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New Flap-Legged Forest Gecko (Genus *Luperosaurus*) from the Northern Philippines

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ABSTRACT.—**We describe a new species of *Luperosaurus* from the Luzon faunal region, northern Philippines. The new species is most similar to, and has long been confused with, *Luperosaurus cumingii* from Luzon Island but differs from this and all other *Luperosaurus* by numerous characters of scalation, color pattern, and a suite of variables related to its small body size. The new species has been recorded at four localities along the eastern seaboard of Luzon and on Camiguin Norte, a small island just northeast of Luzon; it may also occur on Polillo and Lubang Islands. Data from our recent survey work suggest that some *Luperosaurus* species may be adapted to low elevation, coastal forest and that these species may now be encountered rarely now because this habitat type is so severely imperiled by centuries of deforestation and near complete development of virtually all Philippine coastlines.**

Philippine lizards of the family Gekkonidae comprise 47 species (Taylor, 1915, 1922; Brown and Alcala, 1978) in 10 genera: *Gehyra* (1), *Gekko* (12), *Hemidactylus* (5), *Hemiphyllodactylus* (2), *Lepidodactylus* (6), *Luperosaurus* (7), *Ptychozoon* (1), *Pseudogekko* (4), and *Cyrtodactylus* (9), (Brown et al., 2007, 2010a; Welton et al., 2009, 2010a, 2010b; Zug, 2011). Approximately 85% of Philippine gekkonid species diversity is endemic to the archipelago; as species diversity continues to increase, new descriptions include both highly distinctive species discoveries (Roesler et al., 2006; Brown et al., 2009, 2010b; Linkem et al., 2010a) and morphologically conservative or even ''cryptic'' forms, characterized by slight but consistent diagnostic characters of morphology and high levels of genetic divergence (Siler et al., 2010; Welton et al., 2010a,b).

The genus *Luperosaurus* contains 12 species (Brown et al., 2000, 2007, 2010b), and most are known only from one or two specimens (Ota et al., 1996; Brown and Diesmos, 2000). Philippine members include seven endemic species: *Luperosaurus corfieldi*, *Luperosaurus cumingii*, *Luperosaurus gulat*, *Luperosaurus joloensis*, *Luperosaurus kubli*, *Luperosaurus macgregori*, and *Luperosaurus palawanensis* (Brown et al., 2007, 2010b; Gaulke et al., 2007). The Philippine taxa and their Bornean relatives *Luperosaurus yasumai* and *Luperosaurus sorok* (Ota et al., 1996; Das et al., 2008) are robust-bodied and morphologically distinct from the slender, elongate-bodied non-Philippine species *Luperosaurus browni* (Peninsular Malaysia and Borneo), *Luperosaurus brooksii* (Sumatra), and *Luperosaurus iskandari* (Sulawesi; Brown et al., 2000). In a phylogenetic analysis of morphological characters Brown et al. (2000) found that the robust-bodied members of the genus (the Philippine species plus Bornean *L. yasumai*, and, by implication, *L. sorok*) formed a clade that was distinct from, and reciprocally monophyletic with, the slender-bodied forms.

One species, *L. cumingii*, has formerly been considered relatively widespread (Brown and Diesmos, 2000; Gaulke et al., 2007). It has been recorded at multiple localities on both the Luzon and Visayan Pleistocene Aggregate Island Complexes (PAICs; Brown and Diesmos, 2002, 2009) and possibly the small associated islands of Polillo, Camiguin Sur, and Lubang Islands (Brown and Alcala, 1978; Brown and Diesmos, 2000; Gaulke et al., 2007). This apparently widespread species has been collected with moderate frequency over the last 30 years and, thus, appeared to be the more commonly encountered member of the genus (Brown and Diesmos, 2000; Brown et al., 2007; Gaulke et al., 2007).

Recently Gaulke et al. (2007) demonstrated the specific status of the Visayan populations (Negros and Panay Islands; see also Dolino et al., 2009) and described the Panay + Negros Island lineage as a distinct species, *L. corfieldi*. *Luperosaurus corfieldi* was distinguished from *L. cumingii* on the basis of large body size in adults, color pattern, and reduction or absence of ornamental tubercles on the body, tail, and edges of dermal fringes bordering limbs. During the course of that and subsequent (Brown et al., 2007, 2010b) investigations it has become clear that the remaining specimens (from Luzon, Polillo, Lubang, and Camiguin) fall into two size and phenotypic categories. The *L. cumingii* syntypes (BMNH 1946.8.22.41 and 1946.8.22.42; the largest of which is a female, 85.0 mm SVL) lack specific locality data but were convincingly matched by Gaulke et al. (2007) to the large-bodied, ornately scaled phenotype with a bright yellow venter from the Bicol Peninsula of Luzon (exemplified best by a recent specimen from Mt. Malinao, Albay Province: TNHC 61910, 74.1 mm). All remaining specimens from Luzon and satellite islands (Fig. 1) are markedly smaller (mature adults are approximately 55–65 mm SVL), nontuberculate, with reduced interdigital webbing, less dermal fringes bordering the limbs, and lack the conspicuous coloration of true *L. cumingii* from the presumed site of original collection (the Bicol Peninsula). Previous workers have considered these smaller size class individuals to be immature representatives of *L. cumingii* but close examination reveals many of the relevant specimens to be adults with mature testes in males and fully formed oviducts with mature eggs in females.

In this paper, we describe the smaller, widespread form as a new species. One consequence of this action is to limit the known range of *L. cumingii* to a very small part of southern Luzon Island. This has important implications for conservation and adds yet another endemic lineage (true *L. cumingii*) to the biogeographically unique and severely imperiled forests surrounding the volcanoes of the Bicol Peninsula.

MATERIALS AND METHODS

RMB scored data from fluid-preserved specimens deposited in collections in Europe, the United States, Japan, and the Philippines (Leviton et al., 1985; Appendix 1). Sex was determined by gonadal inspection or by scoring of prominent secondary sexual characteristics (Brown et al., 1997, 2000; Brown, 1999) when dissection was not possible. Measurements (to the nearest 0.1 mm) were taken with digital calipers following character definitions by Brown et al. (1997), Brown (1999), and Brown et al. (2007, 2009, 2010a). Characters include: snout–length, tail length, head length, head width, head depth, snout length, eye diameter, eye–narial distance, internarial distance, interorbital distance, axilla–groin distance, femur

