New Species of *Lipinia* (Squamata: Scincidae) from Borneo, Revealed by Molecular and Morphological Data

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ABSTRACT.—A new species of scincid lizard of the genus *Lipinia* is described from isolated localities in Borneo, from Sabah, Sarawak, and Kalimantan. The species was formerly allocated to *Lipinia quadrivittata* (Peters, 1867), a species known from the southern Philippines and Sulawesi in eastern Indonesia. The new species is compared with congeners from Borneo and other parts of Southeast Asia and the South Pacific and is diagnosable in showing the following combination of characters: small body size (SVL to 40.6 mm); external ear opening absent; lower eyelid with a clear spectacle; midbody scale rows 20; longitudinal scale rows between parietals and base of tail 46–50; lamellae under toe IV 16–17; supralabials 6; infralabials 6–7; subcaudals 68–74; and dorsum tan brown with dark gray-brown stripes. Although morphologically similar to the arboreal *L. quadrivittata*, the new species from Borneo differs in coloration and its preference for terrestrial habitats. In addition, analysis of DNA sequence data from 293 base-pairs of the *cytochrome b* gene for the new species and four congeners (*Lipinia leptosoma*, *Lipinia pulchella*, *Lipinia noctua*, and *L. quadrivittata*) demonstrates it is a separate lineage (> 15% sequence divergence from its sister taxa *L. quadrivittata*) with an independent evolutionary history.

The scincid genus *Lipinia* Gray, 1845, which was revived from the synonymy of *Lygosoma* Hardwicke and Gray, 1827 by Mittleman (1952), contains 26 nominal species ranging from the Andaman and Nicobar Islands of India, east to Thailand and Cambodia, the Malay Peninsula, Sumatra, Borneo, the Philippines, to New Guinea and the Republic of Belau (formerly, Palau; Brown and Alcala, 1980:80–107; Welch et al., 1990; Austin, 1995; Das and Greer, 2002). Members of the genus are characterized by the following suite of characters: small body size (SVL to 58 mm); lower eyelid with a clear window (except in *Lipinia leptosoma*); auricular lobules absent; body scales smooth; longitudinal scale rows at midbody ≤ 28; basal subdigital lamellae expanded (slightly in some taxa); postorbital absent; vomers fused; pterygoid teeth absent; dorsal color pattern typically comprising a pale (rarely dark) middorsal stripe at least anteriorly; visceral fat bodies absent (except in *Lipinia noctua*); brood size of two (exceptionally one, as in *Lipinia rouxi*) (Das and Greer, 2002). A biogeographic origin in the Philippines or Southeast Asia, rather than New Guinea, was suggested by Austin (1998).

A few species are taxonomically cryptic, here meaning a reproductively independent unit that is not morphologically discernable from some other recognized species (see Toda et al., 2000; Ota et al., 2001). For instance, Greer and Mys (1987) revived *L. rouxi* (Hediger, 1934), from New Ireland Island, from the synonymy of *L. noctua* (Lesson, 1826). This species is diagnosed by the loss of the left oviduct. Four species of *Lipinia* have been reported from Borneo (Das, 2004). *Lygosoma* (*Mocoa*) *nitens* Peters (1871) was described from ''Sarawak'' (in East Malaysia), this taxon at present known with certainty only from Gunung Pueh and Gunung Matang, and allocated to the genus *Scincella* Mittleman, 1950, by Mittleman (1952) and to *Sphenomorphus* Fitzinger, 1843, by Bauer et al. (1995:64). Das and Greer (2002) allocated this nominal species to *Lipinia*. The second Bornean species was originally described as *Lygosoma vittigerum* Boulenger, 1894, from ''Sereinu (Sipora), Mentawei Islands'' (= Pulau Sipura, Mentawai Archipelago, off Sumatera, Indonesia), was reported from the Baram District, Miri Division, Sarawak by de Rooij (1915:232, based on BMNH 97.3.4.2), and was subsequently collected from various other localities on the island. The rarest Bornean species, *Lygosoma* (*Liolepisma*) *miangense* Werner, 1910, is known from the lost holotype collected from ''Pulo Miang, Ostküste von Borneo'' (= Pulau Miang, Kalimantan Timur, Indonesia). The fourth species was allocated to *Lygosoma* (*Cophoscincus*) *quadrivittatum* Peters, 1867 (type locality: Mindanao in the Philippines) by Brown and Alcala (1956). This

latter species was also reported from Borneo (as *Siaphos quadrivittatum*) by Lloyd et al. (1968) and (as *Lipinia quadrivittata*) by Tan (1993). Brown and Alcala (1956), who examined the Bornean specimens available to them (FMNH 72448, from East Coast Residency, southeast end of Dewhurst Bay, Sabah, East Malaysia; and FMNH 63678 from Pulau Nunukan, Kalimantan Timur, Indonesia), allocated them to *Lygosoma quadrivittatum*, upon failing to find systematic characters to separate them from the nominate populations in the Philippines, although the population from Sulawesi, eastern Indonesia, was allocated to the subspecies *infralineolatum*.

