



Range extension of the rare agamid, *Pseudocalotes austeniana* (Annandale, 1908) (Reptilia, Sauria, Draconinae) in the East Himalaya, with comments on its ontogenetic shift

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Abstract

Despite its recognition since the early 1900s, the agamid lizard *Pseudocalotes austeniana* remains known based on 3 vouchered specimens only from the East Himalaya, and little is known about its general biology. During herpetological surveys of Tibet, China, we collected 3 specimens of *P. austeniana* from Medog County, southeastern Tibet, including the first juvenile specimen ever vouchered. We provide a detailed description based on new material of this enigmatic species, report on a range extension of 400 km northeastward from its type locality, its ontogenetic shift, and clutch size.

Key words

Agamidae, Himalaya, *Mictopholis*, *Salea*, synonym.

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Introduction

The Subfamily Draconinae represents a diverse group of agamid lizards in Asia (Manthey 2010). Although studies have shed light on higher-level phylogenetic relationships among genera within Draconinae (Moody 1980, Macey et al. 2000, Grismer et al. 2016, Wang et al. 2019), the taxonomic status of many species remains unknown, in part due to a lack of vouchered specimens and tissue samples. One such case of a poorly understood species is the enigmatic Abhor Hills Agama, *Pseudocalotes*

austeniana (Annandale, 1908), from the East Himalaya.

First described as *Salea austeniana* from the East Himalaya (Annandale 1908), the Abhor Hills Agama was later transferred to its own monotypic genus, *Mictopholis* by Smith (1935). Using morphological data, Mahony (2010) synonymized the monotypic genus as a junior synonym of *Pseudocalotes* Fitzinger, 1843. Due to the political difficulty of working in the region, and difficult terrain to access and navigate, few biodiversity surveys have been done near the type locality of the species since its original description (Agarwal et al. 2010,

Li et al. 2010). As a result, only 6 individuals of *P. austeniana* have even been recorded in the literature, all of which were from the vicinity of the type locality (Venugopal 2013). Furthermore, only 2 of these 6 individuals were ever vouchered (Athreya 2006, Das and Das 2007, Agarwal et al. 2010, Venugopal 2010, 2013). Therefore, to date, little is known about the biology or ecology of this agamid lizard species, including phenotypic variation and its distribution range, and the species is thought to be restricted to the vicinity of its type locality (Das and Das 2007).

During herpetological surveys in 2011, 2013, and 2016, we collected 2 adult females and a juvenile specimen of *P. austeniana* from southeastern Tibet, PR China, about 400 km (linear distance) northeastward from the most easterly known locality of the species (Venugopal 2013). In addition, we photographed another adult and juvenile from the same region in Tibet. Here we describe the specimens of this rare agamid species from this new locality and report on its morphological variation, including ontogenetic shifts in morphology. An expanded description of the species is provided based on the new material.

Methods

Field surveys and taxonomic sampling. Museum abbreviations for specimens examined follow Sabaj (2016) and include: California Academy of Sciences (CAS), USA; Chengdu Institute of Biology, Chinese Academy of Sciences (CIB), China; Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ), and Zoological Survey of India (ZSI). In addition, Arya Vidyapeeth College, India was abbreviated as MAVC, following Mahony (2010), and Tibetan Museum of Natural History was abbreviated as TMNH.

Three specimens of *P. austeniana* were collected and vouchered from Medog County, Nyingchi Prefecture, southeastern Tibet, China, including a juvenile (KIZ 06777) and 2 adult females (KIZ 013873, TMNH 20170001). The juvenile was collected by locals in June 2011. Specimen KIZ 013873 was collected by Ke JIANG and Kai WANG from 80K, Medog County, Tibet, China (29°39'39" N, 095°29'25" E, WGS 84) in August 2013 and TMNH 20170001 was collected by Ping CI, Shiyang WEN, and Weidong ZHU from Medog Township, Medog County, Tibet, China (29°19'14" N, 095°19'03" E) on 15 June 2017. Both adult specimens were fixed in 10% buffered formalin and transferred to 70% ethanol for long-term storage, while the juvenile was preserved and stored in 75% ethanol.

