On the Occurrences of Japalura kumaonensis and Japalura tricarinata (Reptilia: Sauria: **Draconinae**) in China

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ABSTRACT: Although the recognized distribution of *Japalura kumaonensis* is restricted largely to western Himalaya, a single, isolated outlier population was reported in eastern Himalaya at the China-Nepal border in southeastern Tibet, China in Zhangmu, Nyalam County. Interestingly, subsequent studies have recognized another morphologically similar species, *J. tricarinata*, from the same locality in Tibet based on photographic evidence only. Despite these reports, no studies have examined the referred specimens for either record to confirm their taxonomic identifications with robust comparisons to congener species. Here, we examine the referred specimen of the record of J. kumaonensis from southeastern Tibet, China; recently collected specimens from the same locality in southeastern Tibet; type specimens; and topotypic specimens of both *J. kumaonensis* and J. tricarinata, to clarify the taxonomic identity of the focal population from southeastern Tibet, China. Our results indicate that individuals of the referred Tibetan population differ from *I. kumaonensis* in external morphology, but match descriptions and specimens of *I. tricarinata*. We conclude that the previous record of *I. kumaonensis* from Tibet was a misidentification of *I. tricarinata*, and *I. kumaonensis* should be recognized as occurring in western Himalaya only. To facilitate future taxonomic studies of the genus Japalura sensu lato in the Himalaya, we provide a detailed description of *I. tricarinata* and an updated diagnostic key to the genus from the Himalaya.

Key words: Agamidae; Distribution; Species identification; Taxonomy

THE CORRECT identification of historically collected specimens can be problematic, particularly when there is a limited availability of literature and an unresolved taxonomy for the focal groups. For example, many cryptic yet distinct evolutionary lineages described in recent studies were recognized as a single, widespread species, resulting in misidentified distribution records (Zhao et al. 1999; Hausmann et al. 2009). The re-examination of specimens associated with questionable records can clarify taxonomic confusion and inform biogeographic research and conservation objectives (Murray et al. 2008; Grismer et al. 2016).

Among the reptile fauna of Asia, Japalura sensu lato Gray 1853 is a genus with a long and convoluted taxonomic history that has included the recognition of numerous questionable distribution records based on original identification efforts (Zhao et al. 1999). Although the situation has improved over the last decade, the taxonomy of the genus remains based entirely on assessments of external morphology (Manthey et al. 2012; Wang et al. 2017). Historically, a paucity of vouchered specimens in accessible museum collections and the brief descriptions about them led to several ambiguous species diagnoses, literature misinterpretation, and questionable identifications of some populations of Japalura in China (Hu et al. 1987; Zhao et al. 1999; Manthey et al. 2012). This has resulted in confusion over distribution records for some species of *Japalura* currently to thought to have widespread geographic ranges (Manthey et al. 2012; Wang et al. 2015, 2016). An example of such taxonomic confusion concerns a historical specimen of Japalura from southeastern Tibet, China (CIB 2571), and the associated sympatric records of two Japalura species, namely, J. kumaonensis

(Annandale 1907) and J. tricarinata (Blyth 1853), from the same locality (Zhao and Jiang 1977; Hu et al. 1987; Zhao et al. 1999; Manthey 2010).

First reported by Zhao and Jiang (1977), Kumaon Mountain Dragons (Japalura kumaonensis) were recorded from the China-Nepal border in Zhangmu, southeastern Tibet, China. Zhao and Jiang (1977) did not provide any description of the referred specimen, however, nor did they explain the diagnostic characters used for the species-level identification. Ten years later, Hu et al. (1987) followed the taxonomic identification by Zhao and Jiang (1977) and provided the first morphological description of the same referred Tibetan specimen of J. kumaonensis (CIB 2571) of Zhao and Jiang (1977). However, no comparisons were made with any other congeners from the Himalayan region in support of the species identification (Hu et al. 1987). Given that the locality of this Tibetan specimen is isolated and far from the known range of *J. kumaonensis* (roughly 500 km linear distance away from the easternmost recognized population at the time; Swan and Leviton 1962), such a widespread distribution in China remains suspicious. Despite numerous studies on the diversity in the region (Zhao et al. 1999; Kunte and Manthey 2009; Li et al. 2010; Manthey 2010; Ananjeva et al. 2011; Cai et al. 2015), no research to date has investigated this unusual disjunct distribution.

Related to the Tibetan record of Japalura kumaonensis in China, a Chinese distribution record of a morphologically similar congener, J. tricarinata, from the same locality also raises questions concerning the taxonomic identification and distribution record of J. kumaonensis in China. Schleich and Kästle (2002) first referenced a Chinese record of J. tricarinata in Tibet, which at the time they recognized as Oriotiaris tricarinata. Referencing a photograph that Zhao

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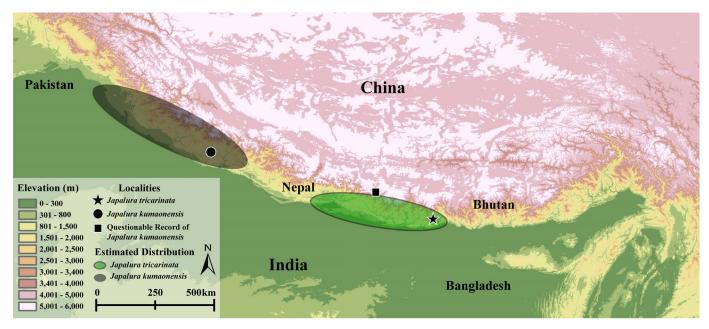


FIG. 1.—Distributions of *Japalura kumaonensis* and *J. tricarinata* in the Himalaya. Different shapes indicate localities of the two species (star = type locality of *J. tricarinata*; circle = type locality of *J. kumaonensis*; square = questionable record of *J. kumaonensis* in Zhangmu, Nyalam County (=Nielamu), southeastern Tibet, China by Zhao and Jiang 1977). Shaded areas represent the estimated distributions of *J. tricarinata* (green) and *J. kumaonensis* (dark gray), following Kästle and Schleich (1998) and Schleich and Kästle (2002). A color version of this figure is available online.

and Adler (1993) reported as *Calotes jerdoni* from Zhangmu, Tibet, China, Schleich and Kästle (2002) suspected that this image was actually a misidentified specimen of *J. tricarinata*. Based on the referenced photograph only, Schleich and Kästle (2002) concluded that *I. tricarinata* should be recognized as part of the herpetofauna of Tibet, China. This record was from the exact same locality as the historical record of *I. kumaonensis* by Zhao and Jiang (1977). Thereafter, online databases (i.e., The Reptile Database; Uetz and Jirí 2017) followed Schleich and Kästle (2002) and added China as part of the distributional range of *I*. tricarinata. Unfortunately, there was no follow-up work that included any examination of vouchered specimens. Furthermore, despite its questionable locality record, no attention has been paid in the literature to the sympatric distribution of out-of-range J. kumaonensis and J. tricarinata in Tibet (Schleich and Kästle 2002; Uetz and Jirí 2017).