During fieldwork in Pulau Manukan, a land-bridge island off the north coast of Sabah, Borneo, four specimens of a *Lipinia* were collected. They differ in subtle aspects of color pattern and are genetically distinct from *L. quadrivittata*. These four specimens and preexisting Bornean specimens formerly allocated to *L. quadrivittata* form the type series of a new species described herein.

MATERIALS AND METHODS

Part of the type series was collected from Pulau Manukan, an island off the north coast of Sabah, at approximately 1100–1130 h, photographed in life, euthanased using pentobarbitol, fixed in buffered formalin approximately 6 h after collection, and subsequently washed in water and transferred to 70% ethanol about two weeks after collection. Geographical coordinates for the type locality were taken with a Garmin eTrek^{TM} Global Positioning System (datum: wgs84). The rest of the type series as well as comparative material were examined on visits to or as loans from museums (see Acknowledgments).

The following measurements were taken with Mitutoyo^{TM} dial vernier callipers (to the nearest 0.1 mm) approximately 24 months after collection in the case of the Pulau Manukan material, approximately 40 years later in the case of the paratype from Sarawak: snout–vent length (SVL); tibia length (TBL), distance between surface of knee to surface of heel, with the knee flexed; head length (HL), distance between angle of jaws and snout-tip; head width (HW), measured across retroarticular process of the mandible; head depth (HD), greatest transverse depth of head, taken posterior of the orbital region); eye diameter (ED), horizontal diameter of the eyes-measured across the anterior and posterior margins of the palpebral margin; interorbital distance (IO), smallest distance between upper eyelids; internarial distance (IN), distance between nostrils; eye to snout distance (E–S), distance between anteriormost

point of eyes and tip of snout; eye to nostril distance (E–N), distance between anteriormost point of eyes and posterior-edge of nostrils; nostril to snout distance (N–S), distance between anteriormost point of nostril and tip of snout; axilla to groin distance (A–G), distance between posterior edge of forelimb at its insertion to body to anterior edge of hind limb at its insertion to body; and body width (BW), greatest width of body. In addition, details of digit scalation were taken on the left limbs. Nomenclature of head scales follows Taylor (1935:71); that of dorsal striping follows Storr et al. (1999:277). Color notes on the holotype were taken from Fujichrome Velvia (50 ASA) 35 mm slide transparency film. Means are given ± 1 SE.

Comparative materials examined are listed in Appendix 1. Sources of additional data on character states and distribution of other species of *Lipinia* are from Alcala (1986), Boulenger (1887, 1894, 1912), Brown and Alcala (1980), Brown and Fehlmann (1958), Das (1997, 2002), Das and Greer (2003), de Rooij (1915), Günther (2000), Manthey and Grossmann (1997), Shea and Greer (2002), Smith (1930), and Zug (1991).

Museum abbreviations, where available (indicated with an asterisk), follow Leviton et al. (1985, 1988). These include: Natural History Museum, London, UK (BMNH*); California Academy of Sciences, San Franciso (CAS*); Field Museum of Natural History, Chicago (FMNH*); Museum of the Department of Biology, La Sierra University, Riverside (LSUHC); Museum of Comparative Zoology, Harvard University (MCZ*); Sarawak Biodiversity Centre, Semenggoh, Sarawak, Kuching, Malaysia (SBC); Sarawak Museum, Kuching, Malaysia (SM*); Sabah Parks Museum, Gunung Kinabalu National Park, Malaysia (SP); ''Borneensis'' Collection, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia (UMS); Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC; the abbreviation used in Leviton et al., 1985, is USDZ*); and Zoological Survey of India, Kolkata, India (ZSI*).

Specimens and Tissues.—Muscle and liver tissue samples were dissected from freshly sacrificed specimens, and stored either at −80°C or in 90% ethanol. DNA was isolated from either muscle or liver tissues following the protocols of Hillis et al. (1990). Appendix 2 provides DNA sequence data from the mitochondrial *cytochrome b* (*cytb*) gene for the new species of *Lipinia* dealt with here (ZRC 2.5728–9), *Lipinia quadrivittata* (topotype material from Mindanao; second author's field number, CCA 1268–70), and three other species (*L. noctua* TNHC 51595 [Papua New Guinea], *L. leptosoma*

SAMA R47903–4 [Palau], and *L. pulchella* TNHC 53979 [Philippines]).