In addition to the vouchered material, an adult and juvenile specimen were photographed by Chao WU and Zheng SHI from the same county in Tibet, but not vouchered. All visible morphological characteristics were recorded based on photographs and recorded notes in the field, including dorsal and lateral pholidosis characteristics and coloration in life.

Representatives of other *Pseudocalotes* species were examined for morphological comparisons (Appendix). For the type and topotypic specimens of *P. austeniana* and comparative genera that we do not have access to, morphological data were obtained from published literature (Smith 1935, Mahony 2010, Denzer et al. 2015).

Morphological Data. For maximum comparability, we selected and measured morphological characters based on Manthey (2010) (morphometric data were measured using a digital caliper to the nearest 0.01mm by KW). The following morphological characters were examined, with abbreviations provided in parentheses: snout-vent length (SVL); tail length (TAL); head width (HW); head length (HL); head depth (HD); interorbital distance (IO); maximum diameter of orbit (OrbD); maximum diameter of tympanum (TymD); trunk length from axilla to groin (TrL); Finger IV length (F4L); Toe IV length (T4L); distance from tip of snout to insertion of fore-limb (SnForeL); hand length (HandL); upper arm length (UpArmL); lower arm length (LowArmL); upper leg length (UpLegL); crus length (CrusL); foot length (FootL); number of supralabials (SL); number of infralabials (IL); number of mid-dorsal scales (MD); circum-marginal scale row count at midbody (MB); subdigital lamellae count beneath Finger IV (F4S); and subdigital lamellae count beneath Toe IV (T4S). All paired measurements were recorded for the left side only, and paired pholidosis counts are given in left/right order.

Furthermore, the following morphological characteristics, which were not used in Mahony (2010) but have been shown to be useful in taxonomic studies of agamid reptiles (Wood Jr et al. 2009, Wang et al. 2016), were also recorded, including: snout length (SEL), length of snout measured from rostral to the anterior corner of eye; length of the longest nuchal crest (CL), length of the longest nuchal crest measured from the tip to the base; and suborbital scale rows (SOR), number of scale rows inferior to the lower edge of orbit, excluding the small granular scales around eyes. The total fore- and hind limb lengths were each the sum of three sections, respectively ($FLL = UpArmL + LowArmL + HandL$; $HLL = UpLegL + CrusL + FootL$). Descriptions of coloration in life are based on field notes, photographs of live specimens, and published accounts (Athreya 2006, Das and Das 2007, Manthey 2010).

Results

New records (Fig. 1). China: Tibet Autonomous Region: Nychi Prefecture: Medog County: 80K (29°39'39" N, 095°29'25" E, WGS 84), collected by Kai Wang, Ke Jiang, and Jing Che on August 10, 2013 (female, KIZ 013873).

China: Tibet Autonomous Region: Nychi Prefecture: Medog County: near Medog Township (29°19'14" N, 095° 19'03" E), collected by Ping Ci, Shiyang Wen, and Weidong Zhu on 15 June 2017 (female, TMNH 20170001).

