

A NEW *INGERANA* (ANURA, DICROGLOSSIDAE) WITH NO EXTERNAL TYMPANUM FROM BORNEO, INDONESIA

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ABSTRACT. – *Ingerana rajae*, new species, is found in Bukit Baka-Bukit Raja National Park, West Kalimantan, Borneo, and is characterised by its large size, dorsum covered with tubercles, no clear distinction of the dorsolateral area, tympanum completely concealed under skin, and fingers and toes ornamented with widely enlarged tips with a circum-marginal groove. Toes are completely webbed to the base of enlarged tips, except for the outer side of penultimate phalanx of the fourth toe, which is essentially free from webbing. The species is contrasted with other members of the genus and some taxonomic confusion is discussed and clarified.

KEY WORDS. – Anura, Dicroglossidae, systematics, *Ingerana*, West Kalimantan, Indonesia.

INTRODUCTION

The genus *Ingerana* was erected to accommodate more or less small, plump frogs with flattened and expanded toe and fingertips with or without circum-marginal grooves (Dubois, 1986, 1992). The genus was initially divided into two subgenera, *Ingerana* (Southeast Asia) and *Liurana* (Indo China and Southern China), as a part of Dicroglossinae, Ceratobatrachini (Dubois, 1986, 1992), but now its members have been placed into different genera and even different families based on genetic analysis but only using samples of *Ingerana baluensis* and without much other reasonable evidence (Frost et al., 2006). Furthermore, Frost (2011; Amphibian Species of the World: ASW, 2008) placed *Liurana* and *Taylorana* in *Limnonectes*, *Ingerana baluensis* in Ceratobatrachidae and all other members of the group in Dicroglossidae, Occidozyginae. As even the familial position of this genus is unclear, we consider here that the genus consists of members of the subfamily Dicroglossidae and may be polyphyletic. We follow ASW proposition concerning *Liurana* and *Taylorana* in placing them in *Limnonectes* for the time being but are fully cognizant that this is merely a convenient and short-term solution and will need to be revisited when more data is made available.

In Southeast Asia, the genus *Ingerana* can be divided into two groups. The first group is composed of species with

relatively smooth skin, relatively narrow finger and toe tips, without circum-marginal groove and much reduced toe webbing. This first group consists of *I. charlesdarwini* (Das, 1998) (Andaman), and *I. borealis* (Annandale, 1912) (India, Myanmar and China (Sailo et al., 2009)). The second group consists of species with rounded, more or less distinctly tuberculated dorsal skin, wide finger tips and at least half webbed toes, including *I. tenasserimensis* (Sclater, 1892) (type of the genus, found in Myanmar and Thailand), *I. tasanae* (Smith, 1921) (Thailand), *I. mariae* (Inger, 1954) (Palawan), and *I. baluensis* (Boulenger, 1896) (Borneo).

During fieldwork in the heart of Borneo, we collected a form represented by three specimens from the second group too large to be included in *Ingerana baluensis*. A literature review showed that another name was associated with a specimen from Sarawak, *Rana sariba* Shelford 1905, based on a single female specimen of 38 mm, again, too large for *I. baluensis* (females max 34.5 mm, vide Inger, pers. comm.). As our specimens represent a larger species, consideration was addressed to the identity and range extension of *Rana sariba*, a species described from Mt Saribou, Sarawak. Despite differences in size, we follow Inger (1966) in placing *R. sariba* as synonym of *I. baluensis*, as no other characteristics to differentiate this form can be found. However, our specimens are over 40 mm as adults and do not

fit most of the original *I. baluensis* description. Judging from comparisons with *I. baluensis* and the original description of *I. sariba* and also to *I. mariae*, our specimens are distinct from all other species in lacking external tympana and having toes that are fully webbed to the widely enlarged toe tips (except for the outer side of the fourth toe). The new species is clearly distinct, but morphologically more closely related to *I. mariae* from Palawan, based on its close similarity in size and extent of toe webbings.

The holotype and one paratype (on which the description is based), are deposited in Museum Zoologicum Bogoriense (MZB), Indonesian Institute of Sciences, Cibinong, Bogor, Indonesia. A juvenile paratype is deposited in Raffles Museum of Biodiversity Research (RMBR), National University of Singapore.