DNA Isolation, Amplification, and Sequencing.—Polymerase chain reaction (PCR) was used to amplify a 293 base-pair region of the *cytb* gene. The protocols of Hillis et al. (1990) were followed to amplify double-stranded PCR products. The specific thermal cycle used is as follows: (1) one cycle at 94°C × 3 min, 47°C × 1 min, and 72°C × 1 minute; (2) 34 cycles at 94°C × 45 sec, 47°C × 45 sec, and 72°C × 1 min; (3) one cycle at 72°C × 6 min. The primers used were L14841 5′AAA AAG CTT CCA TCC AAC ATC TCA GCA TGA TGA AA3′ and H15149 5′AAA CTG CAG CCC CTC AGA ATG ATA TTT GTC CTC A3′ (Kocher et al., 1989). *Cytochrome b* was chosen because of its general utility for resolving divergences among Australasian skinks (Graybeal, 1994; Austin, 1999; Austin and Zug, 1999). PCR products were sequenced using ABI Big Dye version 3 terminator cycle sequencing kit and run on an ABI 3100 automated DNA sequencer.

Genetic Analysis.—To assess the genetic distinctiveness of the new species as an independent lineage, in particular compared to *Lipinia quadrivittata* with which it had long been confused, we performed genetic comparisons with other *Lipinia* for which we had tissue samples. *Lipinia quadrivittata* was hypothesized to be the sister taxa to the new Bornean species. *Lipinia* is presumed to be monophyletic and is a member of the *Sphenomorphus*-group of lygosomine skinks (Greer, 1974), and we chose the genus *Sphenomorphus* as an outgroup based on previous morphological and molecular work (Greer, 1974; Austin, 1995, 1998; CCA unpubl. data). We use both maximum likelihood (ML) and maximum parsimony (MP) methods to generate hypotheses of phylogenetic relationships.

DNA sequences were aligned using Clustal X (Thompson et al., 1997). Maximum likelihood (ML) and maximum parsimony (MP) were the two optimality criteria used to assess phylogenetic relationships (Edwards, 1972; Felsenstein, 1981). All phylogenetic analysis were done using PAUP* 4 (Swofford, 1999). The presence of a bias in the type of base substitutions for DNA sequences has been well documented (Wakeley, 1994, 1996). To take into account transition/transvertion bias and among-site rate variation that can sometimes lead to an underestimation of the transition/transversion bias as the GTR + I + Γ model of sequence evolution was chosen using Modeltest (Posada and Crandall, 1998). All searches were done using the heuristic search options in PAUP* with 20 random addition sequences, with initial trees obtained by stepwise addition, followed by branch swapping using the tree bisection-reconstruction (TBR) method implemented in PAUP*. In both MP and ML analyses, the branch-and-bound algorithm, which guarantees to find the optimal tree or trees, was used to search tree space. Tree reliability for both ML and MP criteria was evaluated by the nonparametric bootstrap resampling method (Felsenstein, 1985; Hillis and Bull, 1993).

RESULTS

Two hundred ninety three base-pairs from 10 individuals were aligned using Clustal X (Thompson et al., 1997). Of these, 116 sites were variable, and 83 sites were parsimony-informative (GenBank accession numbers). No insertions or deletions (indels) were observed. An open reading frame for both genes was observed by alignments based on codon positions by translating DNA sequence into protein sequences using MacClade (version 4). Using the maximum likelihood GTR + I + Γ model, among-site rate variation was incorporated. Maximum likelihood analyses resulted in a single optimal tree (−ln likelihood = 1260.669). Maximum parsimony analyses resulted in a single most parsimonious tree with the same topology as the ML optimal tree (tree length = 275, consistency index = 0.77, homoplasy index = 0.23, rescaled consistency index = 0.58; Fig. 1). Bootstrap proportions are for 100 and 500 pseudoreplicates, for ML and MP, respectively. The matrix for both uncorrected pairwise genetic distances are presented in Table 1.

All nodes on the tree are well supported (≥ 70). Phylogenetic results suggest that the new species from Borneo being described here and *L. quadrivittata* are sister taxa. Genetic distances between the two species are substantial (15–16%; Table 1) and correspond to typical levels of species level differentiation in lizards (Thorpe et al., 1994; Gonzalez et al., 1996; Thorpe, 1996; Thorpe and Malhotra, 1998).

SYSTEMATICS

Lipinia inexpectata sp. nov.
Figures 2–3

Lygosoma quadrivittatum: de Rooij, 1915. Reptiles Indo-Australian Arch. 1:271 (in part).