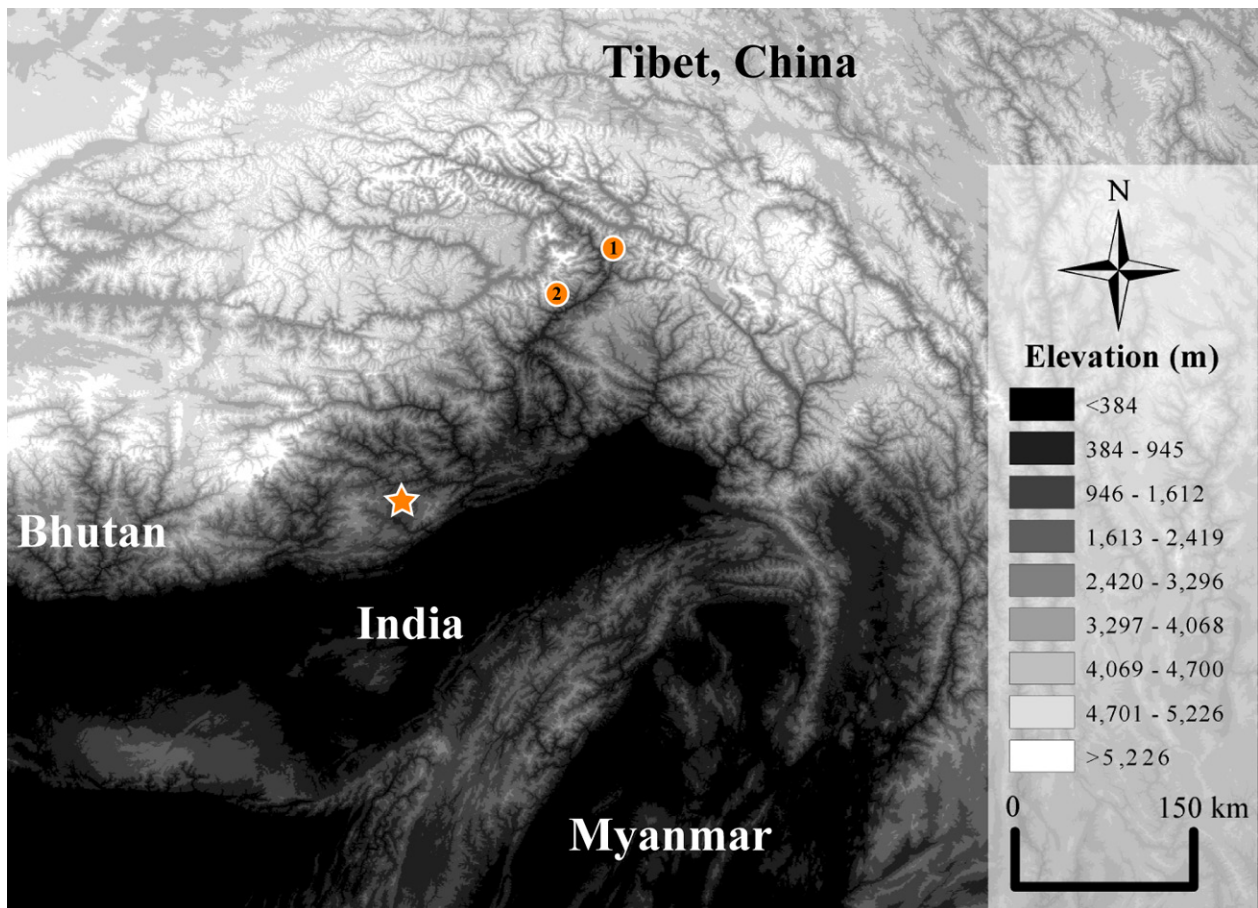


Figure 1. Distribution of *Pseudocalotes austeniana* in the East Himalaya. Orange star indicates the type locality of the species, and circles (1: 62K, Medog County; 2: Hanmi, Medog County) represent new localities for the species in Tibet, China.