Recently, Cai et al. (2015) followed previous authors and included Japalura tricarinata as a member of herpetofauna of China. The record was based on two previously published studies by Macey et al. (2000) and Kunte and Manthey (2009), however, without providing details about referred specimens or their corresponding localities (Cai et al. 2015). Records published in both of these studies are problematic with respect to the occurrence of *J. tricarinata* in China for at least two reasons. Firstly, Kunte and Manthey (2009) did not examine vouchered specimens of the species from Tibet, and they cited incorrectly the distribution record for *I*. kumaonensis in China as being roughly 600 km east of the actual locality by Zhao and Jiang (1977; Kunte and Manthey 2009:fig. 1). Secondly, although Macey et al. (2000) showed the Tibetan Japalura specimen (noted as J. tricarinata, but collected from the same locality as the previous record of *I*. kumaonensis) is phylogenetically closely related to J.

variegata, they did not compare the DNA sequence of Tibetan specimen against topotypic *J. tricarinata* or provide morphological evidence to support their taxonomic identification of the Tibetan specimen. Therefore, the phylogenetic results from Macey et al. (2000) cannot be used as the direct evidence for the species-level identification of *Japalura* specimen from Tibet, as inferred by Cai et al. (2015).

Because the locality of such controversial records of *Japalura* in southeastern Tibet is at the proximate range of *I*. tricarinata, but far away from known range of *J. kumaonensis* (Swan and Leviton 1962; Kästle and Schleich 1998; Khan 2002; Schleich and Kästle 2002), such an out-of-range, isolated record in Tibet is suspicious. Furthermore, given that the females of the two species are morphologically similar (Schleich and Kästle 2002), it is possible that the historical female specimen of J. c.f. kumaonensis from Tibet is a misidentification of J. tricarinata, and the putative sympatric distribution of both species from the same locality in Tibet is a result of misidentification. Therefore, with no direct re-examination of the referred specimens of the records of J. kumaonensis (Zhao and Jiang 1977; Hu et al. 1987) and J. tricarinata (Macey et al. 2000; Kunte and Manthey 2009) from Tibet, the assumed sympatric distribution of both species in southeastern Tibet, China, remain suspicious.

During herpetofaunal surveys in 2011 and 2016, two specimens of *Japalura* were collected from the previously reported locality by Zhao and Jiang (1977) at Zhangmu, Nyalam County (=Nielamu), Tibet, China, and four specimens of *J. kumaonensis* were collected near the species' type locality in India. Additionally, we examined a series of museum specimens of *Japalura* from Zhangmu, southeast Tibet, China (including specimens of previously identified *J.* c.f. kumaonensis and *J.* c.f. tricarinata), and type material of both species and other Himalayan congeners. The information from these specimens was combined with a review of the literature, which allowed us to re-evaluate the taxonomic status of populations of *Japalura* in southeastern Tibet, China. We also discuss future directions for taxonomic studies of the genus in the region, and provide an updated diagnostic key of *Japalura* sensu lato from the Himalaya.

MATERIALS AND METHODS

Museum abbreviations for specimens examined follow Sabaj (2016), and include the British Museum of Natural History (BMNH), the California Academy of Sciences (CAS), the Center for Ecological Sciences, Indian Institute of Science (CESG), the Chengdu Institute of Biology, Chinese Academy of Sciences (CIB), the Kunming Institute of Zoology, Chinese Academy of Sciences (KIZ), the University of Kansas Biodiversity Institute (KU), the Field Museum of Natural History (FMNH), the Museum of Comparative Zoology (MCZ), and the Zoological Survey of India (ZSI).

Two individuals of *Japalura* were collected from Zhangmu, Nyalam County, Tibet, China, in July 2011, including a single male (KIZ 011132) and a single female (KIZ 011133). Four additional specimens of *J. kumaonensis* were collected from India in August 2013, in which an adult pair (CESG 567, 568) was from Mussoorie, India, and another adult pair (CESG 569, 570) was from Glacier Trek, India (see Appendix). After being euthanized, tissue samples were removed from each specimen and placed in 90% ethanol. These samples were fixed in 10% buffered formalin in the field and transferred to 70% ethanol after fieldwork. Available specimens of both J. kumaonensis and J. tricarinata in museum collections were examined, including the type specimens of both species (Appendix). In addition, specimens of most recognized congeners from the Himalayan region were examined, including J. andersoniana Annandale 1905, J. major (Jerdon 1870), J. planidorsata Jerdon 1870, J. sagittifera (Mahony 2009), and J. variegata Gray 1853 (Appendix). For congeners that we did not have access to, morphological characteristics were taken from literature, including for J. dasi (Schleich and Kästle 2002) and J. otai (Mahony 2009).

Specimens were measured with digital calipers by KW and VD (± 0.01 mm). Focal characters follow Wang et al. (2015, 2016), and include (definitions given after abbreviation in parentheses): snout-vent length (SVL); tail length (TAL; from vent to tip of tail); head length (HL; measured from rostral to the jaw joint); head width (HW; measured at the widest point); snout-eye length (SEL; from rostral to the anterior corner of eye); forelimb length (FLL; axillary to the end of the longest finger, excluding claw); hindlimb length (HLL; groin to the end of Finger IV, excluding claw); supralabial count (SL); infralabial count (IL); middorsal scale count (MD; count of dorsal crest scale, from the beginning on occipital of head to position above vent); Finger IV subdigital lamellae count (F4S; subdigital lamellae count from the base to the tip of Finger IV); Toe IV subdigital lamellae count (T4S; subdigital lamellae count from the base to the tip of Toe IV); Toe IV length (T4L); trunk length (TRL); number of scales between nasal and first supralabials (NSL; lowest number of scales, counted in straight line, between the nasal and the first supralabial); number of scale rows between supralabials and orbit circle (SOR; counted from the midpoint of lower edge of orbit circle); enlarged, modified, postoccipital scale count (POS); enlarged, modified, posttympanic scale count (PTY); and enlarged, modified, postrictal scale count (PRS). Measurements were taken on the left side of the specimen only (unless the left side was damaged, then the right side was used), and values for paired pholidosis characters (SL, IL, NSL, SCL, SOR, PTY, and PRS) were recorded from both sides of the body, with counts provided in left/right order. We also assessed the following morphological characteristics: (1) shape of enlarged, modified, postrictal scale (SMP; conical vs. subpyramidal); (2) protuberance of enlarged, modified, postrictal scale (PMP; strongly protruding vs. weakly protruding or not protruding); (3) protuberance of vertebral crests/ridges (PNC; strongly protruding vs. not protruding); (4) texture of ventral head scales (TVH; keeled vs. smooth); and (5) continuousness of dorsolateral ridges on the body (CDR; continuous vs. discontinuous). For descriptions of coloration, we followed Köhler (2012).

