, three medially, followed by one diagonal scale on each side. Two gular folds.

General coloration of dorsum is light brown with five light bars on back. Flanks have reticulated pattern.

CAS 220033 (juvenile), SVL 29.5 mm, TailL 61 mm; five postrostral scales; 'Y'-shaped pattern on snout consists of five enlarged scales, three along midline and one on either side of third scale pointing diagonally. Two gular folds on either side of midline. Fifteen enlarged nuchal crest scales.

Upper head with two wide dark brown bars, anterior bar between middle portion of superciliaries, posterior bar, 'V'-shaped, outer margins crossing posterior portion of superciliaries; two stripes radiating diagonally from eye, anterior stripe continuing on to neck. Gular cream colored, speckled with black or dark brown. Dorsum with three indistinct brown saddles, one on neck and two on anterior portion of body; body grayish. Limbs mottled with light and dark brown.

Sexual dimorphism.— The main external morphological difference between males and females is the distinct gular pouch in males whereas in females the pouch is absent, although faint gular folds are still present. Males also have a more developed, higher, nuchal crest.

Etymology.— The specific epithet is derived from the Latin "collum" meaning neck and "cristatus" meaning crested and refers to the nuchal crest.

Natural history and distribution.— *Ptyctolaemus collicristatus* has thus far only been found on the slopes of Mt. Victoria, Chin State, Myanmar (Fig. 11). Although thorough surveys in Chin State have not been conducted, recent (July–August, 2003) surveys carried out by the