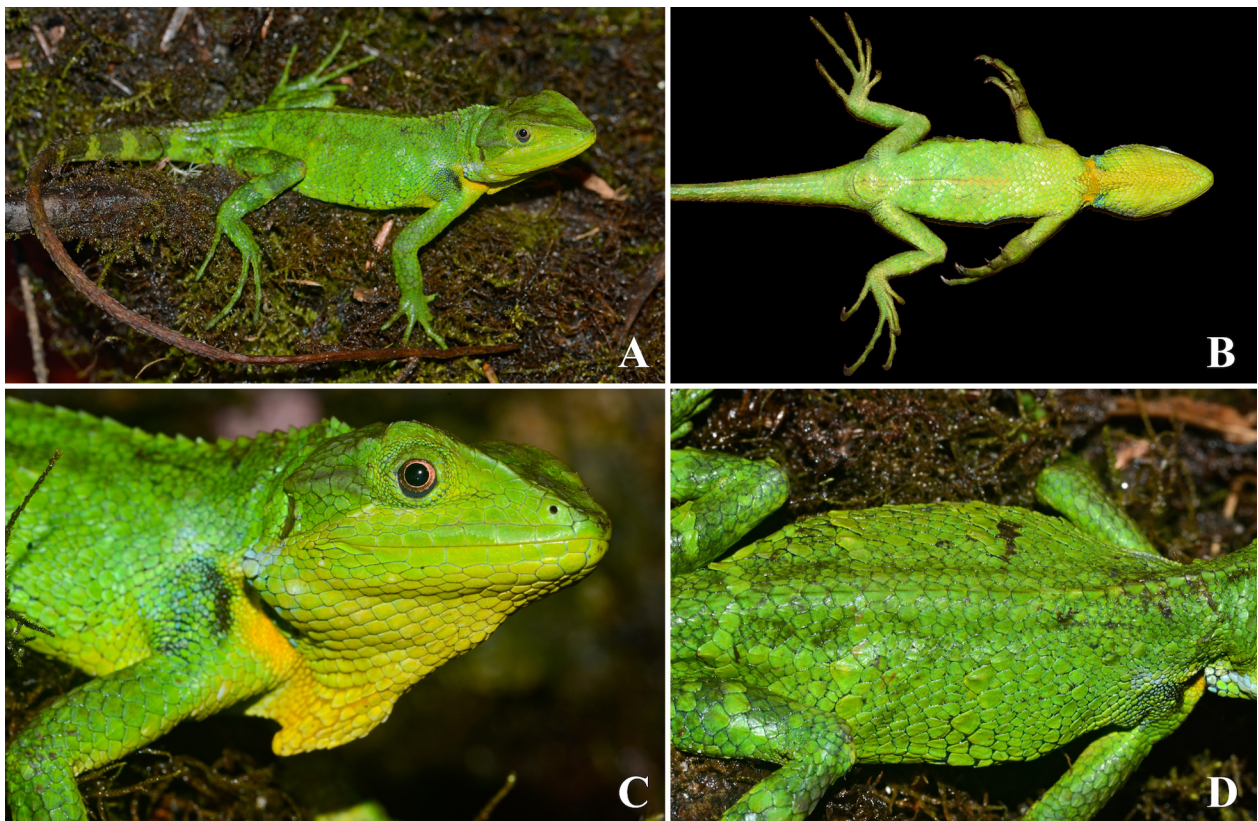


Figure 2. Adult female *Pseudocalotes austeniana* (KIZ 013873) in life. **A.** Dorsolateral view of body. **B.** Ventral view of body. **C.** Lateral, close-up view of head. **D.** Dorsal, close-up view of body. Photographs by Kai Wang.

China: Tibet Autonomous Region: Nychi Prefecture: Medog County: near Hanmi (29°21'54" N, 095°07'50" E), collected by locals on June 2011 (juvenile, KIZ 06777).

Identification. The recently collected adult and juvenile specimens from Tibet resemble closely the pholidosis characteristics of the vouchered holotype and topotypic specimen of *P. austeniana* (Table 1). In summary, these specimens are identified as *P. austeniana* based on the following morphological characters (following Mahony 2010): (1) tympanum exposed; (2) sub-ocular scale row singular, or multiple but one distinctively enlarged; (3) head robust, HW/HL > 59.7%, HD/HW > 72%, HD/HL > 43%; (4) distinct, strongly-developed cranial ridges present on dorsal and lateral surfaces of occipital region of head, forming rectangular, convex areas on temporal region of head and triangular concave area on posterior

lateral region of head; (6) postorbital and postoccipital spines absent; (7) nuchal crest in triangular shape or short lanceolate shape, not strongly differentiated from dorsal crests; (8) mid-dorsal scale count less than 39; (9) longitudinal gular fold present, highly developed in dewlap, with a distinct, pointy tip toward posterior end; (10) transverse gular fold absent; (11) dorsal scales heterogeneous in size and shape, flat, feebly keeled or smooth, arranged irregularly in most parts, some enlarged ones in approximate transverse rows; (12) enlarged scales of dorsum not arranged into clear dorsolateral or V-shaped rows; (13) ventral body scales smooth or feebly keeled, larger than background dorsal scales, distinctively heterogeneous in size and shape, irregularly arranged; (14) antehumeral fold present; and (15) axillary fold present.

For the morphometric data, the adults differed from

Table 1. Morphological data of *Pseudocalotes austeniana*. All morphometric measurements are in mm. Data of previously collected specimens (ZSI 3976, 24841, and MAVC L31) were taken from Mahony (2010). "—" indicates missing data from Mahony (2010) or due to difficulties in accurate measurements (poor specimen condition of the juvenile specimen KIZ 06777). "?" indicates missing data for one of the each paired pholidosis characters from Mahony (2010).