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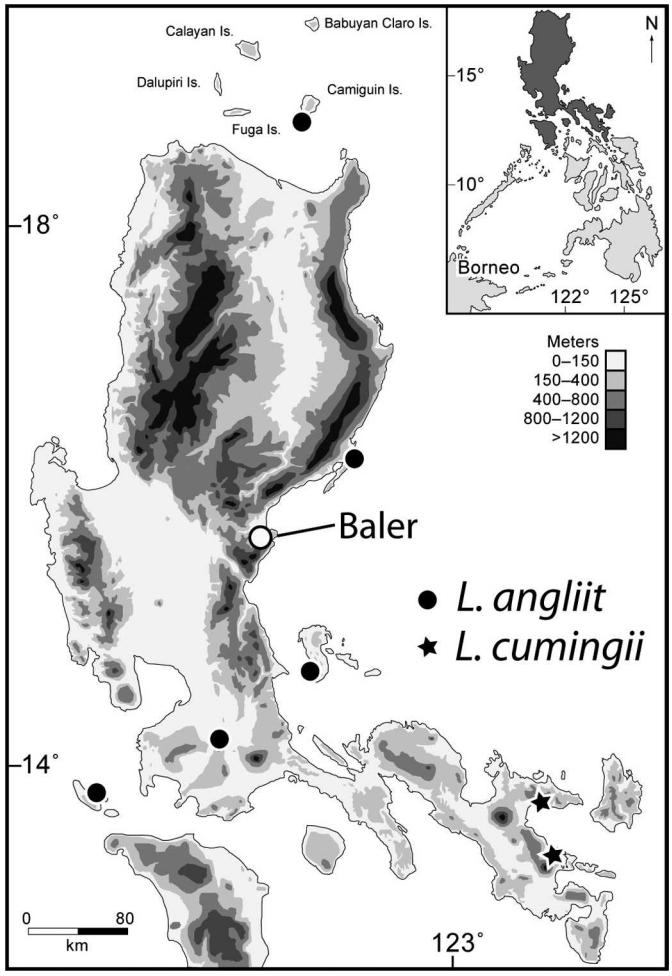

FIG. 1. Map of Luzon Island in relation to the Philippines (inset) with the type locality of *Luperosaurus angliit* (Municipality of Baler, Aurora Province) indicated with an open circle. Comparison of the *Luperosaurus cumingii* syntypes (BMNH 1946.8.22.41 and 1946.8.22.42) to recent collections (UF 77829, TNHC 61910) suggests that Cuming's (1836–1840) types most probably originated on the Bicol Peninsula (Gaulke et al., 2007).

length, tibia–fibula length, first and fourth toe lengths, tail width, tail depth, number of supralabials and infralabials posteriorly to the point labials are no longer differentiated; preanofemoral pore-bearing scales, subdigital lamellae under fingers and toes, transverse midbody scales, paravertebral and midventral scales between midpoints of limb insertions, tail annuli, and subcaudals. We employ lineage-based species concepts (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990; de Queiroz, 1999) in an effort to recognize ancestor-descendent population segments with a distinct evolutionary history, evidence of lineage cohesion, and in cases where the hypothesis of conspecificity can be confidently rejected (Brown and Diesmos, 2002; Brown and Guttman, 2002; Gaulke et al., 2007).

SYSTEMATICS

Luperosaurus angliit sp. nov.
Figures 2–4

Holotype.—PNM 9702 (Field Collection number ACD 3678), adult female, collected at 1930 h by Arvin C. Diesmos 5 April 2008, 91 m above sea level, Barangay Zabali, Municipality of Baler, Aurora Province, Luzon Island, Philippines (15.742°N; 121.576°E; Fig. 1). The holotype was captured on the perimeter fence surrounding the main administration building on the campus of Aurora State College of Technology.

Paratypes.—KU 321815 (ACD 4901), PNM 9703 (ACD 4902), adult males, collected 5 July 2009, by Arvin C. Diesmos on tree trunks in coastal forest at sea level, Sitio Casapsapan, Barangay Culat, Municipality of Casiguran, Aurora Province, Luzon Island (16.293°N; 122.186°E); KU 308023 (RMB 7343), collected 12 February 2007 by J. Fernandez and C. Oliveros on a primary forest tree trunk, 350 m above sea level, Barangay Balatubat-Kauringan, Municipality of Calayan, Cagayan Province, Camiguin Norte Island.

Referred Specimens.—We tentatively refer the following specimens to *L. angliit* with the caveat that the absence of reliable locality data, or the immature or poorly preserved state of the material, render identification somewhat questionable: KU 326160: approximately 800 m on Mt. Makiling, University of the Philippines at Los Baños upper campus, forestry nursery area, Barangay Batong Malake, Municipality of Los Baños, Laguna Province, Luzon Island; PNM 7242: Municipality of Looc, Oriental Mindoro Province, Lubang Island; CAS 62453–62454: vicinity of Polillo Town; Polillo Island, Municiplity of Polillo, Quezon Province, Polillo Island; NMW 17985:1: ''Camiguin'' (presumably Camiguin Norte Island, Cagayan Province, northeast of Luzon island); SMF 9044: ''Central Luzon, Philippines''; ZMB 5578: ''Philippines.''

Diagnosis.—The new species is distinguished from all species of *Luperosaurus* by (1) its relatively small, slender body; (2) reduced interdigital webbing; (3) reduced cutaneous expansions bordering the limbs; (4) absence of ventrolateral body tubercles; (5) absence of spinose tubercles on edges of cutaneous expansions ordering the limbs; (6) the presence of only a few ventrolateral tubercles on the caudal margin of each tail whorl; (7) postrictal and nuchal tubercles absent; (8) precloacofemorals 17–19; (9) relatively low numbers of supralabials and infralabials; and (10) low subdigital scansors counts. A summary of the distribution of diagnostic character states in Philippine *Luperosaurus* is presented in Table 1.

Comparisons.—The critical comparison for the recognition of the new species is to *L. cumingii*, the taxon with which *L. angliit* has so long been confused. *Luperosaurus angliit* differs from *L. cumingii* by SVL 59.4–64.7 (vs. 73.4–82.7), enlarged scales in the precloacofemoral series 17–19 (vs. 20–28), midbody scales 162–182 (vs. 184–199), supralabials 12–15 (vs. 15–17), Toe I scansors 9–10 (vs. 12–14), Toe IV scansors 11–13 (vs. 15–16), the absence (vs. presence) of spinose postrictal, nuchal, and ventrolateral body tubercles, reduction (1/3–1/2) of interdigital webbing between fingers and toes (vs. 1/2–2/3), limitation of ventrolateral tail tubercles to one or two small tubercles on the caudal margin of each tail segment (vs. entire ventrolateral tail margin lined with highly spinose, recurved tubercles), and reduction of cutaneous expansions bordering the limbs (vs. cutaneous expansions extensive throughout limbs; Table 1).