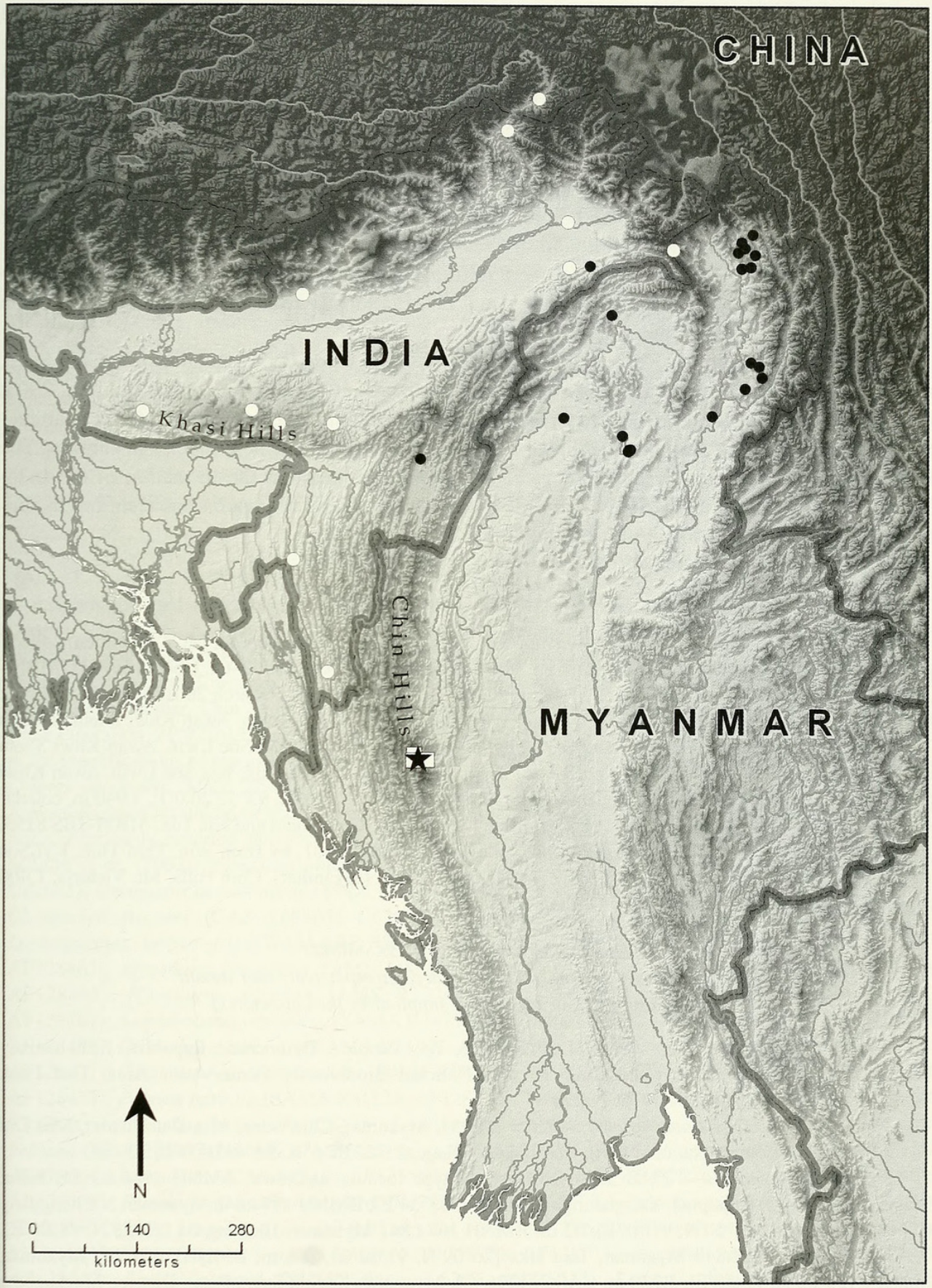


FIGURE 11. Map showing the distribution of *P. collicristatus*, sp. nov. (open squares with the type locality represented by a star) and *Ptyctolaemus gularis* (closed circles represent specimens examined; open circles represent literature records [Boulenger 1890; Wall 1908; Huang 1980; Mathew 1995; Pawar and Birand 2001]). Map prepared by Michelle S. Koo.

Myanmar Herpetological Survey team in the vicinity of Hakha (northern Chin State) failed to find individuals of either species of *Ptyctolaemus*. All specimens of *P. collicristatus* were found in dry mountain forest with deciduous hardwoods and pine between elevations of 790 m and 1,940 m. All specimens were found in areas of secondary forest in close proximity to human habitation. Two specimens were found on trees approximately 2 m above ground, the others were active on the ground.

The CAS specimens of *P. gularis* from Kachin State and Sagaing Division were collected in subtropical evergreen forest, in vegetation, 1–4 m above ground. Smith (1940) also reported that specimens from Kachin State were found in trees and bushes.

The distribution of *P. gularis* in southern northeastern India (Fig. 11) is in close proximity to *P. collicristatus*. These localities represent visual observations (Pawar and Birand 2001) and can not been confirmed by the authors.

Although the Myanmar Herpetological Survey has only made two excursions into Chin State, the collections have resulted in three new species of lizards (*Calotes chincollium* Vindum, 2003; *Cyrtodactylus gansi* Bauer, 2003 and *Ptyctolaemus collicristatus*, sp. nov.). Preliminary examination of other specimens from these collections includes a possible five new species of anurans. The number of new and possibly endemic species supports the idea that the formation of the Indo-Burman Range caused disruption of gene flow among closely allied populations resulting in subsequent vicariant speciation (Vindum et al. 2003).

Material examined

Ptyctolaemus collicristatus sp. nov.— Paratypes (7 specimens). All (except for MCZ specimen) collected from Myanmar, Chin State, Min Dat District, Min Dat Township. **CAS 220560–61**, **USNM 559811**, **MBM-JBS 8312**, 21°22′20.1″N, 93°58′34.6″E, 1,482 m: CAS 220560 collected 16 March 2001, by Kyi Soe Lwin; CAS 220561 collected 18 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; USNM 559811, collected 19 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; MBM-JBS 8312, collected 5 April 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; CAS 219991, from Baw Khue Plantation, 21°23′ 20.9″N, 93°52′20.0″E, 1,940 m, collected 19 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; **MBM-JBS 8195**, 21°26′4.6″N, 93°49′29.6″E, 1,663 m elevation, collected 23 March 2001, by Htun Win, Thin Thin, Kyi Soe Lwin, Awan Khwi Shein and Hla Tun; **MCZ 44747** from Burma [Myanmar], Chin Hills, Mt. Victoria, 1,400 m elevation, collected 1 July 1938 by G. Heinrich.

Additional Material Examined

Geocoordinates in brackets were added retrospectively and should not be considered original data supplied by the collector(s).

Mantheyus phuwuanensis.— FMNH 262581–82, Lao People's Democratic Republic, Bolikhamxay Province, Thaphabat District, Phou Khao Khouay National Biodiversity Conservation Area, That Leuk Waterfall, 18°23′42″N, 103°04′17″E, 200 m.

Ptyctolaemus collicristatus sp. nov.— CAS 220033, Myanmar, Chin State, Min Dat District, Min Dat Township, Nat Ma Taung National Park, Hee Laung Village, 21°22′07.6″N, 93°49′04.0″E, 709 m.