	ZSI 3976	MAVC L31	ZSI 24841	KIZ 013873	KIZ 06777	TMNH 20170001
Gender	F	F	M	F	Juvenile	F
SVL	93.4	87.4	86.6	85.33	47.25	83.67
TAL	226	191	215	177.33	114.46	189.00
HL	28.2	29.2	26.8	27.67	15.85	23.7
HW	17.6	17.6	16	17.31	10.64	15.29
HD	15.2	12.8	13.7	15.23	8.59	13.30
SnL	36.3	30.2	36.7	37.40	18.69	36.04
SEL	—	—	—	10.79	6.57	9.13
IN	6	—	5.7	5.16	3.23	4.59
IO	10.6	9.8	8.7	11.39	7.47	13.57
TymD	3.7	3	3.5	3.22	2.02	3.34
UpArmL	14.9	14.4	13.9	13.77	9.22	12.60
LowArmL	17.6	14.1	13.4	12.48	7.99	13.27
HandL	20	19.4	18.6	17.98	11.83	18.33
FLL	52.5	47.9	45.9	44.23	29.04	44.20
UpLegL	22.7	20.5	21.1	20.15	11.93	19.42
CrustL	22.1	20.3	20.4	18.09	11.67	18.30
FootL	36.3	34	32.7	29.78	17.99	30.77
HLL	81.1	74.8	74.2	68.02	41.59	68.49
F4L	—	—	—	11.73	8.03	11.43
T4L	22.9	21.8	20.6	19.18	12.86	19.77
TRL	29.7	45.1	35	35.85	—	40.26
CL	—	—	—	1.02	—	1.47
HW/HL	62.41%	60.27%	59.70%	62.56%	67.13%	64.51%
HD/HW	86.36%	72.73%	85.63%	87.98%	80.73%	86.98%
HD/HL	53.90%	43.84%	51.12%	55.04%	54.20%	56.12%
SEL/HL	—	—	—	39.00%	41.45%	38.52%
CL/HL	—	—	—	3.69%	—	6.20%
TAL/SVL	241.97%	218.54%	248.27%	207.82%	242.24%	225.89%
FLL/SVL	56.21%	54.81%	53.00%	51.83%	61.46%	52.83%
HLL/SVL	86.83%	85.58%	85.68%	79.71%	88.02%	81.86%
SL	5/6	6	7/8	7/7	7/6	6/6
IL	7/8	7	8	7/8	7/7	6/6
NSL	—	—	0/?	0	0	0
MB	51	53	—	50	—	52
MD	33	30	39	35	33	35
F4S	19/?	23/?	23/?	21/20	21/21	24/23
T4S	31/?	29/?	25/?	26/27	24/24	27/30
SOR	—	—	2/?	2/3	2/3	2/2



Figure 3. Photographed individuals of *Pseudocalotes austeniana* (not voucher) in Medog County, Nyinchi Prefecture, Tibet, China. **A.** Dorsal view of an adult female from 62K, Medog. **B.** Lateral view of the same adult female from 62K, Medog. **C.** Juvenile from Hanmi, Medog. Photographs by Chao Wu and Zheng Shi.

the juvenile specimen in the following characters: juvenile specimen has a more robust and less pointed head (HW/HL 67.13% vs HW/HL < 64.51%), indistinct nuchal crests and dorsal head ridges (vs distinct), and a less distinctive convex area on temporal region and the triangular concave area on posterior lateral region of head (vs. distinctively convex and concave regions on posterior dorsal and lateral regions of head). Additionally, coloration and ornamentation vary between juveniles and adults, with the juvenile specimen having less conspicuous color patterns than adults (Fig. 3). Specific color pattern differences include: juveniles possess Smoky White lip stripes (vs light green in adults), distinct olive brown to dark reddish brown radial stripes around the eyes (vs. absent or indistinct in adults), a brownish background coloration on the dorsal and lateral surfaces of the head, body, and limbs (vs light grass green in adults),

and distinct, light grass green transverse streaks on the lateral body and dorsal hind limb surfaces (vs absent in adults; Figs 3, 4).