Snout–vent length of the new species (59.4–64.7) distinguishes it from *L. corfieldi* (70.0–95.0), *L. kubli* (105.4), *L. palawanensis* (43.7, 52.0), *L. joloensis* (27.5, 32.4), and *L. gulat* (81.3). The number of differentiated (enlarged) scales in the precloacofemoral series of *L. angliit* (17–19) distinguishes it from *L. kubli* (16), *L. palawanensis* (28–32), *L. joloensis* (30–31), and *L. gulat* (40). Supralabials (12–15) distinguish the new species from *L. gulat* (11); infralabials (14–15) distinguish *L. angliit* from *L. corfieldi* (12–14), *L. kubli* (12), *L. palawanensis* (10–11), *L. joloensis* (10–12), and *L. gulat* (11). The number of Toe I scansors (9–10) and Toe IV scansors (11–13) distinguishes *L. angliit* from *L. corfieldi* (Toe I: 10–14; Toe IV:14–20) and *L. kubli* (Toe I: 12; Toe IV: 16); the number of Toe III scansors (11–13) distinguishes the new species from *L. corfieldi* (14–20) and *L. kubli* (16). The absence of postrictal and nuchal tubercles distinguishes *L. angliit* from *L. palawanensis* and *L. joloensis*, and the absence of ventrolateral body tubercles distinguishes *L. angliit* from *L.*

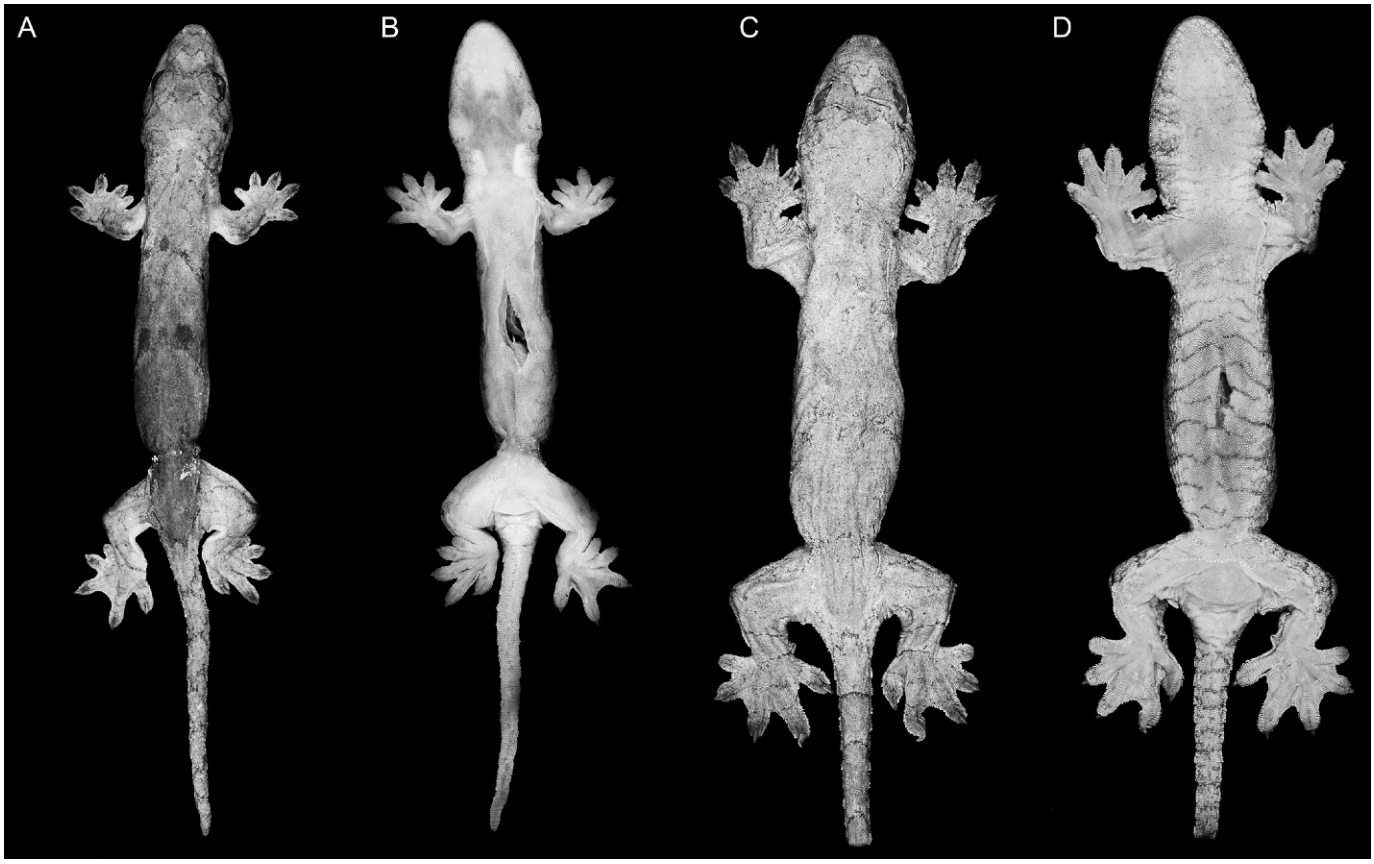

FIG. 2. Dorsal (A) and ventral (B) views of the body of the holotype of *Luperosaurus angliit* (PNM 9702; adult female, SVL = 62.9 mm; from Barangay Zabali, Municipality of Baler, Aurora Province, northeastern Luzon) and *Luperosaurus cumingii* (TNHC 61910, SVL = 71.4 mm; from Municipality of Tiwi, Albay Province, Bicol Peninsula). Note differences in ventral color pattern and extent of cutaneous expansions of the posterior margin for the forelimb in *L. cumingii*.

corfieldi, *L. macgregori*, *L. palawanensis*, *L. joloensis*, and *L. gulat*. *Luperosaurus angliit* is further distinguished from *L. joloensis* by the absence of spinose scales on the margin of the cutaneous expansion on the anterior surface of the forelimb. The absence of dorsal trunk tubercles distinguishes the new species from *L. corfieldi* (present, convex), *L. palawanensis* (present, spinose), *L. joloensis* (present, spinose), and *L. gulat* (present, flat to convex). The presence of one or two elongate, spinose ventrolateral tail tubercles along the caudal margin of each tail segment (whorl, annulus) distinguishes *L. angliit* from *L. joloensis* (vs. entire ventrolateral margin of each tail segments lined with spinose tuberles), *L. corfieldi*, *L. macgregori*, and *L. kubli* (ventrolateral tail tubercles absent or limited to only 1 or 2 very small tubercles per tail segment), *L. palawanensis* (tail tubercles highly spinose, encircling each tail segment along caudal edge), and *L. gulat* (enlarged, flat or convex tubercles encircling tail along caudal edge of each tail segment). The number of midbody scales (162–182) in *L. angliit* distinguishes it from *L. kubli* (157), *L. macgregori* (135–146), *L. palawanensis* (99–106), *L. joloensis* (128–133), and *L. gulat* (82). The absence of differentiation between ventrals and dorsals distinguishes *L. angliit* from *L. corfieldi*, *L. kubli*, *L. palawanensis*, *L. joloensis*, and *L. gulat* (ventrals slightly to moderately enlarged). The presence of undifferentiated (small) postmental chin shields distinguishes the new species from *L. kubli*, *L. palawanensis*, *L. joloensis*, and *L. gulat* (vs. chin shields slightly to moderately enlarged). The extent of interdigital webbing between Toes III and IV (1/3–1/5 length of digits) distinguishes *L. angliit* from *L. kubli* (1/6–1/4) and *L. gulat* (1/10–1/8). Finally, the reduced extent of cutaneous expansions bordering the limbs of *L. angliit* distinguishes the new species from *L. corfieldi* and *L. joloensis* (vs. expansions much more extensive; Table 1), *L. kubli*, *L. palawanensis*, *L. macgregori*, and *L. gulat* (markedly less extensive; Table 1).