The topographic map to illustrate biogeography (Fig. 1) was created by KW in ArcMap v10.3.1 with the use of the digital elevation model (DEM) layers based on NASA's Shuttle Radar Topographic Mission. Estimated distribution ranges of *Japalura kumaonensis* and *J. tricarinata* follow previous published works (Kästle and Schleich 1998; Schleich and Kästle 2002) and our examination of vouchered type and reference material.

RESULTS

The Tibetan specimens, including the previously identified J. c.f. kumaonensis, have feebly developed crest scales that are not serrated or erected, well-developed PRS, and continuous dorsolateral ridges of modified scales on the dorsum, particularly on the anterior half of the body (Figs. 2, 3). The examined males of Tibetan specimens possess smooth scales on the ventral surface of the head and an almost uniform Light Caribbean Blue (Color 163) to Sky Blue (Color 167) in preservation (Fig. 3). For individuals collected in the wild from Tibet, the male was uniform Grass Green (Color 110) in life, where the female was Light Pratt's Rufous (Color 71) to Pratt's Rufous (Color 72) in life, with few Light Grass Green (Color 109) or Dark Brownish Olive (Color 127) speckles. For type, topotype, and Nepalese specimens of *J. tricarinata*, the morphological and pholidosis characteristics resemble the Tibetan specimens in most respects (Tables 1 and 2). The type and topotype specimens possess better-developed, modified scales on the dorsum and on the posterior surfaces of thighs comparing to the Nepalese and Tibetan specimens (Fig. 2).

Topotypic and types of *Japalura kumaonensis* possess discontinuous dorsolateral ridges on the dorsum, serrated and erected crest scales, and inconsistent presence of conical scales postrictus. For the examined males, individuals have distinctively keeled ventral head scales, distinct Pale Buff (Color 1) dorsolateral stripes, distinct Burnt Umber (Color 48) to Jet Black (Color 300) triangle patches, and a Beige (Color 254) background coloration of head and body (Figs. 2–4).

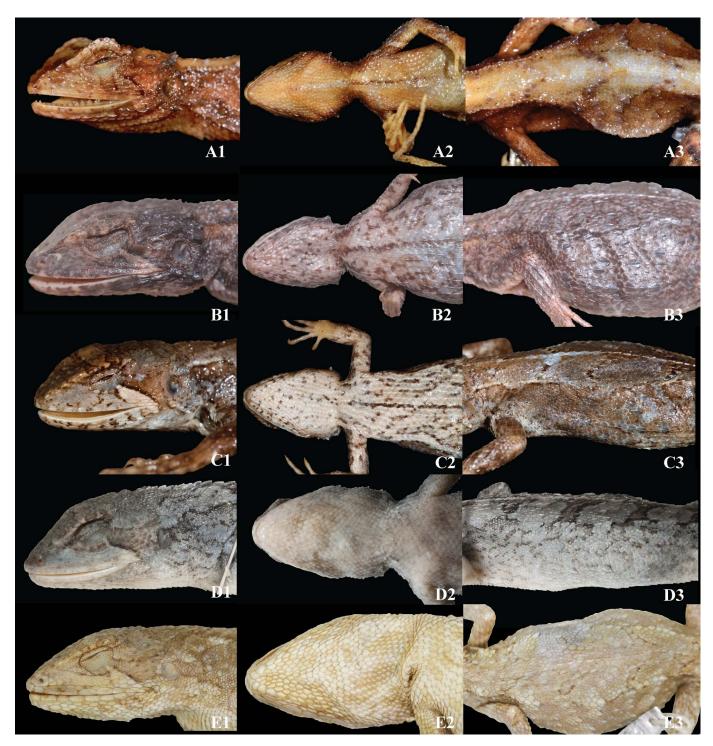


FIG. 2.—Comparisons of lateral (Column 1) and ventral (Column 2) views of the head, and lateral views of the body (Column 3) among topotypic specimen of *Japalura tricarinata* (MCZ 58288; Row A), an historically identified female specimen of *J. c.f. kumaonensis* from Zhangmu, Nyalam County (=Nielamu), Tibet, China (Chinese Academy of Sciences [CIB] 2571; Row B), female *J. c.f. tricarinata* specimen collected recently from the same locality in Zhangmu, Nyalam County, Tibet, China (California Academy of Sciences [CAS] 177533; Row C), topotypic female specimen of *J. kumaonensis* from Kumaon, Uttarakhand, India (Center for Ecological Sciences, Indian Institute of Science [CESG] 568; Row D), and syntype specimen of *J. kumaonensis* (British Museum of Natural History [BMNH] 1946.8.13.94, Row E). Photos by K. Wang, K. Jiang, and V. Deepak. A color version of this figure is available online.