?*Lygosoma quadrivittatum*: Smedley, 1928. Malayan Br. Roy. Asiatic Soc. 6(3):77. (non-*Lygosoma* [*Cophoscincus*] *quadrivittatum* Peters, 1867).

Lygosoma quadrivitatum: Brown and Alcala, 1956. Occ. Pap. nat. Hist. Mus. Stanford University (3):3 (in part).

?*Saiphos quadrivittatum*: Taylor, 1963. University of Kansas Sci. Bull. 44:1053.
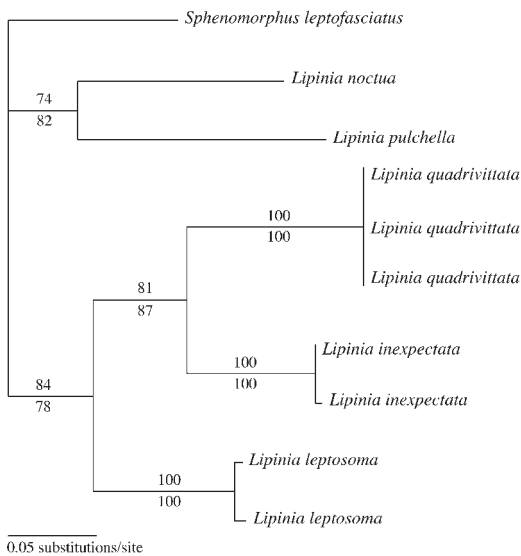
FIG. 1. Phylogram of the maximum likelihood tree obtained from PAUP* searches using *Sphenomorphus leptofasciatus* sequences as an outgroup. Maximum parsimony searches resulted is a single tree with the same topology as the ML tree. Support for inferred clades is assessed by nonparametric bootstrap values for 100 ML and 500 MP pseudoreplicates, above and below each branch, respectively.

Siaphos quadrivittatum: Lloyd, Inger, and King, 1968. American Natural. 202(928):499 (non-*Lygosoma* [*Cophoscincus*] *quadrivittatum* Peters, 1867).

Lipinia quadrivittata: Tan, 1993. Checklist Lizards Sabah:6. (non-*Lygosoma* [*Cophoscincus*] *quadrivittatum* Peters, 1867).

Lipinia quadrivittata: Iskandar, 2004. Amphibians and Reptiles Malinau Region:14;20 (non-*Lygosoma* [*Cophoscincus*] *quadrivittatum* Peters, 1867).

Lipinia undescribed species: Das, 2004. Lizards of Borneo:6;60.

Lipinia quadrivittata: Hikida and Ota, 2005. Curr. Herpetol. 24(1):46. (non-*Lygosoma* [*Cophoscincus*] *quadrivittatum* Peters, 1867).

Holotype.—ZRC 2.5728 (field number ID–7191; holotype) from Pulau Manukan (05°58′N; 115°59′E), Kota Kinabalu District, Sabah, East Malaysia, C. C. Austin and I. Das, collectors, 5 December 2000. Adult female (with paired shelled ova in the oviducts).

Paratypes.—ZRC 2.5729–30 (field numbers ID–7192–93), SP uncataloged (field number ID–7190), three paratopotypes, other data as for holotype; FMNH 138538, Nanga Tekalit Camp on Sungei Mengiong (01°37′N; 113°38′E), Kapit Division, Sarawak, East Malaysia, R. F. Inger, B. Greenberg, and F. W. King, collectors, 16 September 1962.

Diagnosis.—A small (SVL to 40.6 mm) species of *Lipinia*, diagnosable from congeneric species in having the following combination of characters: external ear opening absent; lower eyelid with a clear spectacle; 20 midbody scale rows; 46–50 longitudinal scale rows between parietals and base of tail; 16–17 lamellae under toe IV; 6 supralabials; 6–7 infralabials; 68–74 subcaudals; dorsum tan brown with dark gray brown stripes; dorsum tan brown with a series of dark gray brown stripes; a series of dark spots arranged in a longitudinal series bilaterally on each outer side of the paravertebral stripes; labials unbarred; venter yellowish-cream with pale gray smudges, and a unique *cytb* gene sequence.