MATERIAL AND METHODS

Specimens used for this study were measured with abbreviations as follows: Snout-vent length (SVL) – from cloaca to tip of snout; head width (HW) – widest distance between posterior ends of lower jaws; head length (HL) – from ends of lower jaw to the tip of the snout; femoral length (FE) – between cloaca to end of femur at right angle to body; tibial length (TI) – from end of tibia with foot 90° perpendicular to tibia up to the fold of the upper tibia; foot length (FL) – from tibia-fibula end to tip of 4th toe; inner metatarsal tubercle (IM); upper arm length (UA) – from the base of arm to end of humerus; lower arm length (LA) – from the joint to the base of middle palmar tubercle; hand length (HA) – first toe tip width (T1W); third finger tip width (3FW); fourth toe tip width (T4W); snout length (SL) – measured from bony border of eye socket to tip of snout; diameter of tympanum (TY) – widest diameter of outer tympanum border; diameter of eye (EY) – outer diameter, measured from bones bordering the eye; inter-orbital distance (IO) – between borders of bones bordering the eyes; eye-narial distance (EN) – eye socket border to posterior border of the nostril; internarial distance (IN) – shortest distance between nostrils; nostril to tip of snout (NT); eye mouth distance (EM). Institutional abbreviations are as listed in Leviton et al. (1985). Statistical analysis was performed with a Kruskal Wallis test at $p < 0.001$ and 0.01 level of significance. The holotype specimen is deposited in MZB, with paratypes in MZB and RMBR. For comparative materials, some other species were examined from FMNH, Chicago; BPBM, Hawaii; RMBR (ZRC), Singapore and in Institute of Technology, Bandung reference museum collection (ITB).

SYSTEMATICS ACCOUNT

Ingerana rajae, new species
(Figs.1–4)

Material examined: *Holotype*. – MZB Amph. (FN RMBR 001153), SVL 40.1 mm, an adult female without eggs in the oviduct,

collected from near Bakam stream along forest trail near Ella river watershed (0°36.240'S; 112°14.506'E) at 220 m asl., near km 37 (logging road marker), Kecamatan (=District) Menukung, Kabupaten (=Department) Melawi, Bukit Baka-Bukit Raya National Park, West Kalimantan Province, Indonesia, by D. P. Bickford and A. Rahmansah coll., 19 Aug.2007.

Paratypes. – MZB Amph. (FN RMBR 001127) 1 ex, an adult female without eggs in the oviduct from near Semunga Stream (0°35.228'S; 112°14.195'E) at 240 m asl., Kecamatan Menukung, Kabupaten Melawi, West Kalimantan, by D. P. Bickford and A. Rahmansah coll, 19 Aug.2007. RMBR (FN RMBR unnumbered) juv. of 16 mm SVL, from near Semunga Stream (0°35,228'S; 112°14,195'E) at 240 m asl., Kecamatan Menukung, Kabupaten Melawi, West Kalimantan, by D. T. Iskandar coll., 20 Aug.2007.

The description is based on two adult females and one juvenile specimen.

Diagnosis. – A large *Ingerana* with essentially fully webbed toes, dorsum is uniformly coloured, no lighter dorsolateral stripe, no dark blotch at the midbody below the scapular region, fingers and toes with wide expansion at tips, all toes webbed to penultimate phalange except the outer side of the fourth toe, which is only webbed up to the position of second subarticular tubercle; tympanic annulus hidden under skin and completely covered under temporal musculature.



Fig. 1. Lateral side of *Ingerana rajae* (Holotype, SVL 40.1 mm) in the natural habitat. Photo by D. P. Bickford.



Fig. 2. The ventral aspect of the holotype (SVL 40.1 mm) and adult paratype (SVL 34.6 mm) of *Ingerana rajae*.