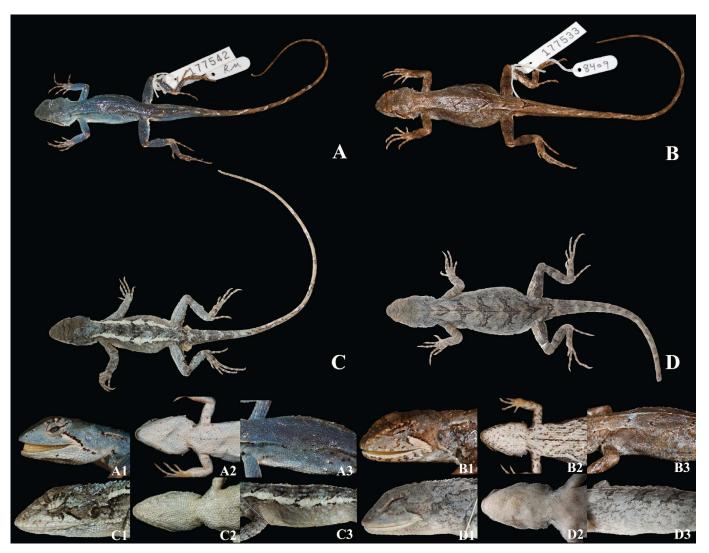


FIG. 3.—Comparisons among preserved male and female specimens of *Japalura tricarinata* from Zhangmu, Nyalam County, Tibet, PR China, and *J. kumaonensis* from Dhanaulti, Mussoorie, India. The male (California Academy of Sciences [CAS] 177542) and female (CAS 177533) of *J. tricarinata* are represented by images labeled (A) and (B), respectively; the male (Center for Ecological Sciences, Indian Institute of Science [CESG] 567) and female (CESG 568) of *J. kumaonensis* are represented by images labeled (C) and (D), respectively. Numbers 1, 2, and 3 represent lateral and ventral views of the head, and lateral views of the body, respectively. Photos by K. Wang and V. Deepak. A color version of this figure is available online.

DISCUSSION

Sympatric Records of *Japalura kumaonensis* and *J. tricarinata* in China

Zhao and Jiang (1977) first reported *J. kumaonensis* from Zhangmu, Tibet, China, without a detailed description of the referred specimen. Hu et al. (1987) provided the first description of that specimen (CIB 2571), in which they reported the specimen as having an exposed tympanum, a relatively long tail (TAL/SVL > 200%), a dorsolateral ridge parallel to vertebral midline on each side of body, chevron- or V-shaped ridges along body midline formed by enlarged scales, and no transverse gular fold. Although these morphological characteristics could distinguish the Tibetan *Japalura* specimen from all other known congeners from East Asia (Wang et al. 2016), they cannot be used to diagnose the specimen from the Himalayan congeners because many of these taxa share these characteristics (including *J. tricarinata*; Schleich and Kästle 2002; Mahony 2009).

Upon detailed morphological examination of the specimen reported by Zhao and Jiang (1977), and additional specimens from the same locality, we found that Tibetan specimens possess a suite of characteristics that can differentiate them from type and topotypic specimens of Japalura kumaonensis (Figs. 2 and 3; Tables 1 and 2). Given that the morphological characteristics of the previously identified J. c.f. kumaonensis from Tibet and all examined *Japalura* specimens from the same locality differ from *J*. kumaonensis, but resemble J. tricarinata, we identify the Japalura populations in Zhangmu, Tibet, China as J. tricarinata. Furthermore, we conclude that the historical Tibetan specimen of *I. kumaonensis* reported by Zhao and Jiang (1977) is a misidentification of J. tricarinata. To our knowledge, J. kumaonensis does not occur in China. Here we provide a detailed description of *I. tricarinata* based on examined specimens.

TABLE 1.—Morphological comparisons of sex-specific characteristics among the historical specimen of *Japalura* c.f. *kumaonensis* from Zhangmu, Nyalam County (=Nielamu), Tibet, China (Chinese Academy of Sciences [CIB] 2571); recently collected specimens of *J. c.f. tricarinata* from the same locality in Tibet (California Academy of Sciences [CAS] 177391–394, 177400, 177402, 177403, 177405, 177533, 177542, Chinese Academy of Sciences [KIZ] 011132, 011133, KIZ 8855); specimens of *J. c.f. tricarinata* from Nepal (Field Museum of Natural History [FMNH] 167397, 167398); specimens of *J. kumaonensis* from Mussoorie and Glacier Trek, India (Center for Ecological Sciences, Indian Institute of Science [CESG] 567–570, University of Kansas Biodiversity Institute [KU] 180691, 180693, 180694); type specimens of *J. kumaonensis* (British Museum of Natural History [BMNH] 1909.7.12.38, 1909.7.12.39); and topotypic specimens of *J. tricarinata* from Darjeeling, West Bengal, India (Museum of Comparative Zoology [MCZ] 58288, FMNH 15804). The mean value (±1 SD) of each character is given in parentheses following the range. See Materials and Methods for descriptions of measurement acronyms.