Description of Holotype.—Gravid female, SVL 40.0 mm, TL 37.7 mm; snout acute (IN:IO ratio 0.54), slightly projecting beyond lower jaws; nostril laterally oriented, oval, situated closer to snout-tip than to orbit (E–N:E–S ratio 0.72); head relatively long, slightly longer than wide, HL 5.1 mm, HW 4.7 mm (HL:HW ratio 1.09), slightly flattened, HD 3.3 mm (HL:HD ratio 1.55); rostral broad, projecting only moderately onto snout; posterior border of rostral nearly straight; frontonasal trapezoid, wider than long; frontal elongated, arrow-shaped, wider anteriorly; frontoparietals fused; prefrontals small, widely separated; interparietal single, subequal

TABLE 1. Summary of the mean inferred uncorrected pairwise genetic distances for the mitochondrial *cytb* gene for *Lipinia inexpectata* and four congeners.

|	1	2	3	4	5	6	7	8	9	10
1 TNHC 51595	—									
2 SAMR 4195	0.18771	—								
3 CCA1269	0.19113	0.19795	—							
4 CCA1268	0.19454	0.20137	0.00341	—						
5 CCA1270	0.19113	0.19795	0.00000	0.00341	—					
6 ID7190	0.23549	0.20478	0.15358	0.15700	0.15358	—				
7 ID7191	0.23891	0.20819	0.15700	0.16041	0.15700	0.00341	—			
8 SAMA R47903	0.21502	0.18430	0.19113	0.19454	0.19113	0.16041	0.16382	—		
9 SAMA R47904	0.20819	0.17747	0.19454	0.19795	0.19454	0.16382	0.16724	0.01024	—	
10 TNHC 53979	0.20819	0.20478	0.22184	0.22526	0.22184	0.23208	0.23549	0.20137	0.20819	—
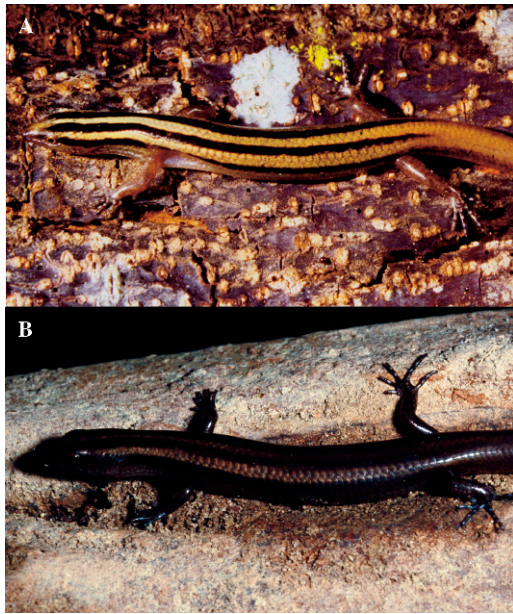
FIG. 2. Dorsolateral view of holotype of *Lipinia inexpectata* sp. nov. (ZRC 2.5728) in life compared with its sister taxa *Lipinia quadrivittata*. (A) *Lipinia quadrivittata* (CCA 1263) from southern Mindanao, Philippines. (B) *Lipinia inexpectata* (ZRC 2.5728).
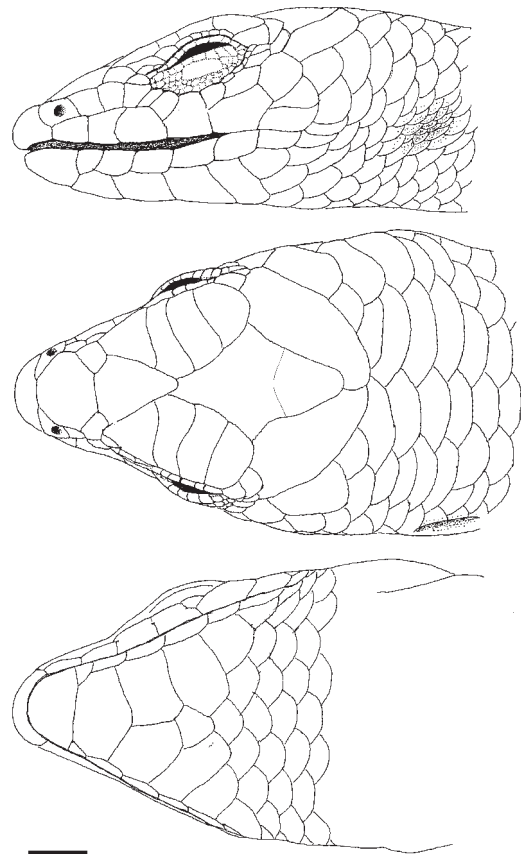

FIG. 3. Head scalation in the holotype of *Lipinia inexpectata* sp. nov. (ZRC 2.5728). (Top) Lateral view. (Middle) Dorsal view. (Bottom) Ventral view. Scale marker = 2 mm.

to frontonasal; parietals in narrow contact posterior to interparietal; parietal eye spot situated at posterior half of interparietal; four supraoculars; three supraciliaries; nostrils located within nasals; postnasal absent; loreals squarish, two in number; equal in height; two presuboculars, separating supralabial III from orbit; six supralabials (supralabial IV contacting orbit of eye); three postsuboculars; three postoculars; two pretemporals; three temporals, the dorsal largest; two pairs of nuchals; seven infralabials; one scale separates second pair of enlarged chin shields; three scales separate third pair of chin shields; enlarged chin shields contact infralabials; external ear opening absent, its location indicated by a shallow depression; eyes relatively large; pupil rounded; lower eyelid with a clear window, approximately one-half eye diameter; scales on upper row of lower eyelid small, 10 in number; tongue short, undivided anteriorly, pointed; teeth small, somewhat obtuse.