Description of Holotype.—Adult female in excellent condition (Figs. 2–4). Body 62.9 mm snout–vent; habitus elongate, slender; limbs stout, tail original, relatively short; head at widest point 1.2 times wider than body (Figs. 2, 3); all limbs with expanded lateral cutaneous flaps or dermal folds covered with undifferentiated, minute scales on dorsal and ventral surfaces; anterior margins of forelimb with moderate crenulate flaps; posterior margins of forelimb with minute, narrow fold; anterior margins of hind limb with similar narrow folds; posterior margins of hind limb with moderate flaps.

Head moderate, elongate, with only slightly hypertrophied temporal and adductor musculature; snout subelliptical, rounded at tip in dorsal and lateral aspect (Fig. 2A,C); head width 71% of head length and 18% of snout–vent length; snout length 66% of head width and 47% of head length; dorsal surfaces of head smooth, homogenous, with only slight postnasal, prefrontal, interoribital, and parietal concavities; auricular opening subcircular; tympanum deeply sunken; orbits moderate, with slightly pronounced supraorbital crests; palpebra only slightly raised above parietal surface; eye moderate, pupil vertical, margins wavy (Fig. 2C); tympanic annulus diameter 41% of eye diameter; limbs stout and relatively short, femoral segments of hind limbs robust, musculature hypertrophied; tibia length 13% of snout–vent length, 77% of femur length.

Rostral large, subrectangular 1.5 times as broad as high, with slight dorsomedial depression; nostril surrounded by rostral, first labial, an enlarged squareish supranasal, and two postnasals, each smaller than adjacent supranasals; dorsal

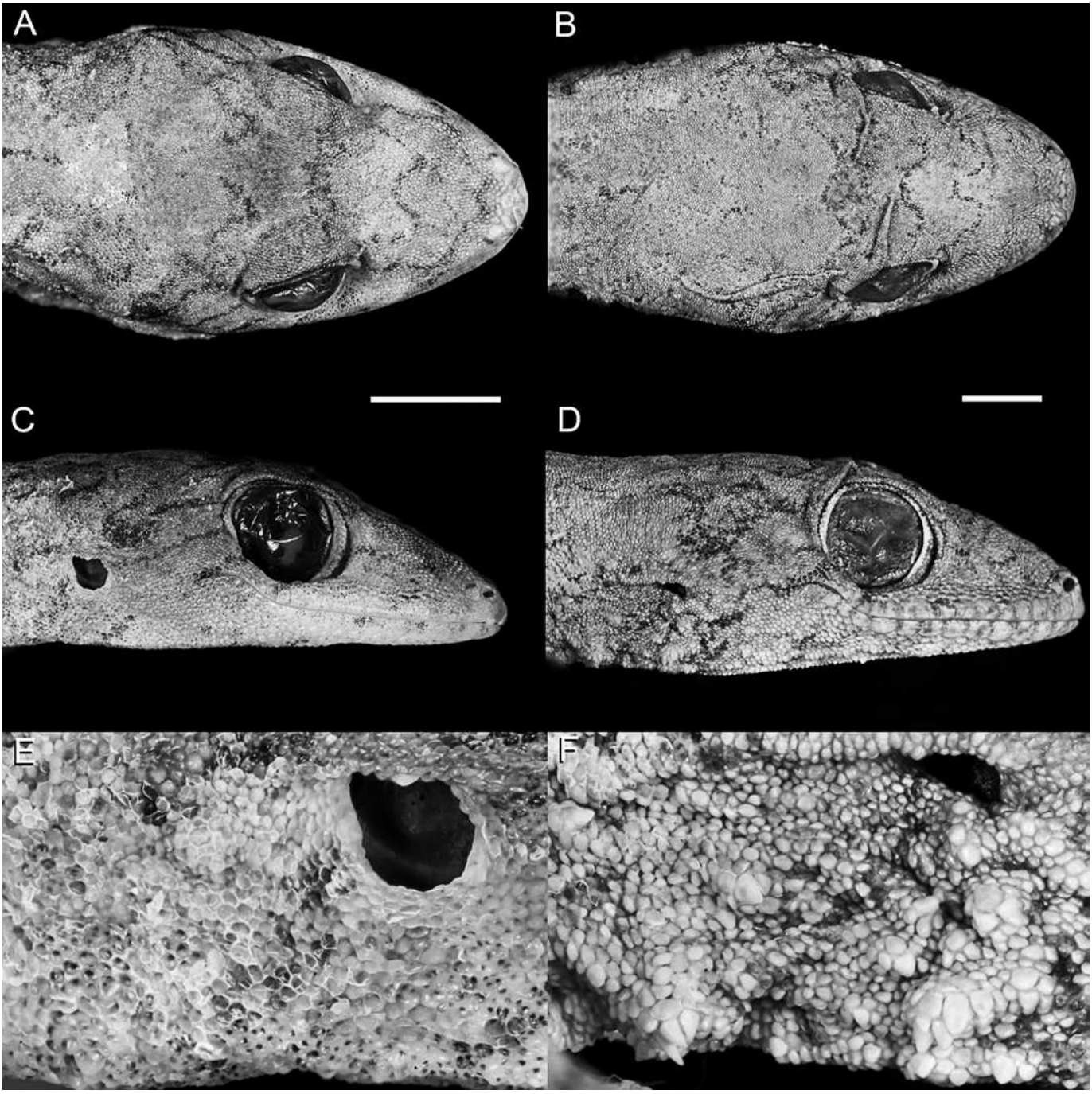

FIG. 3. Dorsal aspect of head of (A) *Luperosaurus angliit* (holotype, PNM 9702) and (B) *Luperosaurus cumingii* (TNHC 61910); lateral views of sample specimens (C, D); enlarged view of postrictal (infra-auricular) regions of same specimens, showing absence of recurved, highly spinose tubercles in *L. angliit* (E) and their presence in *L. cumingii* (F). Note differences in configuration of auricular opening and the concave preoccular and loreal region in *L. angliit*. Scale bars = 5 mm.

postnasal (on dorsopostero edge of nares) smaller than ventral postnasal on posterior margin of nares; supranasals separated by a single enlarged, hexagonal internasal; supranasals, internasal, and postnasal followed posteriorly by one row of slightly enlarged, convex snout scales, subsequent to which snout scales are undifferentiated (Fig. 2A,C); dorsal and lateral snout and head scales small, juxtaposed, granular, uniform.

Supralabials 15/15 (9–15 subocular), bordered dorsally by one row of very slightly elongate, similarly flattened snout scales; infralabials 13/13 (last one concealed in postrictal pocket), bordered by three rows of slightly differentiated chin scales (more than 2 or 3 times the size of undifferentiated, minute gular scales), first row elongate to ovoid, second row elongate posteroventrally and pentagonal to hexagonal anteroventrally in postmental position; third row of ventral chin scales only slightly enlarged; subsequent rows indistinguishable from uniformly small, granular gulars and nuchals; postrictal scales slightly enlarged, approximately 2 times the size of scales of temporal region; postrictals and scales of infraauricular and nuchal regions irregular and slightly heterogeneous but with enlarged tubercles absent; mental very small (smaller than adjacent infralabials).