Ptyctolaemus gularis.— ZMB 5004 (Holotype), type locality unknown; BMNH 1946.8.1.14, India, Manipur, 22.5 km N of Imphal, Kanglatongbi [24°59′N; 93°54′E]; BMNH 1974.846 Myanmar, N Chengyang [if N'Chang Yang = 25°50′N, 97°48′E], 62 m; BMNH 1974.847 Myanmar, Hkawng Ga [25°58′N, 98°00′E], 1,311 m; BMNH 1974.848 Myanmar, Tara Hka [26°09′N, 97°52′E], 366 m; BMNH 1974.849 Myanmar, Mahtum [26°06′N, 97°58′E], 1,220 m; CAS 221296–97, Myanmar, Kachin State, Putao District, Machanbaw Township, between Alonga and Ahtonga, 27°16′51.3″N, 97°45′31.8″E; CAS 221433, Myanmar, Kachin State, Putao District, Naung Mon Township, Aureinga camp, 27°17′49.8″N, 97°51′58.1″E; CAS 221515, Myanmar,

Kachin State, Putao District, Naung Mon Township, Rabaw, 27°26′28.4″N, 97°55′07.5″E; CAS 224431, Myanmar, Kachin State, Putao District, Nagmung Township, Hkakabo Razi National Park, between Pannandin Village and Shin San Ku camp, 27°41′07.7″N, 97°53′38.6″E, 1,188 m; CAS 224652, Myanmar, Kachin State, Putao District, Nagmung Township, Nagmung Town, 27°31′22.5″N, 97°47′56.1″E, 569 m; CAS 224704, Myanmar, Kachin State, Putao District, Nagmung Township, between Kasanku Village and Hton Hlar Village, 27°35′31.3″N, 97°45′25.4″E, 573 m; CAS 224733, Myanmar, Kachin State, Putao District, Nagmung Township, Ma Za camp, 27°28′06.8″N, 97°42′59.5″E, 976 m; CAS 225240, Myanmar, Kachin State, Putao District, Nagmung Township, Au Yin Ga camp, 27°17′51.4″N, 97°51′57.1″E; CAS 225592, Myanmar, Sagaing Division, Hkamti Township, Htamanthi Wildlife Sanctuary, beside Natesu stream, 25°28′46.0″N, 95°37′13.5″E; CAS 226687, Myanmar, Kachin State, Hukaung Valley Wildlife Sanctuary, 26°42′40.8″N, 96°11′35.6″E, 308 m; CAS 226688, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, Hepu stream, 25°05′20.5″N, 96°24′16.1″E, 253 m; CAS 226689, Myanmar, Kachin State, Mohynyin Township, Indawgyi Wildlife Sanctuary, Kyar Phu stream, 25°04′28.4″N, 96°23′30.8″E, 268 m; CAS 226690, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, 25°05′55.5″N, 96°25′11.0″E, 652 m; CAS 226691, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, 25°15′44.6″N, 96°19′20.1″E, 172 m; MBM-JBS 17893, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, Hepu stream, 25°05′31.5″N, 96°24′06.0″E, 246 m; MBM-JBS 18089, Myanmar, Kachin State, Mohnyin Township, Indawgyi Wildlife Sanctuary, Hepu stream, 25°05′25.2″N, 96°24′18.2″E, 263 m; FMNH 42675, Myanmar, Kachin State, Myitkyina District, Myitkyina [25°30′N, 97°24′E]; USNM 123425, India, 12 mi E Ledo [27°18′N, 95°56′E].