Body slender, BW 7.8 mm (BW:SVL ratio 0.20); head slightly distinct from neck and from body; 48 longitudinal scale rows from parietal to above level of anterior margin of hind limb; 58 ventrals, counted from first postgular to last scale before preanals; body scales smooth, subcycloid; 20 transverse scale rows at midbody; 74 subcaudals; abdominal scales larger

than throat and pectoral scales, the median ventral scales also enlarged relative to scales on flanks; preanals enlarged, median pair of preanals overlap lateral preanals; tail relatively long (TL:SVL ratio 0.94), tip rounded, tail base not wider than rest of tail; tail gradually tapering to a point; median row of subcaudals slightly enlarged.

Limbs relatively short; pentadactyle and clawed; all lamellae smooth and enlarged; adpressed limbs failing to meet; lamellae under finger I–6; II–10; III–10; IV–12; V–9; lamellae under toes I–8; II–9; III–12; IV–13; V–10.

Coloration (in Preservative).—Dorsum tan brown (= pale) with a series of dark gray brown (= dark) stripes. A pale vertebral stripe extends from the interorbital region, across nape and midbody, to the tail, and down to the tip; on midbody, it is half a scale wide and lies on half of each of the two paravertebral scale series; the paired dark paravertebral stripes extend from the level of second supraocular, and

extend to the tail tip; dark spots arranged in a longitudinal series bilaterally on each outer side of the paravertebral stripes; the paired pale dorsal stripes start from the level of the second supraoculars and terminate at the inguinal region; and finally, the paired dark laterodorsal stripes extend from postocular region to groin. All stripes are broadest at midbody and show reduced contrast towards posterior of body. Snout-tip dark gray; labials unbarred; tongue dark gray; venter yellowish-cream with pale gray smudges, forming a longitudinal stripe, especially along pectoral region; limbs unbanded; scales on undersurface of limbs light gray; manus and pres dark gray; undersurface of tail yellowish-cream.

Measurements (in Millimeters; Holotype with the Variation Shown in the Type Series in Parentheses).—SVL 40.0 (38.0–40.6, mean 39.00 ± 0.54); HL 5.1 (4.7–5.1, mean 4.94 ± 0.707); HW 4.7 (4.0–4.8, mean 4.58 ± 0.15); HD 3.3 (3.1–3.3, mean 3.22 ± 0.05); BW 7.8 (5.4–7.8, mean 6.30 ± 0.41); TBL 4.3 (4.2–5.5, mean 4.46 ± 0.28); ED 1.6 (1.2–1.6, mean 1.50 ± 0.08); UE 1.9 (1.4–1.9, mean 1.52 ± 0.10); IN 1.3 (1.1–1.3, mean 1.22 ± 0.50); IO 2.4 (2.2–2.5, mean 2.38 ± 0.05); E–S 2.5 (2.5–2.6, mean 2.52 ± 0.02); E–N 1.8 (1.4–1.8, mean 1.54 ± 0.07); N–S 1.0 (0.6–1.0, mean 0.76 ± 0.07); A–G 23.6 (18.8–23.6, mean 21.74 ± 0.86); TL 37.7 (35.7–46.2, mean 38.87 ± 2.48; TL of ZRC 2.5730 is a regenerated nubbin, 12.6 mm long and was not considered).

Variation (Holotype with the Variation Shown in the Type Series in Parentheses).—Transverse scale rows at midbody 20 (no variation); longitudinal scale rows 48 (46–50, mean 47.80 ± 0.66); ventral scale rows 58 (49–58, mean 53.60 ± 1.50); supralabials 6 (no variation); infralabials 7 (6–7, mean 6.20 ± 0.20); subcaudals 74 (68–74, mean 71.25 ± 1.25); lamellae under toe IV 17 (16–17, mean 16.40 ± 0.25). Additional material of the new species examined are in Appendix 1. No variation in characters listed were observed between the populations on Pulau Manukan and those on Borneo.

Etymology.—The species name (an adjective in feminine form) refers to the unexpected nature of the discovery of the type series. This species was referred to *Lipinia quadrivittata* for 90 years since the work of de Rooij (1915).