| | Species | | | | | | |
|----------------------------|--|--|--|---|--|---|--|
| | Japalura kumaonensis (topotypic and types) | | Japalura tricarinata (topotypic) | <i>Japalura</i> cf. <i>kumaonensis</i> (Zhangmu, Tibet, China) | Japalura cf. tricarinata (Zhangmu, Tibet, China, and Nepal) | | |
| Measurements and ratios | M $(n = 5)$ | F $(n = 4)$ | $\mathbf{F} (n = 2 \text{ [subadults]})$ | F(n = 1) | M $(n = 9)$ | F $(n = 6)$ | |
| SVL | 50.81-60.90 (55.33 ± 4.23) | 50.46-70.52 (62.75 ± 8.81) | 42.51 - 45.56 (44.04 ± 2.16) | 58.55 | 42.47-53.43 (47.57 ± 3.24) | 48.11-61.32 (54.80 ± 4.71) | |
| TRL | 23.53-30.19 (26.47 ± 3.39) | 23.11 - 34.85 (30.11 ± 4.97) | 20.04-24.23 (22.14 ± 2.96) | 29.6 | 17.18-24.87 (21.32 ± 2.37) | 22.39-29.73 (25.46 ± 2.76) | |
| TAL | 103.8-129.8 (119.19 ± 9.91) | 117.7 - 135.7 (126.82 ± 9.02) | 93.5-104.2 (98.81 \pm 7.57) | 119.1 | 106.12-152.0 (124.80 ± 14.12) | 102.53 - 134.67 (112.16 ± 12.83) | |
| HL | 14.20-17.22 (16.09 ± 1.33) | 15.07-20.02 (17.54 ± 2.23) | 12.52-12.76 (12.64 ± 0.17) | 15.78 | 12.79-15.85 (14.25 ± 0.98) | 14.41-17.25 (15.86 ± 1.03) | |
| HW | 9.41-11.36 (10.80 ± 0.80) | 10.56-13.89 (12.15 ± 1.82) | 9.06-9.35 (9.21 ± 0.21) | 11.74 | 8.66-11.01 (9.54 ± 0.71) | 10.08-11.64 (10.83 ± 0.55) | |
| SEL | 5.56-6.45 (6.02 ± 0.41) | 6.18 - 7.35 (6.72 ± 0.59) | (0.21 ± 0.21) 4.85-4.99 (4.92 ± 0.10) | 6.61 | (5.03-6.07) (5.44 ± 0.39) | (5.35-6.29) (5.99 ± 0.34) | |
| FLL | (3.62 ± 0.11) 23.42–28.61 (25.35 ± 2.16) | (0.12 ± 0.05) 26.17–31.96 (29.62 ± 2.53) | (1.02 ± 0.10) 20.54–24.90 (22.72 ± 3.08) | 22.82 | (0.11 ± 0.05) 20.93–25.71 (22.95 ± 1.65) | (24.62 ± 0.01) (24.62 ± 1.40) | |
| HLL | (20.03 ± 2.03) 38.52-45.75 (42.04 ± 3.01) | (13.31 - 48.77) (46.55 ± 2.38) | (22.12 ± 0.06) 35.90-42.10 (39.00 ± 4.38) | 41.36 | (12.00 ± 1.00) 38.25-44.70 (41.21 ± 2.16) | (40.59 - 48.30) (44.72 ± 3.16) | |
| T4L | (12.01 ± 0.01) 10.40-12.19 (11.43 ± 0.67) | (10.35 ± 2.35) 11.16-13.54 (12.24 ± 1.06) | (0.80-12.34) (11.57 ± 1.09) | 12.09 | 10.13-14.12 (12.26 ± 1.19) | 12.20-13.36 (12.72 ± 0.46) | |
| TAL/SVL | (211.15 ± 0.01) 204.35-240.01% $(215.73\% \pm 15.66\%)$ | (12.21 ± 1.00) 201.47 - 233.25% $(212.50\% \pm 17.99\%)$ | (11.57 ± 11.65) 219.83–228.62% $(224.23\% \pm 6.22\%)$ | 203.43% | (12.23 ± 1.13) 245.75–298.33% $(261.93\% \pm 15.86\%)$ | (12.12 ± 0.10) 213.12–230.49% $(221.97\% \pm 7.67\%)$ | |
| TrL/SVL | $\begin{array}{l} (215.15\% \pm 16.00\%) \\ 43.53-51.62\% \\ (47.75\% \pm 3.61\%) \end{array}$ | $(212.50\% \pm 11.00\%)$ 45.80-49.59% $(47.85\% \pm 1.94\%)$ | $(224.25\% \pm 0.22\%)$ 47.14-53.18% $(50.16\% \pm 4.27\%)$ | 50.56% | $(201.05\% \pm 10.00\%)$ 40.60-48.70% $(44.83\% \pm 3.13\%)$ | $\begin{array}{c} (221.01\% \pm 1.01\%) \\ 44.35 - 50.37\% \\ (46.42\% \pm 2.21\%) \end{array}$ | |
| SEL/HL | $(47.16\% \pm 0.01\%)$ 35.62-39.15% $(37.49\% \pm 1.37\%)$ | $(41.56\% \pm 1.04\%)$ 36.71-41.54% $(38.50\% \pm 2.10\%)$ | $(36.10\% \pm 4.21\%)$ 38.74-39.11% $(38.92\% \pm 0.26\%)$ | 41.89% | $(41.05\% \pm 0.15\%)$ 36.85-39.95% $(38.36\% \pm 1.02\%)$ | $(40.42\% \pm 2.21\%)$ 36.46-39.64% $(37.82\% \pm 1.31\%)$ | |
| HW/HL | $(57.45\% \pm 1.57\%)$ 64.34-71.84% $(67.21\% \pm 2.89\%)$ | $(53.50\% \pm 2.10\%)$ 64.71-72.48% $(69.16\% \pm 3.25\%)$ | $(38.32\% \pm 0.20\%)$ 71.00-74.68% $(72.84\% \pm 2.60\%)$ | 74.40% | $(53.30\% \pm 1.02\%)$ 62.49-69.95% $(67.34\% \pm 2.70\%)$ | $(51.52\% \pm 1.51\%)$ 66.19-70.13% $(68.31\% \pm 1.53\%)$ | |
| HL/SVL | $(01.21\% \pm 2.05\%)$ 27.09–30.95% $(29.09\% \pm 1.48\%)$ | $(05.16\% \pm 3.25\%)$ 26.15-29.87% $(28.05\% \pm 2.01\%)$ | $(12.34\% \pm 2.00\%)$ 27.48–30.02% $(28.75\% \pm 1.79\%)$ | 26.95% | $(01.34\% \pm 2.10\%)$ 28.38–32.25% $(29.88\% \pm 1.20\%)$ | $(00.01\% \pm 1.00\%)$ 28.13-29.95% $(28.99\% \pm 0.64\%)$ | |
| FLL/SVL | $(25.05\% \pm 1.43\%)$ 42.44-48.63% $(45.83\% \pm 2.31\%)$ | $(23.03\% \pm 2.01\%)$ 45.32-51.86% $(47.50\% \pm 2.97\%)$ | $\begin{array}{c} (23.13\% \pm 1.13\%) \\ 48.32 - 54.65\% \\ (51.48\% \pm 4.48\%) \end{array}$ | 38.98% | $(29.36\% \pm 1.20\%)$ 45.60-51.29% $(48.35\% \pm 1.59\%)$ | $(23.95\% \pm 0.04\%)$ 40.28-48.92% $(45.09\% \pm 2.93\%)$ | |
| HLL/SVL | $(45.85\% \pm 2.81\%)$ 70.47-83.46% $(76.76\% \pm 4.82)$ | $(47.50\% \pm 2.91\%)$ 67.77-85.83% $(74.98\% \pm 7.69\%)$ | $(51.43\% \pm 4.43\%)$ 84.45-92.41% $(88.43\% \pm 5.63\%)$ | 70.64% | $(48.35\% \pm 1.59\%)$ 81.92-94.49% $(86.91\% \pm 3.97)$ | $(45.09\% \pm 2.95\%)$ 73.99-87.84% $(81.83\% \pm 5.16\%)$ | |
| TVC | Distinctively keeled | Distinctively keeled | Distinctively keeled | Distinctively keeled | (80.91% ± 3.97) Smooth or weakly keeled | Distinctively keeled | |

Species Account for Japalura tricarinata

Synonyms.—Calotes tricarinatus Blyth 1853:650. Tiaris elliotti Günther 1860:151. Oriotiaris elliotti Günther 1864:150. Acanthosaura tricarinata Anderson 1871:167. Japalura kumaonensis Zhao and Jiang 1977:68, Hu et al. 1987:113, Zhao et al. 1999:117, Kunte and Manthey 2009:51, Li et al. 2010:115–116, Manthey 2010:71, Ananjeva et al. 2011:121, Cai et al. 2015:Appendix 1. Japalura tricarinata Macey et al. 2000:255, Kunte and Manthey 2009:51. Japalura tricarinata Manthey 2010:71, Cai et al. 2015:368, Appendix 3. Oriotiaris tricarinata Schleich and Kästle 2002:633.