Dorsal cephalic scales round, uniformly small, granular, juxtaposed, predominantly homogenous, excepting slight en-

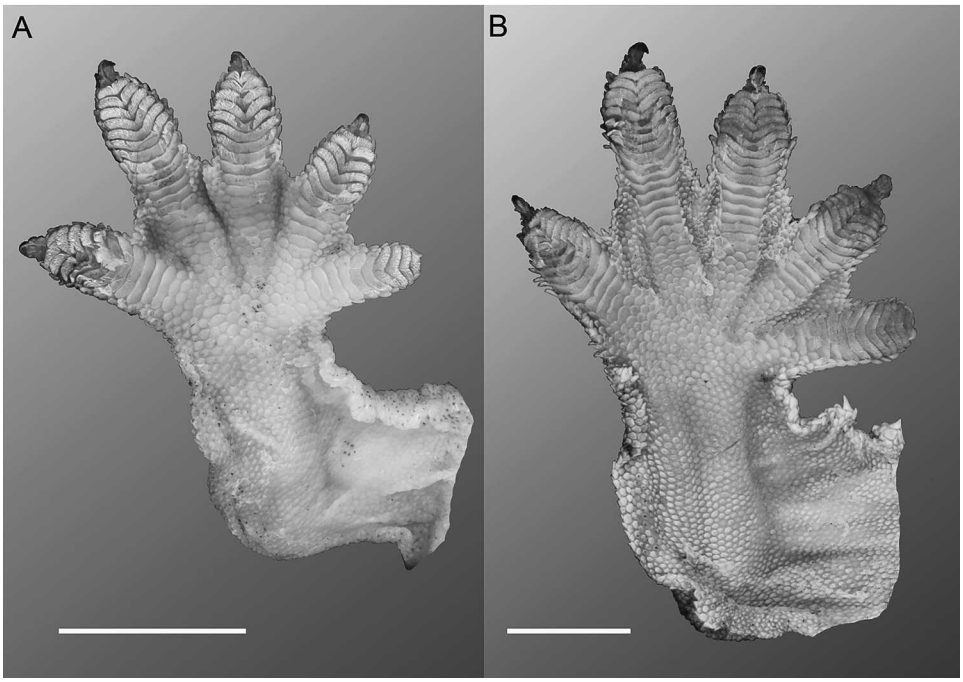

FIG. 4. Inferior view of right forelimbs of (A) *Luperosaurus angliit* (holotype, PNM 9702) and (B) *Luperosaurus cumingii* (TNHC 61910). Note differences in extent of interdigital webbing, extent of cutaneous expansions trailing from the posterior margin for the forelimb, and presence of spinose tubercles on the lead edge of cutaneous expansions of the anterior margin for the forelimb in *L. cumingii*. Scale bars = 5 mm.

largement on distal portions of snout, loreal, and prefrontal regions; preorbital region lacking differentiated scales; temporal and parietal region free of enlarged tubercles; circumorbitals differentiated slightly into 18/16 undifferentiated circumorbitals in preorbital series, 24/25 slightly enlarged circumorbitals in supra- and postorbital series, followed by 8/10 undifferentiated circumorbitals encircling eye posteroventrally; circumorbitals undifferentiated in shape, true spiny ciliaries absent; 45 interorbital scales arranged transversely at palpebral midpoints.

Nuchals granular, uniformly very small, strongly convex, with a few enlarged, lateral tubercles; dorsals enlarged, cycloid, tightly juxtaposed, lacking interstitial granules, with few scattered convex tubercles; minute throat and chin scales gradually transition in pectoral region to slightly enlarged ventrals; throat with moderately enlarged endolymphatic sacs; ventral trunk scales nonimbricate, juxtaposed, slightly convex.

Axilla–groin distance 52% of snout–vent length; undifferentiated dorsal body scales round, convex, nonimbricate, transversely undifferentiated, juxtaposed, lacking interstitial granules; transverse midbody scales 162 (including 34 slightly enlarged ventral rows); paravertebrals between limb insertion midpoints 202; ventrals between limb insertion midpoints 126; dorsal body tuberculation nearly absent, with flat to convex slightly enlarged scales thinly scattered over posterior two-thirds of body trunk, slightly more apparent laterally.

Scales on dorsal surfaces of limbs flat, uniformly granular, small, round, convex, juxtaposed, similar in size to dorsal trunk scales; forelimb scalation homogenous, completely lacking tuberculation; scales of ventral surfaces of forelimbs homogenous, round, granular, juxtaposed, transitioning distally to scales that extend onto the palmar surfaces of the manus and gradually increase in size distal to digits; scales on ventral surfaces of thigh similar, with slight enlargement closer to groin; scales of ventral surface of tibia and ankle moderately enlarged, flat, subimbricate, gradually transitioning to slightly enlarged scales on ventral surface of pes; scales on dorsal surfaces of manus and pes similar to those on dorsal limb and trunk; scales on both dorsal and ventral surfaces of cutaneous expansions bordering limbs minute, uniformly granular.

Differentiated, slightly dimpled, and enlarged scales of the precloacofemoral pore-bearing series (pores absent in females) arranged in a continuous, nearly straight configuration across the precloacal region, and extending laterally onto the distal portions of the thigh; scales anterior to precloacofemorals composed of one row of similarly sized, slightly dimpled scales, and three preceding rows that gradually decrease in size until becoming indistinguishable from surrounding ventrals in groin region; scales posterior to precloacofemorals undifferentiated; a single, moderately enlarged, spinose cloacal spur follows the vent on either side of the tail base.

Digits widely dilated and covered on palmar/plantar surfaces by wide, bowed scansors (Fig. 4A); penultimate 2 or 3 scansors deeply notched (not divided); digits moderately webbed, with web extending one-third to one-half the length of digit from base, and ending well below the dilated hyperextensible portions of digits; scales on dorsal surfaces of digits uniformly small, granular, juxtaposed; those on ventral surfaces of digits transversely widened and slightly imbricate below proximal portions of digits; distal subdigitals differentiated to form bowed, smoothly curved, flattened adhesive scansors; subdigital scansors of manus: 8/8, 9/19, 12/13, 13/12, and 10/11 on left/right digits I–V respectively; pes: 10/10, 11/12, 11/12, 13/13, and 11/10 on left/right digits I–V respectively; all digits but first (inner) clawed; inner digits of both manus and pes with enlarged flattened nail in claw position; remaining terminal claw-bearing phalanges compressed, with large recurved claws (claws sheathed), rising free at distal end, extending beyond dilated distal portion of digit.