Ecological Notes.—Part of the type series was collected from under two fallen tree trunks, approximately 10 m from the beach, at the edge of a disturbed primary forest. Two individuals were found under each log. Pulau Manukan is one of the more well-explored islands off the coast of Sabah, within the Tunku Abdul Rahman National Park (see Repin and Sundaling, 2000). Although a large number of congeners are arboreal (e.g., *Lipinia leptosoma*, *L. pulchella*,

L. quadrivittata, *L. rouxi*, *L. semperi*, *L. subvittata*, and *L. vittigera*; see Brown and Fehlmann, 1958; Brown and Alcala, 1980:89, 95–96; Greer and Mys, 1987), the new species being described here is terrestrial, a trait shared by a few congeneric species, such as *L. macrotympanum*, *L. surda*, and some populations of *L. noctua* (Greer and Mys, 1987; Das, 1998). The holotype is a female, containing one ova in each oviduct.

This landbridge island is underlaid by folded sandstone and sedimentary rocks, and was presumably detached from the Crocker Range of the Sabah mainland by a rise in sea level during the last Pleistocene post glaciation event (Voris, 2000). A number of vegetation types are represented, depending on local conditions. The coastal beach vegetation and mangroves are replaced in the interior by primary rain forests, comprising a rich dipterocarp flora. The adjacent primary forest is dominated by dipterocarps, including *Dipterocarpus grandiflorus*, *Dipterocarpus acutangulus*, as well as *Shorea falciferoides*, *Shorea macroptera*, *Shorea laxa*, *Shorea angustiflorus*, and *Shorea confusca* (floral inventory in Repin and Sundaling, 2000). The only other species of lizard found on Pulau Manukan was *Hemidactylus frenatus* Duméril and Bibron, 1836 (ZRC 2.5301). However, Nanga Tekalit in Sarawak, where the FMNH paratype of the new species of *Lipinia* was also collected, is a lowland dipterocarp forest, with a rich herpetofauna, including as many as 40 species of lizards (see Lloyd et al., 1968; Inger, 1980).

We are unclear of the systematic status of populations referred to *Lipinia quadrivittata* from southern Thailand (referred to as *Saiphos quadrivittatum* by Taylor, 1963:1053), the Malay Peninsula (Boulenger, 1912; Taylor, 1963; Denzer and Manthey, 1991), and from Pulau Siantan, in the Anambas Archipelago (referred to as *Lygosoma quadrivittatum* by Smedley, 1928), because no specimens from these localities could be examined.

Comparisons.—The new species of *Lipinia* from Borneo is most similar in gross morphology and coloration to *L. quadrivittata* (Peters, 1867; distribution: Mindanao [type locality] as well as Negros, Bohol, Palawan, Siquijor, Little Govenen, Cebu, Leyte, and Camiguin Islands in the southern Philippines). *Lipinia quadrivittata* has a light brown to yellow base color with dark, longitudinal dorsolateral stripes. In contrast, *L. inexpectata* has a dark brown base color with light longitudinal dorsolateral stripes (Fig. 1). In addition, *L. inexpectata* has a series of longitudinal dark spots lateral to the paravertebral stripe, which are lacking in *L. quadrivittata*. Additionally, in *L. inexpectata*, only supralabial IV contacts the orbit, as opposed to supralabials IV and V contacting the orbit in *L.*

quadrivittata; and *L. inexpectata* is terrestrial (as opposed to arboreal). The two species show a high level of sequence divergence (15.4–16.0%), and character based genetic analysis demonstrates that *L. inexpectata* is distinct and a separate evolutionary lineage (Table 1). Because all specimens previously identified as *L. quadrivittata* from Borneo are referable to *L. inexpectata* (see Appendix 1), we confirm that there are no authentic records of *L. quadrivittata* for Borneo.