Description. – A large *Ingerana*, SVL 40.1 and 34.6 mm in adult holotype and paratype respectively, body robust and plump, with a continuous depression along the vertebrae. Head slightly wider than length, eye diameter slightly shorter than snout, pupil diamond shaped; snout rounded, canthus rostralis straight from above and rounded in profile, lores concave; nostrils slightly below canthus rostralis, closer to tip of snout than to eye; distance between eyes narrower than internarial distance, interorbital narrower than internarial distance, tympanic annulus hidden under skin and covered with muscle, but a rounded soft area could be located after incision of the skin covering the tympanic area; a distinct supratympanic fold extending from slightly below the position of the middle part of eye, curving straight down to dorsal part of fore limbs and not looping above the position of the tympanic annulus as usually seen in most frogs. Vomerine teeth present, tongue with a median cleft, tips not narrowing so that the tongue is essentially rounded. Upper arm with small tubercles, longer than lower arm; limbs short, hands with two palmar tubercles; subarticular tubercles distinct. Fingers have narrow fringes of skin, with wide truncated and flattened tips bearing circum-marginal grooves; a rounded inner and elongated outer metacarpal tubercle, but no supernumerary metacarpal tubercles. First finger shorter than second, in length order $1 < 2 < 4 < 3$. Disk of toes about equal to fingers, also with wide flattened tips bearing circum-marginal grooves with extensive webbing, only the penultimate phalange on the outside of fourth toe is free from extensive webbings, a single inner metatarsal tubercle, flattened, the length slightly greater than its distance to the base of the widened toe tip, no outer metatarsal tubercle. Tibia not meeting each other when adpressed with femur perpendicular to body, slightly shorter than femur; toes fully webbed up to the base of flattened toe tips except for the outer side of fourth finger with the penultimate phalange free from extensive webbings (Fig. 3). Toes in length order $1 < 2 < 5 < 3 < 4$. Dorsal skin covered with rounded tubercles narrowly interspaced from each other, head and snout with distinct rounded or oval tubercles, eyelids with tubercles, all are about same size as those on the head and body. Lower part of body, gular surface and ventrum are equally

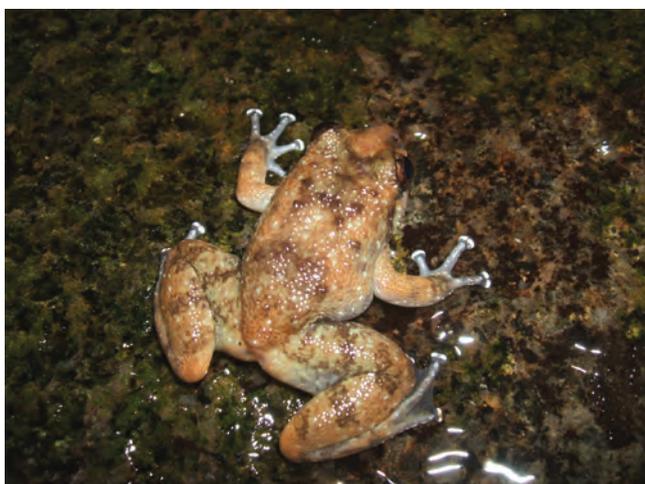


Fig. 3. A very pale female from the type locality, photographed in 2008 (not collected). Photo by Mediyansyah.

tuberculated but tubercles not as tightly packed compared to dorsal parts.

Coloration in life. – All three specimens were essentially uniform dark brown or blackish without any specific markings or pattern or mottling. Lower parts are mottled with dark brown and gular surface is more heavily marked (Fig. 2). Lips uniform as other parts of head and body, not barred although the region below the eyes is distinctly darker, bearing a single white dot exactly below the eyes. A similar darker area is on the lips below the nostril. Upper arm essentially uniform, with no bands visible. The femur and tibia have three indistinct darker cross bands dorsally. Few white spots are scattered on the sides of body and head and lower parts of sides and some on the hands and limbs (Fig. 1). All fingers and toes have a white cross bar straddling middle of the truncated, flat disk and a brownish tint in the middle of the white bar. The iris is dark brown with indistinct reticulation.

Variations. – A light brown specimen having all the characteristics of this species was photographed (not sampled) from the type locality in 2008. However it differs from the type series by having darker areas at the head between the eyes and extending to the scapular area, along the supratympanic fold and another darker area at the pelvic region (Fig. 3). The tip of snout is reddish, and so is the area above the vent. Otherwise all other characters fit with the type specimens.

Etymology. – The specific epithet refers to the type locality Bukit Baka-Bukit Raya National Park. Bukit Raya is the highest and largest mountain (2278 m asl) in Kalimantan, Indonesian part of Borneo. The specific epithet originates from Indonesian language, *raja* (or *raya*) signifies majesty or king, big or huge, also referring to its large size compared to other members of the genus as the most conspicuous feature of the new species.