Specimens examined.—ZSI 5300 (holotype), subadult, from Darjeeling, West Bengal, India; MCZ 58288 (topotype), young adult female, from Darjeeling, West Bengal, India; CAS 177533, 177400, 177392–394, adult females; CAS 177391, 177402, 177403, 177405, 177542, adult males; collected by J. R. Macey and T. J. Papenfuss along the Lhasa-Zhangmu Road between the Chinese checkpoint and Nepal border in Tibet Autonomous Region, China (28°07'N, 85°59'E; in all cases datum = WGS84; elevation 2100–2300 m) on 5 September 1990. FMNH 167397, 167398, adult males, collected from Newakot District, Nepal; FMNH 15804 (topotype), young adult female, from Darjeeling, West Bengal, India; CIB 2571, adult female, collected by E. Zhao and Y. Jiang in Zhangmu, Tibet Autonomous Region, China. KIZ 011133, young adult female; KIZ 011132, subadult male, collected by KJ and JC near the China–Nepal border in Zhangmu, Tibet Autonomous Region, China (27°58'39''N, 85°58'24''E; elevation 2117 m) on 16 July 2010.

Diagnosis.—*Japalura tricarinata* can be diagnosed from congeners by a combination of the following morphological characteristics: (1) body size small, SVL 42.47–53.43 mm in males, 42.51–61.32 mm in females; (2) tail long, TAL 247.75–298.33% SVL in males, 203.43%–230.49% in females; (3) MD 36–46; (4) T4S 22–28; (5) V-shaped ridges present along body midline from neck to pelvis, formed by enlarged, keeled scales (more distinct in females); (6)

TABLE 2.—Pholidosis comparisons among the historically collected specimen of *Japalura* c.f. *kumaonensis* from Zhangmu, Nyalam County (=Nielamu), Tibet, China (Chinese Academy of Sciences [CIB] 2571); recently collected specimens of *J. c.f. tricarinata* from the same locality in Tibet (California Academy of Sciences [CAS] 177391–394, 177400, 177402, 177405, 177533, 177542); specimens of *J. c.f. tricarinata* from Nepal (Field Museum of Natural History [FMNH] 167397, 167398); specimens of *J. kumaonensis* from Mussoorie and Glacier Trek, India (Center for Ecological Sciences, Indian Institute of Science [CESG] 567–570, University of Kansas Biodiversity Institute [KU] 180691, 180694); types of *J. kumaonensis* (British Museum of Natural History [BMNH] 1909.7.12.38, 1909.7.12.39); and topotypic specimens of *J. tricarinata* from Darjeeling, West Bengal, India (Museum of Comparative Zoology [MCZ] 58288, FMNH 15804). The mean value (±1 SD) of each character is given in parentheses following the range. See Materials and Methods for descriptions of trait acronyms.

| | Species | | | | | |
|------------------|--------------------------|---------------------------|----------------------------|----------------------------|--|--|
| | Japalura kumaonensis | Japalura cf. kumaonensis | Japalura tricarinata | Japalura cf. tricarinata | | |
| Pholidosis trait | n = 9 | n = 1 | n = 2 | n = 12 | | |
| SL | 6 or 7 (6.56 \pm 0.51) | 5 or 6 | 5 or 6 (5.75 \pm 0.50) | $5-7 (6.04 \pm 0.46)$ | | |
| IL | $6-8 (6.83 \pm 0.51)$ | 6 | 5 or 6 (5.5 ± 0.58) | $5-8(6.25 \pm 0.61)$ | | |
| NSL | $0 (0.00 \pm 0.00)$ | 0 | $0 (0 \pm 0.00)$ | $0 (0.00 \pm 0.00)$ | | |
| SOR | 3 or 4 (3.78 \pm 0.43) | 3 | $3(3 \pm 0.00)$ | 3 or 4 (3.17 \pm 0.38) | | |
| MD | $39-47 (44.00 \pm 3.52)$ | 38 | $41-46~(43.5~\pm~3.54)$ | $36-44 \ (40.00 \pm 2.41)$ | | |
| F4S | $17-22 (19.00 \pm 1.10)$ | _ | $20-22 (20.75 \pm 0.96)$ | $16-23 (19.00 \pm 1.95)$ | | |
| T4S | $20-28(25.00 \pm 2.37)$ | 23 | 26 or 27 (26.5 \pm 0.58) | $22-28 (25.92 \pm 1.64)$ | | |
| POS | $1-6 (3.83 \pm 1.29)$ | 2 | 4 or 5 (4.5 \pm 0.58) | $1-5 (2.88 \pm 0.95)$ | | |
| PTY | $3-8(5.72 \pm 1.49)$ | 2 | $6-8 (7 \pm 0.82)$ | $3-8$ (5.54 \pm 1.28) | | |
| PRS | $3-8(5.33 \pm 1.61)$ | 3-5 | $4-6 (5 \pm 1.15)$ | $3-7$ (5.08 \pm 0.93) | | |
| SMP | Subpyramidal | Tall pyramidal or conical | Tall pyramidal or conical | Tall pyramidal or conical | | |
| PMP | Weak | Strong | Strong | Strong | | |
| PNC | Protruding | Not protruding | Not protruding | Not protruding | | |
| CDR | Irregular, discontinuous | Regular, continuous | Regular, continuous | Regular, continuous | | |