Tail relatively short, 63% of snout–vent length; tail height (not including basal denticulate lobes) 75% of tail width; tail not depressed, subcylindrical, with flattened ventral surface due to protrusion of ventrolateral edge composed of a few enlarged scales per tail segment (whorl or annulus) and one or two spinose posteriorly oriented tubercles on the caudal margin of each segment, 17 fracture planes (autotomy grooves) delineating borders of segments, with 15–15 undifferentiated dorsal caudals and 7–9 ventrals per tail segment; dorsal

TABLE 1. Distribution of diagnostic characters states (+, present; −, absent) in *Luperosaurus angliit* and remaining Philippine species of *Luperosaurus*. See Brown et al. (2007: table 1) for distribution of character states distinguishing the morphologically similar group of Philippine species from the remaining, phenotypically divergent non-Philippine species (*Luperosaurus iskandari*, *Luperosaurus browni*, *Luperosaurus brooksi*, and *Luperosaurus yasumai*). Bilaterally symmetrical characters are presented from the right side of specimens. Measurements are presented in millimeters and all specimens (with the exception of the *Luperosaurus joloensis* paratype) were mature adults. Sources of data (all confirmed by examination of specimens) include 1, Brown et al., 2000; 2, Ota et al., 1996; 3, Brown and Alcala, 1978; 4, Brown et al., 2007; 5, Gaulke et al., 2007; 6, Brown et al., 2010b; and 7, this study.

	angliit (*N* = 6)	*cumingii* (*N* = 4)	*corfieldi* (*N* = 7)	*kubli* (*N* = 1)	*macgregori* (*N* = 4)	*palawanensis* (*N* = 2)	*joloensis* (*N* = 2)	*gulat* (*N* = 1)
Snout–vent length	59.4–64.7	74.1–85.0	70.0–95.0	105.4	57.4–58.9	43.7, 52.0	27.5, 32.4	81.3
Precloaco-femorals	17–19	20–28	11–19	16	16–18	28–32	30–31	40
Supralabials	12–15	15–17	14–16	13	13–15	11–13	11–13	11
Infralabials	14–15	13–15	12–14	12	14–16	10–11	10–12	11
Postrictal and nuchal tubercles	–	Numerous highly spinose	–	–	–	Few, conical	Few conical	–
Spinose scales on margin of anterior forelimb	–	+	–	–	–	–	−, +	–
Tail height/tail width	0.75	0.90	0.82–0.95	0.76	0.75–0.87	0.80	0.50	0.82
Internasals contacting rostral	1–3	1–3	1–2	1	1–3	1–3	1	2
Scales contacting nostril	5	5–6	4	5	5	5	5	5
Head length/head width	1.4–1.5	1.2–1.3	1.2	1.2	1.4	1.2	1.3–1.4	1.3
No. scansors on toe I	9–10	12–14	10–14	12	10–11	9–11	8–9	9
No. scansors on toe IV	11–13	15–16	14–20	16	12–14	12–13	9–13	13
Extent of web between digits III and IV of pes	1/3–1/2	1/2–3/4	1/3–1/2	1/6–1/4	1/5–1/3	1/5–1/4	1/5–2/3	1/10–1/8
Auricular opening	Circular large	Oval, oblique small	Subcircular large	Oval oblique small	Oval, oblique small	Subcircular large	Oval oblique small	Subcircular oblique small
Penultimate scansors	Deeply notched	Deeply notched	Deeply notched	Deeply notched	Few, divided	Bowed	Deeply notched	Bowed
Dorsal tubercles	–	Spinose	Convex	–	–	Spinose, recurved	Spinose recurved	Flat to convex
Ventrolateral body tubercles	–	Many, spinose	Few, convex to conical	–	Few, convex	Few, spinose	Many, spinose	Few, flat to convex
Ventrolateral tail tubercles	1 or 2 per whorl, on caudal edge of tail segments	Numerous, highly spinose, along ventrolateral edge of whorl	–	–	Absent or limited to 1 or 2 small tubercles per whorl	Numerous, highly spinose, encircling each whorl	1 or 2 per whorl, highly spinose, along caudal edge of tail segments	Few, convex encircling each whorl
Ventrals enlarged	No	Yes	Slightly	Yes	No	Yes	Yes	Yes
Midbody Scales	162–173[a]	184–199	165	157	135–146	99–106	128–133	82
Anteriormost chin scales	Small	Small	Small	Slightly enlarged	Small	Slightly enlarged	Slightly enlarged	Moderately enlarged
Anterior forelimbs expansions	Moderate flaps	Wide flaps	Wide flaps	–	Narrow folds	–	Moderate folds	–
Posterior forelimbs expansions	Narrow folds	Wide flaps	Wide flaps	Minute folds	Moderate flaps	–	Moderate folds	–
Anterior hind limbs expansions	Narrow folds	Narrow folds	Wide flaps	–	–	–	Narrow folds	–
Posterior hind limbs expansions	Moderate flaps	Wide flaps	Wide flaps	Moderate flaps	Moderate flaps	Wide flaps	Wide flaps	Minute folds
Source	7	1,3,5	5	4	3,4,6	1,3,6	1,3,6	6

[a] Specimens of *Luperosaurus angliit* examined by us had 162–173 midbody scales (vs. 184–199 in three *Luperosaurus cumingii* specimens from known localities on the Bicol Peninsula). Specimens in European collections without precise locality data (i.e., ZMB 5578, "Philippines," SMF 9044 "Central Luzon") both have 182 midbody scale rows (Gaulke et al., 2007).

caudals uniformly granular, juxtaposed; subcaudals 122, small to moderate, slightly larger than dorsal caudal scales, squareish, flat to convex, subimbricate.

Measurements of Holotype.—Measurements in millimeters. Snout–vent length 62.5; tail length 39.4; head length 16.4; head width 11.6; head depth 7.0; snout length 7.7; eye diameter 3.9; eye–narial distance 5.5; tympanic annulus diameter 1.6; internarial distance 3.0; interorbital distance 3.6; axilla–groin distance 32.7; femur length 10.9; tibia length 8.4; Toe I length 3.3; Toe IV length 6.4; tail width 4.4; tail height 3.3.

Coloration in Preservative.—Dorsum medium gray, darker gray blotches, a few blotched and indistinct transverse dark bands, and numerous irregular thin dark brown lines originating in vertebral region and extending posteroventrally across flanks; dorsal nuchal region and head slightly lighter gray than body, but with denser congregation of thin radiating brown lines; lateral portions of head flat light gray, with thin brown lines in interorbital region, irregularly traversing snout, and radiating posteriorly from orbit; dark brown lines converge in large brown spot anterodorsal to auricular opening; labial and loreal regions nearly white; postrictal and infraauricular region gray with thin brown lines. Dorsal surfaces of limbs medium gray with irregular thin brown lines and dark blotches on elbows and knees; limbs lacking transverse banding; dorsal surfaces of manus and pes light gray; digits darker gray with very dark gray distal portions; innermost digits slightly lighter; dorsal and lateral portions of tail light gray with six dark gray ''X''-shaped markings (not corresponding to tail annuli); distal portions of tail not conspicuously lighter; ventral surface of tail light gray with faint midventral stripe.

Infralabial region and chin flat cream; gular region light gray, with white endolymphatic sacs and black melanic pigment of interior buchal cavity visible through somewhat translucent throat, giving impression of dark gray throat coloration; gular region flanked by slightly lighter gray ventrolateral jaw coloration; sternal region and venter medium gray with indistinct gray flecks; ventral body light gray; ventral surfaces of limbs slightly lighter, nearly dirty cream; ventral surfaces of scansors of fingers and toes dark gray.