Comparison. – In the field, *Ingerana rajae* is difficult to distinguish from juvenile frogs of the genus *Limnonectes*, except for the widely enlarged finger and toe tips with a conspicuous white bar on each flattened tip and also the uniformly tuberculated skin texture. *Ingerana rajae* is distinct compared to other members of the genus by lacking tympanic annulus and by having fully webbed toes. Considering the size, *I. rajae* is almost like a giant *I. baluensis* (Fig. 4). The head is slightly broader than long compared to *I. baluensis* which is equal or slight narrower than long, interorbital space is narrower in *I. rajae* compared to *I. baluensis*. *Ingerana rajae* has relatively shorter limbs compared to *I. baluensis*, and also relatively shorter snout and smaller eyes compared to *I. baluensis*. Skin texture is similar in both species (Table 1). The gular surface is heavily marked with large blotches or mottled in *I. rajae* but it is dusted or only lightly spotted in *I. baluensis*. All *I. baluensis* seen have a more or less clear distinction of a lighter dorsolateral region and frequently a pair of dark spot below the scapular area middorsally. *Ingerana rajae* lacks such dorsolateral light markings and middorsal dark markings. *Ingerana tasanae* has a darker gular surface with rounded light markings up to the breast area. The limbs have two or three dark bars.

In *I. baluensis*, the limbs are moderately mottled so that the dark bars are not clearly evident. *Ingerana rajae* has very dark brown limbs with slightly distinct darker bars. Toe webbings are much more extensive in *Ingerana rajae* (compared to the rest of the genus), all the toes is essentially fully webbed, but the penultimate phalange of fourth toe is essentially free from wide webbings at the outer side. In *I. baluensis* the two last phalanges of the fourth toe are free from webbing. *Ingerana tasanae* has toe webbings about the same extent as *I. baluensis*, and the head has a distinct pineal spot, absent in *I. rajae*. *Ingerana charlesdarwinii* is an equally large species, but has narrow toe and finger tips devoid of circum-marginal grooves.

Ingerana mariae from Palawan is slightly smaller compared to *I. rajae*, although the number of known specimens is too low to give an accurate assessment for the species. Both species have very wide truncated disks on fingers and toes. Heads of both species are also wider than long, but the eyes are smaller in *I. mariae* than in *I. rajae*. The toe webbing of *I. mariae* is slightly less extensive compared to *I. rajae*, as it does not reach the inner side of the fourth toe disk. The other differences of *I. rajae* compared to *I. mariae* are the absence of tympanum and the depression along the vertebrae. *Ingerana tasanae* has the same tuberculated skin and the type has a conspicuous pineal spot on the snout which is not clearly present in *I. rajae*. *Ingerana tasanae* is unique in having a pair of tarsal folds commencing of the outer and inner sides converging towards the heel as parallel folds so that the species is readily recognisable compared to other species. *Ingerana tasanae* has reduced webbings on essentially all toes while it is essentially fully webbed in *I. rajae*, except for the tip of fourth toe. *Ingerana tenasserimensis* is quite distinct from other species in having small finger and toe tips and the toes are only webbed at the base, so that no confusion could be raised from this Burmese species. *I. rajae* differs from *I. tenasserimensis* by the nature of finger and toe tips which are very small but bearing circum-marginal grooves. The webbings of *I. rajae* are also more extensive compared to *I. tenasserimensis* which is only webbed at the base or at most to the first subarticular tubercle. The skin is covered with rounded tubercles in *I. rajae* to contrast to the essentially

smooth, or with fine skin folds, *I. tenasserimensis*. The size of *I. rajae* is larger compared to that species as well. In addition, *I. tenasserimensis* has no tarsal fold. *Ingerana charlesdarwinii* from Andaman Island is specific in having smooth skin with hairline ridges. Further *I. charlesdarwinii* differs from *I. rajae* in having fingers without circum-marginal grooves.