The photographed but non-vouchered adult resembles the color patterns of the vouchered adult female specimens, except for having distinct green rectangular patches on the dorsal surface of its body (vs faint or absent; Fig. 3).

Description of recently collected adult females from Tibet. Moderate sized lizard, SVL 83.7–85.3 mm in females; body not compressed dorsally, reuleaux triangle in cross section; tail long, slender, TAL 207.8–225.9% SVL. Limbs moderate, FLL 51.8–52.8% SVL, HLL 79.7–81.9% SVL. Head moderate, HW 62.6–64.5% HL, HD 55.0–56.1% HL. Rostral rectangular, 4 times wider than high, in contact with 4 small scales excluding nasals and first supralabial; nasal large, irregular, pentagonal shape, bordered by 6/7 (left/right) scales including supralabials and rostral; supralabials 6 or 7, smooth, larger than proximal scales dorsally; infralabials 6–8, smooth, roughly same size as supralabials; loreal region slightly concave; loreals heterogeneous in size and shape, smooth or bearing feeble keels; suborbital scales smooth, in 2 or 3 rows above fifth supralabial, middle row (if in 3) or posterior most row (if in 2) enlarged; orbit scales surrounding eyes fine, granular, larger when in direct contact with eyes; supraciliaries imbricate, overlapping $\frac{2}{5}$ to $\frac{1}{5}$ of posterior scale; canthus ridges prominent, raised, running from one scale posterior to nasal to point in line with posterior edge of orbits; 2 enlarged, keeled scales present posterior to orbit, posterodorsal to last supraciliaries, conical oval in shape; tympanum large, exposed, oval in shape, longest diameter 3.2–3.3 mm; modified, subconical scales post-tympanic, 2–4; 4 distinctly enlarged, convex, hexagonal scales in the region between posterior corner of the orbit and anterior-dorsal border of the tympanum, forming single distinct lateral ridge on each side; area in line between posterior-inferior corner of the orbit to rictus forming another ridge on each side; together the 2 ridges sandwich a triangular, concave area anterior to tympanum on each side.

Dorsal head scales keeled, heterogeneous in size, shape; 3 or 4 distinct, enlarged, irregular hexagonal scales arranged in Y-shape on dorsum of snout, largest 2 (tips of Y-shape figure) between anterior corners of orbit dorsally. Three to 6 enlarged, convex, modified scales positioned on each side of interparietal, each side arranged in a butterfly-wing shape, separated from the other side by 2–4 small scales, symmetrical along medial axis, anterior most pair of scales in the modified scale series scapular in shape, with narrower ends facing medially. A distinct, continuous ridge encloses temporal region on each side, forming slightly convex, rectangular area on temporal region of head in life; such convex regions shrunk after preservation, becoming slightly concave compared to surrounding ridges.

Antehumeral fold present, distinct, reaching roughly



Figure 4. Juvenile *Pseudocalotes austeniana* (KIZ 06777) from Hanmi, Medog County, Tibet, China. **A.** Lateral head. **B.** Dorsal head. **C.** Ventral head. **D.** Ventral body. **E.** Lateral body. Specimen was preserved in ethanol. Photographs by Mian Hou.

1 cm superior to fore-limb insertion; axillary fold present, distinct in life. Dorsal body scales heterogeneous in size and shape; background scales smooth or weakly keeled, arranged irregularly; axillary scales granular, much smaller than others of dorsum; distinctly enlarged dorsal scales about 4–10 times larger than smallest proximate scales, each bearing a single weak keel, mostly flat except tip posteriorly, which protrudes upward; some enlarged dorsal scales arranged roughly in 3 transverse rows between axilla and groin; 35 serrated crest scales, triangular in shape; dorsal and nuchal crests not clearly

differentiated, the nuchal crest composed of approximately 13 erected scales, while the dorsal crest is composed of about 22 less erect scales.

Dorsal limb scales strongly keeled; dorsal fore-limb scales roughly homogeneous in size and shape, except on dorsum of elbow and lower arm; dorsal hind limb scales heterogeneous in size, shape, with enlarged scales scattered randomly. Tail scales strongly keeled, carinate in lateral rows.