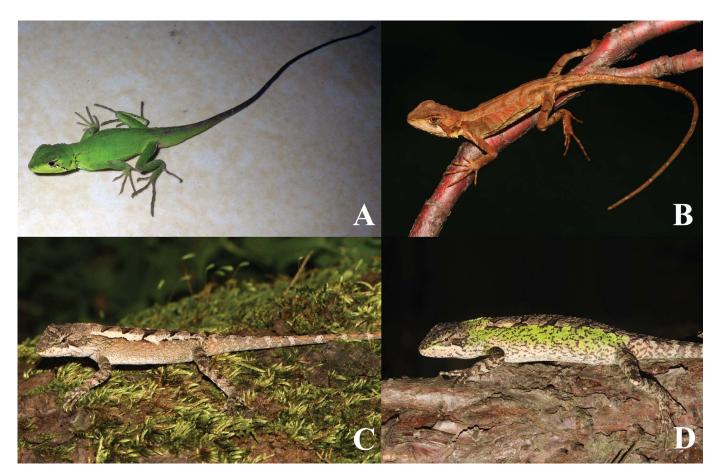


FIG. 4.—Comparisons among live males and females of *Japalura tricarinata* (A: male, Chinese Academy of Sciences [KIZ] 011132; B: female, KIZ 011133) from Zhangmu, Nyalam County (=Nielamu), Tibet, PR China, and *J. kumaonensis* (C: male, Center for Ecological Sciences, Indian Institute of Science [CESG] 567; D: female, CESG 568) from Dhanaulti, Mussoorie, India. Photos by K. Jiang, J. Che, and V. Deepak. A color version of this figure is available online.

dorsolateral ridge present on each side of vertebral ridge, distinct, continuous from neck to pelvis; (7) numerous enlarged, modified scales present postrictal, with one at rear axis of jaw in conical shape, distinctively thick, protruding; (8) tympanum exposed; (9) transverse gular fold absent; (10) gular pouch feeble or absent; (11) ventral head scales smooth or feebly keeled in males; (12) vertebral ridge feebly developed in both sexes, not raised on skin fold or possessing protruding, serrated scales; (13) body coloration in life mostly uniform grass green in males (sometimes speckled with few dark brown spots), light Pratt's rufous or Pratt's rufous in females; (14) series of dark chevron patterns represent dorsally along midline in females, but indistinct in males; (15) gular spots absent in both sexes; and (16) distinct dorsolateral stripes absent in males.

Description of examined specimens.—Body small, dorsally compressed, SVL 42.47-53.43 mm in males, 42.51-61.32 mm in females; tail slender, long, TAL 245.75–298.33% SVL in males, 203.43–230.49% in females; HLL 81.92-94.49% SVL in adult males, 70.64-92.41% in adult females. Head triangular, HL 26.95-32.25% SVL, HW 62.49-74.68% HL. Rostral rectangular, 3-4 times wider than height; nasal flat, large, oval or lacrimal shaped, in direct contact with rostral and first supralabial, bordering more than two-thirds of total length of first supralabials; supralabials 5–7, keeled, elongated, fourth and fifth below orbit; infralabials 5-8, elongated, keeled; loreal scales mostly keeled, heterogeneous in shapes and sizes; suborbital scale rows 3 or 4; numerous modified scales dorsal-anterior to tympanum; tympanum oval, exposed; scales enlarged, distinctively modified, 3-8 posttympanic, 3-7 postrictal; one of postrictal conical scales thick, conical or tall pyramidal in shape, protruding, 2-3 times larger than neighboring scales. Dorsal head scales heterogeneous in size and shape, keeled; Y-shaped ridge present on dorsal snout, formed by keels of individual scales; supraciliaries 6 or 7, overlapping greatly with neighboring ones except the posterior two; single enlarged, subpyramidal scale postorbit on each side; parietal somewhat rectangular, pineal eye present; 1-5 enlarged, subpyramidal, or low conical scales present on occipital region.

Dorsal, lateral body scales distinctively keeled, heterogeneous in size and shape; axillary scales distinctively smaller; vertebral ridge scales feebly developed, not differentiated between nuchal and dorsal, not distinctively raised or serrated; single continuous dorsolateral ridge present on each side of vertebral ridge from neck to tail base; enlarged scales of dorsum arranged in V-shaped ridges from neck to tail base, with tips of V-shaped ridges on dorsal midline (sometimes indistinct in males); keels of individual enlarged scales of Vshaped ridges not oriented along direction of ridges. Scales of limbs distinctively keeled, mostly homogeneous in size and shapes on forelimbs, heterogeneous on hindlimbs, with enlarged, modified scales on posterior thigh and crus.

Ventral head scales smooth or weakly keeled in males, more distinctly keeled in females, homogeneous in size and shape, smaller than ventral body scales; mental triangular shaped, about equal width as rostral; two or three pairs of enlarged postmental symmetrical to vertebral line, first one or two pairs in contact with first infralabial; transverse gular fold absent; gular pouch feebly developed or absent. Ventral body scales homogeneous in size and shape, equal to enlarged dorsal scales in size, distinctively keeled; keels of individual ventral scales in regular lateral rows (Table 1; Figs. 2 and 3).

Coloration.—The species is sexually dichromatic, with dramatic differences in body coloration. In life, males are mostly uniform Grass Green (Color 110) on dorsal and lateral surfaces of head, body, and limbs. Distinct, Jet Black (Color 300) radial stripes are present superior and posterior to eyes, with the posterior downward ones longest and broadest, starting from the lower posterior edges of eyes to the corners of mouth. White coloration is present between black stripes around eyes, with a distinct white stripe inferior to the longest black stripe from the posterior corner of the eye to the corner of the mouth on each side. Sometimes a narrow black stripe is present below the paravertebral ridge on each side of the vertebral ridge, and such black stripes usually end before one fourth of the total length of the ridge from the neck. Coloration of the tail gradually changes from Grass Green (Color 110) to Dark Lavender (Color 203) and Dark Neutral Gray (Color 299) at the base, and the coloration becomes Sepia (Color 286) after one third of its total length. The ventral surfaces of the head, body, limbs, and tail are white, sometimes greenish, with very few dark speckles on the ventral body.

For females, the ground coloration of the dorsal and lateral surfaces of head, body, limbs, and tail is Light Pratt's Rufous (Color 71) to Pratt's Rufous (Color 72). Some individuals possess one or two Dark Brownish Olive (Color 127) transverse stripes between eyes on the dorsal surface of head. Although the ornamentation patterns of lateral head in females are mostly the same as in males, females possess Jet Black (Color 300) radial stripes below eyes, and the loreal and suborbital regions anterior to the downward black stripes are Light Buff (Color 2), different from the coloration of the body. Random Dark Brownish Olive (Color 127) or Grass Green (Color 110) speckles sometimes are present on the dorsal and lateral surfaces of the body, limbs, and the tail. A series of Dark Brownish Olive (Color 127) chevron patterns are present on the dorsal surface of body, overlaying on top of the V-shaped ridges of the dorsum. Ventral surfaces of the head, body, limbs, and tail are Pale Pinkish Buff (Color 3). Jet Black (Color 300) speckles are sometimes scattered randomly on the ventral surfaces of head, body, limbs, and tail. A Sepia (Color 286) ventromedial stripe is present along the ventral midline from the chest to the vent in most individuals of females (Figs. 2, 3).