We performed a more thorough analysis between the new species with three other members of the genus, *I. baluensis*, *I. tasanae* and *I. tenasserimensis*. As the number of specimens is relatively low, only a Kruskal Wallis test can be performed. The results show that except for TY/SVL and IO/SVL, all proportions are significantly different at $p < 0.001$ level. In fact most ratios between species showed minimum overlapping so we treat the Bukit Baka specimens as a distinct species. A number of small *Limnonectes* are about the same size as *Ingerana rajae*, and could easily be confused in the field. Most *Limnonectes*, however, have smooth skin and none has flattened finger and toe tips, hence can be differentiated easily by these two characteristics. *Limnonectes hascheanus* differs in being smaller in size and having very reduced toe webbings. *Limnonectes parvus* is also a small species, with smooth skin and very reduced webbings. *Limnonectes palawanensis* is easily distinguished from this species by having smooth skin and a pair of dorsolateral folds. *Limnonectes nitidus* is a much larger species, and also has smooth skin with dorsolateral folds. *Limnonectes tweediei* is another small species with smooth skin although the dorsolateral folds are absent, and it does not have expanded finger and toe disks. *Limnonectes asperatus* is a rough skinned species, but the skin ornamentation composed of more or less spinous tubercles, different compared to the rounded tubercles in *Ingerana*.

Occidozyga semipalmatus is another species which might be misidentified in the laboratory as it is similar in most respects to *Ingerana* especially in having fingers with flattened disks but no circum-marginal groove. The finger disks have equally a white bar straddling in the middle. However, the lower jaws have a single median cusp at the far end and the palatine has no vomerine teeth, which might serve to distinguish it from most *Ingerana*.

Ecology. – The specimens were located in a microhabitat similar to that of *I. baluensis*, along seepage areas close to small streams, slow moving water and adjacent to swampy forest floor. Judging from the fully webbed toes and absence of tympanic annulus, *I. rajae* may be more aquatic than *I. baluensis*. The absence of external tympana corroborates the possibility that the species also does not vocalise, but males are needed to confirm this behaviour. This is a primary forest habitat, with minimum human exposure, where 62 other amphibians species have been collected. For the same microhabitat, we have collected *Limnonectes rhacodus*, *Chaperina fusca*, *Leptolalax gracilis* and *Microhyla borneensis*. In this forested area, *Ansonia minuta* and *Staurois latopalmaris* are the most abundant species.



Fig. 4. Comparison between adults of *Ingerana rajae* (SVL 40.1 mm) and *Ingerana baluensis* (SVL 21 mm). Photo by D. T. Iskandar.

Table 1. Detailed measurement and ratios of four *Ingerana* species. Upper line, average \pm SD; lower line, range. ** significant at $p < 0.001$ level; *significant at $p < 0.01$ level for all four species based on a Kruskal Wallis test.