Ventral head scales smooth or bearing feeble keels toward tips, heterogeneous in size, shape; longitudinal

gular fold strongly developed, extending as dewlap, with distinct pointed tip at distal end (less distinct after preservation); transverse gular fold absent. Mental pentagonal in shape, bordered posteriorly by first pair of chin shields; first 4 pairs of chin shields differentiated from other ventral head scales, shape and size of chin shields decreases gradually posteriorly before blending with surrounding gular scales by the fifth or six pairs of chin shields; first 1 to 2 pairs of chin shields in contact with infralabials, remaining chin shields separated from infralabials by 1 or 2 rows of small, narrow scales on each side; ventral head scales largely subequal in size, not significantly enlarged toward lateral surfaces of head; smaller scales present on medioposterior and posterior region of longitudinal gular fold and on posterior edge of pointed tip of longitudinal gular fold.

Ventral body scales smooth or weakly keeled, heterogeneous in size, shape, ranging from lanceolate to flabellate in shape, scales arranged irregularly, tips and keels of scales pointing medially, laterally, or parallel to ventromedial line; most ventral scales larger than background scales of dorsum; single medial sulcus running from midbody posteriorly to anterior pelvis. Ventral forelimb and hind limb scales roughly homogeneous in size, shape, arranged in regular rows, ventral thigh scales imbricate, arranged in regular rows. Femoral pores absent. Cloacal scales slightly enlarged, arranged in 2 regular transverse rows.

Coloration in life. The dorsal surface of the head is mostly uniform light grass green, and the lateral surface of the head is uniform yellowish green. Pale cyan patches are present posterior to the rictus on the jaw joint of each side of the head. The tympanum is uniform olive. The ventral surface of the head is greenish yellow, and gradually changes to spectrum yellow toward the posterior end of the throat. The inter-scale surfaces between gular scales in the center of the dewlap have the brightest yellow coloration.

A distinct spectrum yellow patch is present on the lateral surfaces of the neck anterior to the shoulder joint on each side. This patch is followed by a short vertical olive streak superior to the shoulder joint. The fine scales of the axillary region posterior to the olive streak are light cyan, and the inter-scale spaces are jet black. The dorsal surfaces of the body and limbs are largely uniform light grass green, except for 4 darker green transverse bands present on the dorsal surfaces of the hind limbs, and 3 faint lighter green rectangular patches present between the posterodorsal region of the body and the vent. The ventral surfaces of the body change from greenish yellow anteriorly to light grass green posteriorly. The medial sulcus along the ventral midline of the body is more yellowish. The ventral surfaces of the limbs are uniform light grass green.

The background coloration of dorsal and lateral surfaces of the anterior one-fourth of the tail is pale yellow green, with the ventral surface of this region of the tail

light grass green. Four faint brown to olive green, rectangular patches are distributed evenly across the dorsal and lateral surfaces of the tail from the vent to one-fourth of its total length. The dorsal, lateral, and ventral surfaces of the posterior three-fourths of the tail are uniform reddish brown.

Coloration in preservative. For KIZ 013873, most ornamental coloration patterns faded after preservation. The dorsal surfaces of the head and neck, and some of the enlarged scales of the dorsal body surfaces are smoky gray. All the remaining parts of the body and limbs are light blue in preservation. Additionally, the yellow gular spot is pale buff, the ventral surfaces of the body are bluish white, and the dorsal, lateral, and ventral surfaces of the posterior three-fourths of the tail are olive. For TMNH 20170001, all ornamentation faded, and the entire specimen is uniform light to medium gray, except the dewlap, the chest, and ventral surfaces of forelimbs, which are light buff.

Discussion

Distribution range. Prior to our observations of *P. austeniana* in the field, the species was thought to be a rare endemic to the southern parts of Southern Tibet (Mahony 2010, Venugopal 2010, 2013), and the species was not officially listed as a member of the Chinese herpetofauna (Zhao and Jiang 1977, Zhao and Adler 1993, Zhao et al. 1999, Cai et al. 2015). However, the newly discovered populations represent a range expansion of about 400 km northeastward from the species' previous range limits in the East Himalaya. Given the recognized habitat connectivity and similar environment spanning this region, it is likely that *P. austeniana* is currently, or once was, distributed continuously across this area. Future survey efforts for this species should focus on habitat to the west in Bhutan. Additional studies of this enigmatic and secretive lizard are needed to better understand its ecology, population densities, and full geographic distribution.