Coloration in Life.—Little fading occurs with preservation of *Luperosaurus* specimens (Brown et al., 2000, 2007, 2010b; Gaulke et al., 2007). Field notes of ACD match the description above with the following exceptions: dorsum grayish-brown with dark brown lines and blotches; venter pale yellow, groin nearly orange; chin and throat bright white; circumorbital scales bright yellow; iris silver.

Variation.—Very little body size, scalation, or color variation is exhibited by the type series. All specimens are very close in body size and do not differ noticeably in body proportions. Mensural and meristic characters vary as follows: snout–vent length 59.4–64.7 mm ($\bar{x}$ = 62.4 ± 2.2 SD; N = 4); head length 16.0–17.4 ($\bar{x}$ = 16.5 ± 0.6); head depth 6.6–7.1 ($\bar{x}$ = 6.9 ± 0.2); head width 11.5–11.9 ($\bar{x}$ = 11.7 ± 0.2); snout length 7.3–7.8 ($\bar{x}$ = 7.6 ± 0.2); eye–narial distance 5.4–5.5 ($\bar{x}$ = 5.5 ± 0.1); eye diameter 3.3–3.9 ($\bar{x}$ = 3.6 ± 0.3); auricular opening diameter 1.4–1.6 ($\bar{x}$ = 1.5 ± 0.1); internarial distance 2.4–3.0 ($\bar{x}$ = 2.8 ± 0.3); interorbital distance 3.3–3.5 ($\bar{x}$ = 3.4 ± 0.1); axilla–groin distance 28.5–32.7 ($\bar{x}$ = 30.7 ± 1.7); femur length 10.3–11.8 ($\bar{x}$ = 10.9 ± 0.6); tibia length 8.2–8.6 ($\bar{x}$ = 8.4 ± 0.2); Toe I length 3.3–3.5 ($\bar{x}$ = 10.4 ± 0.1); Toe IV length 5.7–6.1 ($\bar{x}$ = 5.9 ± 0.2); tail length 39.4–41.8 ($\bar{x}$ = 40.7 ± 1.2); tail height 3.3–3.7 ($\bar{x}$ = 3.5 ± 0.2); tail width 4.3–4.9 ($\bar{x}$ = 4.5 ± 0.3). Enlarged scales in the preloacofemoral series 17–19 ($\bar{x}$ = 17.8 ± 0.9); supralabials 12–15 ($\bar{x}$ = 13.3 ± 1.5); infralabials 13–14 ($\bar{x}$ = 13.5 ± 0.6); Toe I scansors 9–10 ($\bar{x}$ = 9.5 ± 0.6); Toe IV scansors 11–13 ($\bar{x}$ = 11.8 ± 0.9); midbody scale rows 162–182 ($\bar{x}$ = 167.5 ± 4.9); paravertebrals between midpoints of limb insertions 191–207 ($\bar{x}$ = 199.3 ± 6.9); midventrals between midpoints of limb insertions 125–133 ($\bar{x}$ = 128.5 ± 3.7).

PNM 9793 and KU 321815 (from Casiguran, Aurora Province, northeastern Luzon) have slightly darker overall dorsal coloration. KU 321815 and 308023 (from Camiguin Norte Island) have a few indistinct dark brown blotches on the ventral surfaces of the hind limbs and faint dark striations wrapping on to the lateral surfaces of the venter (contiguous with dark markings traversing the flanks). KU 308023 has greatly enlarged endolymphatic sacs and PNM 9793 is an adult female with two yellowish, greatly enlarged, thickly shelled oviductal eggs dominating the abdominal cavity. KU 308023 has a regenerated tail (length 18.7 mm); the regenerated portion distal to autotomy scar has minute, irregular scalation encircling the tail. Tail segmentation and ventrolateral tubercles absent.

Habitat and Natural History.—Unlike most species of *Luperosaurus,* some information on microhabitat preference and distribution of *L. angliit* is available. Two specimens (KU 308023 from Camiguin Norte Island and KU 326160 from Mt. Makiling, Luzon Island) have been collected in reasonably mature, albeit disturbed, upland forested habitats. Additional specimens (PNM 9702 from the Municipality of Baler, Aurora Province and PNM 7242 from Lubang Island) were collected in highly disturbed second growth vegetation, within less than 5 km from coastal areas. Two specimens (KU 321815 and PNM 9703) from the Municipality of Casiguran, Aurora Province were collected in a fragment of beach forest less than 20 m from the coast. Older specimens from European collections, provisionally assigned to this species lack precise locality data or details of habitat and circumstances of capture. Most specimens with collection data were captured 2–3 m high on tree trunks, although one (PNM 7242 from Lubang Island) was collected from a thin branch of a low, scrubby understory tree, adjacent to a small stream. Other gekkonids collected sympatrically include *Gekko gecko* (at two localities), *Gekko mindorensis* (at two localities), *Gekko* n. sp. (at one locality; Brown et al., 2009), *Cyrtodactylus philippinicus* (at all known localities), *Lepidodactylus lugubris* (at one locality), and the house geckos *Hemidactylus frenatus, H. platyurus,* and *Gehyra mutilata* (at all localities).

Etymology.—The specific epithet is taken from the Tagalog (Filipino) conjugation of the adjective *maliit*, meaning small or little. In colloquial usage, *ang liit* is used to denote or emphasize the small size of a particular object (the new species) in reference to another larger entity (*L. cumingii*) and translates to ''the small one,'' or ''the little one.''

Discussion

The description of *L. angliit* brings the number of Philippine *Luperosaurus* taxa to eight and the total content of the genus to 13 species. Most species of *Luperosaurus* are known only from one or two specimens (Brown and Diesmos, 2000; Brown et al., 2000; Das et al., 2008). The exceptions are *L. cumingii* (now known from only four or five specimens, all presumably from Luzon's Bicol Peninsula), *L. corfieldi* (known from 10 or 11 specimens) and *L. angliit* (possibly known from seven specimens).

The known geographic range of *L. angliit* includes the Sierra Madre Mountains of eastern Luzon and Camiguin Norte Island, just off the north coast of Luzon. Specimens tentatively assigned to the new species include one poorly preserved specimen from Mt. Makiling (southern Luzon), an immature male from Lubang Island (off the coast of southwest Luzon), two hatchings from Polillo Island, and several older specimens in European collections with imprecise locality data. Gaulke et al. (2007) interpreted the locality (''Camiguin Island, Philippines'') accompanying NMW 17985.1 to putatively refer to Camiguin Sur Island, a small island off the north coast of the island of Mindanao, southern Philippines. However, given our

record of *L. angliit* from Camiguin Norte Island, we consider it more likely that NMW 17985.1 may actually have originated on Camiguin Norte, northern Philippines. Although *L. joloensis* does occur on western (KU 314947) and southern Mindanao (MCZ 26118), and *L. corfieldi* has been recorded from southern Negros (Dolino et al., 2009), currently no other specimens are known from the northern coast of Mindanao Island or from the vicinity of Camiguin Sur. Unfortunately, given the present lack of sufficient surveys from Camiguin Sur, there is no way to verify or falsify the possibility of a species of *Luperosaurus* species occurring on this island.