In preservation, ornamentation patterns of specimens remain the same, but coloration fades: The Grass Green coloration (Color 110) of males fades into Light Caribbean Blue (Color 163) to Sky Blue (Color 167), and the Light Pratt's Rufous (Color 71) to Pratt's Rufous (Color 72) coloration of females fades into Amber (Color 51).

Remarks on sexual dimorphism.—As with most congeners, *Japalura tricarinata* is sexually dimorphic. In addition to the sexually dichromatic coloration (Fig. 4), males possess longer tails (245.75–298.33% SVL vs. 203.43–230.49% in females), and smoother scales on the ventral surfaces of heads (vs. more distinctively keeled; Table 1).

Ecology and distribution.—*Japalura tricarinata* is known currently from the eastern Himalaya region, including eastern Nepal (Annapurna region and eastward), China (Zhangmu, Nyalam County, southeastern Tibet Autonomous Region), and northeastern India (Sikkim and Darjeeling of West Bengal). In China, the species is recorded from a single locality in Zhangmu, Nyalam County, Tibet. *Japalura tricarinata* inhabits cloud forests at an elevation of 2100– 2300 m (Fig. 1). On sunny days, individuals were found basking along forest edge. *Duttaphrynus himalayanus*, *Himalayophis tibetanus*, *Ovophis monticola*, and *Trachischium tenuiceps* were found in the same area.

Distributions and Cryptic Diversity of *Japalura* sensu lato in the Himalaya

Over the last few decades, populations of Japalura from the Himalaya have received far less attention than other congener lineages occurring in East Asia. Excluding the present study, there are four taxonomic studies in the past 17 yr that concern only the Himalayan *Japalura* (Kunte and Manthey 2009; Mahony 2009, 2010; Bhosale et al. 2013). Many species from the Himalaya are known from a few specimens or from the type specimens only in the literature (e.g., J. dasi, J. otai, J. planidorsata, and J. variegata). Furthermore, regions of the Himalaya, especially those in the East, have yet to receive systematic surveys for amphibian and reptile diversity. Therefore, the taxonomic identification of many recognized populations of Japalura populations has not been confirmed, including for J. c.f. planidorsata from Myanmar and J. c.f. variegata from Bhutan and Nepal.

Similar to the Japalura flaviceps complex in southwestern China, J. kumaonensis possesses a widespread geographic distribution, spanning multiple recognized faunal regions (Kästle and Schleich 1998; Manthey 2010; Mani 2012), and a complicated taxonomic history that contains questionable records for populations occurring in sympatry with morphologically similar congeners (e.g., J. tricarinata and J. major; Khan 2002; Manthey 2010). Given the strict habitat requirements of this montane lizard species, and the degree of habitat heterogeneity that exists across its current range (Kästle and Schleich 1998), it seems likely that the currently recognized populations of J. kumaonensis represent a complex of distinct evolutionary lineages that might warrant taxonomic recognition. Future integrative and comparative studies are needed to assess the taxonomy and phylogeographic patterns of J. kumaonensis in the western Himalaya further.

As for Japalura tricarinata, morphological variations are evident between the type and topotypic specimens from Darjeeling, India and the specimens from Tibetan and Nepal (Tables 1 and 2). Specifically, the enlarged scales on the dorsal body, posterior lateral thigh, and the posttympanic region of the lateral head on the type and topotypic specimens are more significantly modified than the ones on the Tibetan/Nepalese specimens. Smith (1935) also noted that similar morphological variations were observed among topotypic individuals of *J.* tricarinata in Darjeeling, which suggests that such variation might be intraspecific rather than interspecific. Future phylogenetic studies that include topotypic individuals of the Himalayan species are needed to verify such hypotheses, however, and confirm the taxonomic status of the eastern populations of *J. tricarinata* in Tibet and Nepal.

Here we provide an updated diagnostic key to all species of the genus *Japalura* sensu lato from the Himalaya in an effort to facilitate future taxonomic research of the genus in the region. DIAGNOSTIC KEY TO *JAPALURA* SENSU LATO IN THE HIMALAYA (NINE SPECIES)

5b. Head relatively wide, HW/HL > 65%; body dorsally compressed; nuchal and dorsal crest absent or feeble....7

- 7a. Body coloration mostly uniform green in males; middorsal scale count 53–58 *Japalura sagittifera*
- 7b. Body coloration brown or blackish brown in both sexes

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Appendix

Specimens Examined

Japalura and ersoniana (n = 4).—KIZ 011145, 011147, 011156, 010972, all from Medog, Nynchi Prefecture, Tibet, PR China.

Japalura kumaonensis (n = 9).—BMNH 1909.7.12.38, 1946.8.13.94 (syntypes), Kumaon, Nainital, India; CESG 567, 568, from Dhanaulti, Mussoorie, India; CESG 569, 570, from Gangi Village, Khatling Glacier Trek, India; KU 180691, 180693, 180694, near Mussorie, Uttar Pradesh, India.

Japalura major (n = 5).—BMNH 1946.8.14.7 (type), from Valley of Sutlej, near Kotegurh, India; FMNH 256412–15, all from Northwest Frontier Province, Pakistan.

Japalura planidorsata (n = 4).—CAS 243195, 234859, 233296, 219935, from Chin State, Myanmar.

Japalura sagittifera (n = 6).—BMNH 1946.8.13.96, 1946.8.13.97 (syntypes); BMNH 1946.8.14.97, 1946.8.15.2, 1946.8.14.94/134, 1946.8.15.4 (paralectotypes); all from Pangnamdin, Triangle, Upper Myanmar.

Japalura tricarinata (n = 18).—ZSI 5300 (holotype), Darjeeling, West Bengal, India; KIZ 011132, 011133; CIB 2571; CAS 177391–394, 177400, 177402, 177403, 177405, 177533, 177542; all from Zhangmu, Nyalam County (=Nielamu), Tibet, PR China; FMNH 167397, 167398, Newakot District, Nepal; MCZ 58288, FMNH 15804 from Darjeeling, West Bengal, India.

Japalura variegata (n = 6).—MCZ Herp R-58855, R-58857, R-7196, all from Takdah, Darjeeling District, West Bengal, India; FMNH 190842, 204517, from Nepal; FMNH 11780, from Bengal Pres, India.

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