Ontogenetic shifts in morphology and clutch size. Ontogenetic shifts in morphology (both coloration and ornamentation as well as morphometric characteristics) are common in lizards, including many agamids (Qiu et al. 2001, Mahony 2010, Du et al. 2011, Wang et al. 2015). As ontogenetic shifts in phenotype can be associated with diversification in species-specific niche and predator-avoidance strategies (Qiu et al., 2001, Du et al. 2011, Fresnillo et al. 2016), documentation of such developmental changes lays a foundation for future ecological and evolutionary studies. Unfortunately, such information is often lacking for many reptile species, including agamid reptiles. Based on limited information in published literature, disparate coloration and ornamentation patterns have been documented between adult and subadult *P. austeniana* (Manthey 2010). Manthey (2010) noted that subadult *P. austeniana* possess fawn colored



Figure 5. Eggs of *Pseudocalotes austeniana* (produced by the voucher female TMNH 20170001). Photograph by Shiyang Weng.

radial stripes around the eyes, a white lip stripe that runs from the rostral to the corner of the mouth, a brownish gray posterolateral stripe that runs from the posterior margin of the orbit to the anterior boundary of the tympanum, a pale gray dorsal ground coloration with jet black transverse pigmentation patterns running longitudinally down the body, and a red axillary coloration, whereas adults lack distinct radial stripes around eyes but possess a uniform yellowish green coloration of lateral head without lip stripe, a light grass green dorsal body coloration with darker green rectangular patches, and a light cyan axillary coloration. However, nothing was known about the coloration of juvenile individuals or morphometric differences between different age groups.

The results of our study show, that in contrast to adults, juvenile *P. austeniana* possess longer white lip stripes that extend to the fore-limb insertion (vs indistinct or terminate at the corner of the mouth), more distinct radial stripes or a single stripe (vs absent), a round jet black patch around the fore-limb insertion (vs absent), and a olive to drab dorsal coloration with yellowish green transverse bands and speckles on lateral body (vs mostly uniform light grass green with darker, rectangular patches). For morphometric data, the voucher juvenile possesses a wider head (HW 67.13% HL vs $\leq 64.51\%$) and relatively longer limbs (FLL 61.46% SVL, HLL 88.02% SVL vs $\leq 56.21\%$ and $\leq 86.83\%$, respectively). Based on current data, we suggest that *P. austeniana* goes through ontogenetic shifts in morphology, for both coloration and morphometric measures, and we recommend focused ecological studies on *P. austeniana* to better understand the evolutionary context of the observed ontogenetic changes in phenotype.

Regarding the reproductive biology, nothing is known about the clutch size of *P. austeniana* to date. One of the female specimens that was vouchered in this study (TMNH 20170001), laid 8 eggs in captivity prior to the euthanization (Fig. 5). The eggs are about 15 mm long and appear to be unfertilized. To our knowledge, this represents the first record of clutch size for the species.

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Authors' Contributions

Kai Wang, Ke Jiang, Ping Ci, Shiyang Weng, Weidong Zhu, and Jing Che collected specimens in Tibet; Kai Wang, Shiyang Weng contributed to the collection of morphological and reproductive data; Kai Wang, Ping Ci, Ke Jiang, Jing Che and Cameron Siler wrote the manuscript with others' inputs. Jing Che and Cameron Siler reviewed the final manuscript.

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Appendix

Additional specimens examined.

- Pseudocalotes* sp. ($n = 1$): KIZ 012124, Myanmar.
- Pseudocalotes kakhienensis* ($n = 7$): KIZ 214908, 214949, 027558, 027582, 027584, 027585, 027585, 027576, Gaoli-gongshan, Yunnan, China.
- Pseudocalotes kingdonwardi bapoensis* ($n = 4$): CAS 241965, 242628, 242629, 242000, 242020, Gongshan, Yunnan, PR China.
- Pseudocalotes microlepis* ($n = 3$): KIZ 040631, 040632, 040640, Guangdong, China.
- Salea anamallayana* ($n = 1$): CAS 104247, India.