Material examined in phylogenetic analyses

Newly reported sequences are: *Mantheyus phuwuanensis,* Lao PDR, Bolikhamxay Province, Thaphabat District, Phou Khao Khouay National Biodiversity Conservation Area, near That Xay waterfall, 18°27'N, 103°10'E, 300 m (FMNH 255495; GB AY555836); *Ptyctolaemus gularis,* Myanmar, Kachin State, Putao District, Naung Mon Township, Rabaw, 27°26′28.4″N, 97°55′07.5″E (CAS 221515, GB AY555838), *P. collicristatus,* Myanmar, Chin State, Min Dat District, Min Dat Township, Nat Ma Taung National Park, Baw Khue Plantation, 21°22′20.1″N, 93°58′34.6″E (USNM 559811, GB AY555837). Several corrections are made to the identifications as reported in Macey et al. (2000). *Calotes emma* (MVZ 222144) is *Calotes mystaceus*; *Calotes versicolor* (MVZ 224102) is *Calotes emma*; sequences reported as *Bronchocela cristatella* and *Aphaniotis fusca* should be switched, that is AF128495 is *Bronchocela cristatella* and AF128497 is *Aphaniotis fusca*. Previously reported sequences used here are reported in Macey et al. (1997a,b, 1998b, 2000) and Schulte et al. (2002): *Basiliscus plumifrons* (MVZ 204068, U82680); *Oplurus cuvieri* (MVZ-RM10468, U82685); *Uromastyx acanthinurus* (MVZ 162567, U71325); *Chamaeleo dilepis* (CAS 168922, AF128460); *Chamaeleo fischeri* (CAS 168965, U82688); *Physignathus cocincinus* (MVZ 222159, U82690); *Lophognathus longirostris* (WAM-ERP-R29940, AF128462); *Physignathus lesueurii* (SAMA R33417, AF128463); *Hypsilurus modestus* (AMS R122434, AF128464); *Chelosania brunnea* (AMS R140288, AF128465); *Hypsilurus dilophus* (AMS R122449, AF128466); *Moloch horridus* (SAMA R38770, AF128467); *Amphibolurus muricatus* (SAMA R34770, AF128468); *Chlamydosaurus kingii* (SAMA R34531, AF128469); *Ctenophorus decresii* (SAMA R31008, AF128470); *Ctenophorus adelaidensis* (SAMA R40929, AF128471); *Caimanops amphiboluroides* (WAM R104419, AF128472); *Diporiphora bilineata* (QM J46161, AF128473); *Pogona barbata* (SAMA R41126, AF128474); *Tympanocryptis lineata* (SAMA tissue collection R35B06, voucher may be lost, AF128475); *Leiolepis guentherpetersi* (MVZ 222157, AF128461); *Leiolepis belliana* (MVZ 215497, U82689); *Hydrosaurus* sp. (TNHC 54902, AF128476); *Agama agama* (CAS 199007, AF128504); *Agama atra* (CAS 193436, AF128505); *Agama bibroni* (MVZ-FC501201, voucher frozen whole, AF128506); *Pseudotrapleus sinaitus* (BMNH 1996.201, AF128507); *Trapelus ruderatus* (NHMG Re. ex. 5212, AF128508); *Trapelus agilis* (NHMG Re. ex. 5210, AF128509); *Trapelus persicus* (NHMG Re. ex. 5211, AF128510); *Trapelus sanguinolentus* (CAS 179758, AF128511); *Trapelus savignii* (MVZ RM10471, AF128512); *Laudakia nupta* (NHMG Re. ex. 5209, AF128513); *Laudakia tuberculata* (ZIL 20697.1, AF128514); *Laudakia sacra* (CAS 170554, AF128515); *Laudakia stellio* (MVZ-RM10494, AF128516); *Phrynocephalus interscapularis* (CAS 179151, AF128517); *Phrynocephalus mystaceus* (CAS 179754,

AF128518); *Phrynocephalus raddei* (CAS 179770, U82691); *Laudakia lehmanni* (CAS 183009, AF028677); *Laudakia himalayana* (CAS 183016, AF028676); *Laudakia stoliczkana* (CAS 167878, AF128519); *Laudakia microlepis* (NHMG Re. ex. 5135, AF028678); *Laudakia caucasia* (CAS 184650, AF028683); *Laudakia erythrogastra* (CAS 184400, AF028680); *Draco blanfordii* (MVZ 222156, AF128477); *Japalura tricarinata* (CAS 177397, AF128478); *Japalura variegata* (ZIL 20922, AF128479); *Aphaniotis fusca* (TNHC 57874, AF128497); *Bronchocela cristatella* (TNHC 57943, AF128495); *Gonocephalus grandis* (TNHC 56500, AF128496); *Cophotis ceylanica* (WHT 2061, AF128493); *Lyriocephalus scutatus* (WHT 2196, AF128494); *Ceratophora aspera* (WHT 1825, AF128491); *Ceratophora karu* (WHT 2259, AF128520); *Ceratophora tennentii* (WHT 1633, AF128521); *Ceratophora erdeleni* (WHT 1808, AF128522); *Ceratophora stoddartii* (WHT 1512, AF128492); *Acanthosaura capra* (MVZ 222130, AF128498); *Acanthosaura lepidogaster* (MVZ 224090, AF128499); *Japalura flaviceps* (MVZ 216622, AF128500); *Japalura splendida* (CAS 194476, AF128501); *Pseudocalotes brevipes* (MVZ 224106, AF128502); *Pseudocalotes larutensis* (previously reported as *Pseudocalotes flavigula* – TNHC 58040, AF128503); *Salea horsfieldii* (BNHS-AMB5739, AF128490); *Otocryptis wiegmanni* (WHT 2262, AF128480); *Sitana ponticeriana* (WHT 2060, AF128481); *Calotes emma* (MVZ 224102, AF128489); *Calotes mystaceus* Vietnam (MVZ 222144, AF128487); *Calotes mystaceus* Myanmar (CAS 204848, AF128488); *Calotes calotes* (WHT 1679, AF128482); *Calotes ceylonensis* (WHT 1624, AF128483); *Calotes liocephalus* (WHT 1632, AF128484); *Calotes liolepis* (WHT 1808, AF128485); *Calotes nigrilabris* (WHT 1680, AF128486).

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