Despite escaping recognition by taxonomists and masquerading as *L. cumingii* for more than 150 years, the morphological distinctiveness of *L. angliit* is compelling. How could it have been misidentified by so many workers in past studies? We are convinced that most taxonomists who have studied these specimens assumed that the reduced tuberculation, small size, reduced interdigital webbing and minute cutaneous expansions bordering the limbs were indicative of ontogenetic variation (Brown et al., 2000, 2007; Gaulke et al., 2007) and considered specimens of *L. angliit* to be immature examples of *L. cumingii* (Boulenger, 1885; Brown and Alcala, 1978; Brown and Diesmos, 2000). Gaulke et al. (2007) demonstrated that of all available museum specimens of *Luperosaurus,* only specimens from the Bicol Peninsula of Luzon match the specific suite of phenotypic characters present in Gray's (1845) syntypes and the original description (dense aggregation of spinose nuchal and ventrolateral body tubercles present, wide cutaneous expansions bordering limbs, spinose tubercles present along the anterior margin of the cutaneous expansion bordering the forelimb, venter bright yellow with bold broken black transverse lines). Because of this, we have a high degree of confidence in the proposition that true *L. cumingii* type specimens originated on the Bicol Peninsula, where it is most probably yet another (of many) species restricted and endemic to this biogeographically unique peninsula of southern Luzon (Brown and Gonzales, 2007; Linkem et al., 2010b; Siler et al., 2010). To the best of our knowledge, true *L. cumingii* has been collected only twice in the past century: once by W. Auffenberg on the Caramoan Peninsula (UF 77829) and once by RMB on Mt. Malinao, Albay Province (TNHC 61910).

The rarity of *Luperosaurus* specimens continues to baffle field biologists. For years, we have assumed that *Luperosaurus* species, like some members of the genus *Ptychozoon*, were obligate canopy specialists that seldom were collected because they so rarely visited low vegetation strata (Brown et al., 1997, 2000; Brown, 1999; Brown and Diesmos, 2000). Brown et al. (2007) suggested that the obligate canopy hypothesis may not explain fully *Luperosaurus* rarity. These authors suggested that *Luperosaurus* may have evolved to specialize on mature coastal or beach forests, which are now all but gone from the Philippines. Assuming that coastal forests were the preferred habitat of most *Luperosaurus* species, we now usually find *L. cumingii*, *L. corfieldi*, *L. macgregori*, *L. joloensis*, and *L. angliit* at or below a few hundred meters elevation (in degraded habitat adjacent to intact lower montane forest), suggesting an explanation about why *Luperosaurus* are so rarely encountered and are found at such low densities. It is possible that most species are severely threatened, possibly in decline, with small fragments and regenerating forests representing the last vestiges of suboptimal habitat left to support populations of these evolutionarily and ecologically unique lizards. Because of the fragmented and patchy nature of the suspected preferred habitat and the obvious conservation concerns, we urge immediate and exhaustive survey efforts in the few remaining coastal forests of the Philippines. If our recent experience is any indication, these now rare and imperiled habitats appear to support the last remaining populations of *Luperosaurus* in the Philippines.

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APPENDIX 1

Specimens Examined

Luperosaurus angliit.—See Holotype, Paratypes, and Referred Specimens sections.

Luperosaurus brooksii.—Indonesia, Sumatra Isl., Benkuelen, Lebong Tandai: BMNH 1920.1.16.2 (holotype).

Luperosaurus browni.—Malaysia, peninsular Malaysia, Selangor, Ulu Gombak forest reserve, 35 km north of Kuala Lumpur: FMNH 185106 (holotype); Malaysia, Sarawak (Borneo Isl.), Lambir National Park: KUZ 12835 (*L. serraticaudus* holotype).

Luperosaurus corfieldi.—Philippines, Panay Island, Aklan Province, Municipality of Buruanga, Barangay Tagosip: PNM 7919 (holotype), PNM 7920, 8489 (paratypes); Negros Isl., Negros Oriental Prov., Municipality of Valencia, Lake Balinsasayao: SUR 2211; Saksak Cr., Mt. Cuernos de Negros, ''Camp Lookout'': CAS-SU 24394–24395; Negros Isl., Lake Balinsasayao: CAS 182570.

Luperosaurus cumingii.—Philippines, Luzon Isl., Camarines Sur Province, Municipality of Caramoan, Caramoan Peninsula, Anuling Mountain: UF 77829; Albay Province, Municipality of Tiwi, Barangay Banhaw, Sitio Purok 7, Mt. Malinao, 550 m above sea level: TNHC 61910; Philippines, presumably the Biol Peninsula of Luzon Island: BMNH 1946.8.22.41 and 1946.8.22.42 (syntypes).

Luperosaurus gulat.—PNM 9282, 3.4 km west, 0.60 km south of Mt. Mantalingajan peak, Barangay Ransang, Municipality of Rizal, Palawan Province, Palawan Island, Philippines (holotype).

Luperosaurus iskandari.—Indonesia, Sulawesi Is., Propinsi Sulawesi Tengah (Central Sulawesi Province), Kabupaten Banggai, Kecamatan Pagimana, Kampung/Desa Siuna, approximately 4 km east of Dusun Satu (Region 1), Mt. Tompotika (0°44.5′S, 123°01.1′E): MZB Lace. 2114.

Luperosaurus joloensis.—Philippines, Mindanao Isl., ''Cotobato Coast'': MCZ 26118; Jolo Isl., Siet Lake: CAS 60675 (paratype); Zamboanga Del Sur Province, Barangay Pasonanca, Sitio Canucutan, Pasanonca Natural Park: KU 314947.

Luperosaurus kubli.—Philippines, Quirino Province, Municipality of Nagtipunan, Barangay Disimungal, Sierra Madre Mountain Range, Mt. Lataan (900 m): PNM 9156 (holotype).

Luperosaurus macgregori.—Philippines; Babuyan Islands group, Calayan Isl.: CAS-SU 6263 (paratype), USNM 36191 (holotype); Barit Isl. (near Fuga Isl.): USNM 508306, 508308.

Luperosaurus palawanensis.—Philippines, Palawan Isl., Palawan Province, Malatgaw River, SE of Thumb Peak, approximately 3.5 km westnorthwest of Iwahig (9°44′40.27″N; 118°37′48″E): CAS 134207 (holotype); Thumb Peak, approximately 7 km northwest of Iwahig: (9°45′42.98″N; 118°36′18″E): CAS 136740 (paratype).

Luperosaurus yasumai.—Indonesia, Kalimantan (Borneo Isl.), Bukit Soeharto Experimental Forest, 45 km south-southwest of Samarinda: KUZ 30408 (holotype).

Gekko hokouensis.—''Tablas Island'' (presumably in error) FMNH 17812 (*L. amissus* holotype).