| | <i>Ingerana rajae</i> | | <i>Ingerana baluensis</i> | <i>Ingerana tenasserimensis</i> | <i>Ingerana tasanee</i> |
|----------|-----------------------|-----------------------|-------------------------------|---------------------------------|-------------------------------|
| | RMBR 1153 holotype | RMBR 1127 paratype | (n=8) | (n=3) | (n=4) |
| SVL** | 40.1 | 34.6 | 23.45 \pm 2.97 19.8–27.7 | 29.83 \pm 1.94 27.7–31.5 | 42.70 \pm 0.92 41.5–43.7 |
| HL** | 16.75 | 14.8 | 11.26 \pm 1.15 9.9–13.2 | 12.70 \pm 0.70 11.9–13.2 | 18.38 \pm 0.73 17.3–18.9 |
| HW** | 17 | 15.6 | 10.65 \pm 1.02 9.4–12.6 | 12.30 \pm 1.08 11.4–13.5 | 18.23 \pm 1.05 16.7–19.0 |
| IO | 2.95 | 2.7 | 2.29 \pm 0.39 2.0–3.2 | 2.37 \pm 0.25 2.1–2.6 | 3.13 \pm 0.30 2.8–3.5 |
| ED** | 6.05 | 5.3 | 3.91 \pm 0.28 3.7–4.4 | 5.93 \pm 0.60 5.3–6.5 | 7.95 \pm 0.29 7.7–8.2 |
| SL** | 7.2 | 6.5 | 3.92 \pm 0.40 3.3–4.6 | 4.97 \pm 0.25 4.7–5.2 | 7.73 \pm 0.40 7.3–8.2 |
| EN** | 4.5 | 3.8 | 2.10 \pm 0.34 1.8–2.7 | 2.43 \pm 0.15 2.3–2.6 | 3.80 \pm 0.22 3.5–4.0 |
| NT** | 3.25 | 2.8 | 1.59 \pm 0.47 1.0–2.4 | 2.20 \pm 0.10 2.1–2.3 | 3.95 \pm 0.30 3.6–4.2 |
| IN** | 4 | 3.5 | 2.69 \pm 0.34 2.3–3.1 | 3.63 \pm 0.12 3.5–3.7 | 5.10 \pm 0.24 4.8–5.4 |
| ET* | 0 | 0 | 0.61 \pm 0.40 0.4–1.3 | 0.70 \pm 0.17 0.6–0.9 | 1.20 \pm 0.12 1.1–1.3 |
| TY* | 0 | 0 | 2.30 \pm 0.32 2.0–3.0 | 2.23 \pm 0.23 2.1–2.5 | 3.00 \pm 0.29 2.6–3.3 |
| UA** | 10.9 | 8.4 | 6.40 \pm 0.45 5.8–7.0 | 7.83 \pm 0.40 7.4–8.2 | 12.50 \pm 1.07 11.1–13.6 |
| LA** | 8 | 7.3 | 5.20 \pm 0.67 4.2–6.0 | 6.20 \pm 0.36 5.9–6.6 | 9.23 \pm 0.43 8.7–9.7 |
| HA** | 10.3 | 10 | 6.61 \pm 0.68 5.8–7.7 | 8.40 \pm 0.53 7.8–8.8 | 11.20 \pm 0.65 10.6–11.9 |
| FE** | 19.1 | 19.8 | 13.46 \pm 1.35 11.5–15.5 | 14.87 \pm 0.49 14.3–15.2 | 20.43 \pm 0.97 19.3–21.5 |
| TI** | 18.3 | 17.7 | 12.24 \pm 1.88 10.1–15.1 | 15.27 \pm 0.51 14.7–15.7 | 18.53 \pm 0.81 17.6–19.5 |
| PL** | 25.5' | 24.4 | 17.71 \pm 2.32 15.0–21.5 | 23.20 \pm 1.54 21.5–24.5 | 28.18 \pm 0.63 27.3–28.8 |
| IM** | 2.71 | 2.62 | 1.63 \pm 0.15 1.5–1.8 | 1.90 \pm 0.20 1.7–2.1 | 2.85 \pm 0.34 2.4–3.2 |
| 3FD** | 2.57 | 2.07 | 1.08 \pm 0.10 1.0–1.2 | 1.67 \pm 0.06 1.6–1.7 | 1.90 \pm 0.24 1.4–1.9 |
| 1TD** | 2.0 | 1.8 | 1.00 \pm 0.11 0.9–1.1 | 1.27 \pm 0.06 1.2–1.3 | 1.70 \pm 0.18 1.5–1.9 |
| 4TD* | 2.11 | 1.99 | 1.23 \pm 0.15 1.1–1.4 | 1.27 \pm 0.21 1.1–1.5 | 1.65 \pm 0.21 1.4–1.9 |
| EM* | 2.75 | 1.96 | 1.33 \pm 0.15 1.2–1.5 | 1.50 \pm 0.17 1.4–1.7 | 2.33 \pm 0.05 2.3–2.4 |
| HL/SVL* | 0.42 | 0.43 | 0.48 \pm 0.03 | 0.43 \pm 0.04 | 0.43 \pm 0.01 |
| HW/SVL* | 0.42 | 0.45 | 0.46 \pm 0.03 | 0.41 \pm 0.03 | 0.43 \pm 0.02 |
| HW/HL* | 1.02 | 1.05 | 0.95 \pm 0.02 | 0.97 \pm 0.05 | 0.99 \pm 0.02 |
| IO/SVL | 0.07 | 0.08 | 0.10 \pm 0.01 | 0.08 \pm 0.00 | 0.07 \pm 0.01 |
| ED/SVL* | 0.15 | 0.15 | 0.17 \pm 0.02 | 0.20 \pm 0.01 | 0.19 \pm 0.01 |
| SL/SVL | 0.18 | 0.19 | 0.17 \pm 0.01 | 0.17 \pm 0.02 | 0.18 \pm 0.01 |
| EN/SVL | 0.11 | 0.11 | 0.09 \pm 0.01 | 0.08 \pm 0.01 | 0.09 \pm 0.00 |
| NT/SVL | 0.08 | 0.08 | 0.07 \pm 0.01 | 0.07 \pm 0.00 | 0.09 \pm 0.01 |
| IN/SVL | 0.10 | 0.10 | 0.11 \pm 0.01 | 0.12 \pm 0.01 | 0.12 \pm 0.01 |
| ET/SVL | – | – | 0.02 \pm 0.02 | 0.02 \pm 0.00 | 0.03 \pm 0.00 |
| TY/SVL** | – | – | 0.10 \pm 0.01 | 0.18 \pm 0.03 | 0.16 \pm 0.01 |
| UA/SVL | 0.27 | 0.24 | 0.28 \pm 0.03 | 0.26 \pm 0.02 | 0.29 \pm 0.02 |
| LA/SVL | 0.20 | 0.21 | 0.22 \pm 0.01 | 0.21 \pm 0.01 | 0.22 \pm 0.01 |
| HA/SVL | 0.26 | 0.29 | 0.28 \pm 0.01 | 0.28 \pm 0.03 | 0.26 \pm 0.01 |
| FE/SVL* | 0.48 | 0.57 | 0.58 \pm 0.05 | 0.50 \pm 0.04 | 0.48 \pm 0.02 |
| TI/SVL | 0.46 | 0.51 | 0.52 \pm 0.06 | 0.51 \pm 0.04 | 0.43 \pm 0.01 |
| PL/SVL | 0.64 | 0.71 | 0.76 \pm 0.03 | 0.78 \pm 0.07 | 0.66 \pm 0.01 |

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Comparative material. – *Ingerana tasanae*: ZRC. 1.11795. 1 ex, juv. from Khao-Lak, Phang-Nga Province, Thailand, juv. (identified as *I. tenasserimensis*). FMNH 216071 (1 ex.) from Thailand; FMNH 171414–171416 (3 ex.) from Ranong Province, Thailand; *I. tenasserimensis*: FMNH 21635–21637 (3 ex.) From Trang Province, Thailand; *I. baluensis*: ZRC 1.2737. from Lahad Datu, Danum Valley, Sarawak, Malaysia; ZRC 1.11069, 1.11070. from Kapit Palagus, Sarawak, Malaysia; ZRC 1.3152. from Temburong, Batu Apoi, Brunei. MZB Amph. (3 ex.), from Mt, Lawit, Betung Kerihun National Park, West Kalimantan, Indonesia. ITB coll. (3 ex.) from Sebuku-Sebakung, Kayan Mentarang National Park, East Kalimantan, Indonesia; *I. maria*: FMNH 51359–51360 (2 ex.- Types) from Palawan, the Philippines; *Limnonectes* n. sp. 1: MZB Amph. 2827, 2828–2833, (6 ex.), ITB. unnumbered (12 ex.); ZRC 1.3264, 1 ex. Mt. Kerinci, West Sumatra, Indonesia. *Limnonectes* n. sp 2. MZB Amph. 3035–3037; FMNH 252456; 4 ex. (types), from West Sumatra, Indonesia; *Limnonectes hascheanus*: FMNH 189959; 1 ex., from Bukit Lanjang, Selangor, Peninsular Malaysia; FMNH 190350, 1 ex., from Kuala Lumpur, Selangor, Peninsular Malaysia, RMBR–ZRC 1. 614–619, 6 ex., from Penang Island, Peninsular Malaysia. *Limnonectes limborgii*: FMNH 186355, –358, –365, –370, –373, –377, –378, –418, –448, –885, 12 ex., from Bukit Lanjan, Peninsular Malaysia; FMNH 172787–90, 4 ex., from Bhetong, Yala Province, Thailand; 216054, 1 ex., from Doi Suthep, Chiang Mai Province, Thailand. *L. parvus*: FMNH 50269, 50270, 96073, 131315, Mindanao, the Philippines. *L. microdiscus*: ITB coll, ZRC, FMNH, 104 ex, 61 females and 43 males, from Cibodas, West Java, Indonesia. *L. nitidus*: ZRC 1.849 & 1.850, 2ex, ad and juv. (paratypes) from Cameron highland, Malaysian Peninsula.

L. palavanensis: FMNH 245115, –16, –21, –23, 4 ex., from Sabah, Malaysia; ITB coll., 1 ex., from Central Kalimantan, Indonesia. *L. tweediei*: FMNH 141815, –24, –31, –39, –37, 181845, –23; BPBM 3449, 3448, 4523, 4530, 4567, 4570, 4571, 4873; 15 ex., from Peninsular Malaysia.

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