Lipinia inexpectata is here compared with all other known congeners, listing only opposing suite of characters: *albodorsalis* (Vogt, 1932) (distribution: Papua New Guinea), SVL to 54 mm; external ear opening present; seven supralabials; supralabial five in midorbital position; 22–25 midbody scale rows; 19–23 lamellae under toe IV; and dorsum pale yellow with a dark upper lateral stripe; *auriculata* (Taylor, 1917) (distribution: Philippines: Negros and Masbate Islands), external ear opening present; 22–25 midbody scale rows; and 55–61 longitudinal scale rows between parietals and tail base; *cheesmanae* (Parker, 1940) (distribution: Indonesia: Papua Province; New Guinea), 28 midbody scale rows; five pairs of nuchals; and dorsum coppery with a middorsal row of dark spots forming an interrupted zigzag line from the occiput to tail base, and a dark lateral band along the flanks and tail, with a series of large, semicircular spots along its upper border; *infralineolata* (Günther, 1873; distribution: Indonesia: Sulawesi and Sangihi Islands), SVL to 49 mm; 22 midbody scale rows; 18–25 lamellae under toe IV; and lips and limbs with brown spots; *leptosoma* (Brown and Fehlmann, 1958) (distribution: Palau Islands, at present, the Republic of Belau), external ear opening present; 22–26 midbody scale rows; supralabial five in midorbital position; 7–10 lamellae under toe IV; and arboreal habits; *longiceps* (Boulenger, 1895) (distribution: New Guinea, Fergusson, Misima, and Trobriand Islands), SVL 43 mm; external ear opening present; 24 midbody scale rows; 19 lamellae under toe IV; rectilinear black dorsolateral lines converge at tail base; and tail golden yellow; *macrotympanum* (Stoliczka, 1873) (distribution: India: Andaman and Nicobar Archipelago), 21–23 midbody scale rows; seven supralabials; and coloration of dorsum contrasting black and yellow and tail bright red in life (color photograph in Das, 2002); *miangensis* (Werner, 1910) (distribution: Indonesia: Pulau Miang, Kalimantan Timur; Borneo), external ear opening present; two vertebral series of scales enlarged; 24 midbody scale rows; 62 ventral scales; 21 lamellae on toe IV; dorsal surface golden with two dark brown longitudinal stripes from the snout-tip, over the eyes, to

around the middle of tail; a dark line from eye to base of fore limb; and venter unpatterned greenish-white; *miotis* (Boulenger, 1895; distribution: New Guinea), SVL to 52 mm; external ear opening present; supralabial V in midorbital position; midbody scale rows 24–26; and dorsum golden brown with small dark spots in two longitudinal series; *nitens* (Peters, 1871) (distribution: Malaysia: western Sarawak; Borneo), a small member of the genus, SVL to 33.6 mm; two enlarged paravertebral scale rows; external ear opening replaced by a scaly dimple; subcaudal scales enlarged; dorsal surface metallic green; sides of body spotted with black and green; and pale yellow vertebral stripe, with jagged edged black lines, one on each side from supraorbital to tail base; *noctua* (Lesson, 1826) (distribution: Indonesia: Maluku and Papua Province; also, Papua New Guinea, the Admiralty and Bismarck Archipelago, as well as the Solomon Islands), SVL to 47 mm; 24–28 midbody scale rows; seven supralabials, fifth in midorbital position; and head with a light spot; *nototaenia* Boulenger, 1914 (distribution: Indonesia: West Papua [New Guinea]), SVL to 47.5 mm; external ear opening present; 24–25 midbody scale rows; 52–55 longitudinal scale rows between parietals and base of tail; seven supralabials; *occidentalis* Günther, 2000 (distribution: Indonesia: Papua Province; New Guinea), external ear opening present; 24–26 midbody scale rows; 20–21 lamellae under toe IV; broad brownish dorsal band terminates at tail-base, where it forms a dark tip; and pale dorsal stripes absent; *pulchella* Gray, 1845 (distribution: the Philippines), external ear opening present; 51–58 longitudinal scales between parietals and tail base; 22–26 midbody scale rows; and 24–31 lamellae under toe IV; *pulchra* Boulenger, 1903 (distribution: New Guinea), external ear opening present; 24 midbody scale rows; 22 lamellae under toe IV; supralabial five in subocular position; and dorsum black with five greenish-white longitudinal lines; *rabori* (Brown and Alcala, 1956) (distribution: Philippines: Negros Island), a large member of the genus, SVL to 51.0 mm in males and 54.8 mm in females; external ear opening present; 7–8 supralabials; seven infralabials; 22 midbody scale rows; 52–57 longitudinal scale rows between parietals and tail base; 18–21 lamellae under toe IV; *relicta* (Vinciguerra, 1892) (distribution: Indonesia: Mentawai Archipelago off Sumatra), SVL to 56 mm; 18 lamellae under toe IV; tail thick; a light vertebral stripe present and labials with a small white spot; *rouxi* (Hediger, 1934) (distribution: New Ireland, northeast Papua New Guinea and Bismarck Archipelago), 22–28 midbody scale rows; 8–9 supraciliaries; 22–26 lamellae under toe IV; left oviduct missing;

venter greenish-white in life (fide Greer and Mys, 1987) and arboreal habits; *semperi* (Peters, 1867) (distribution: Philippines: Mindanao and Camiguin Islands), SVL 43.9–49.9 mm; external ear opening present; 22–24 midbody scale rows; seven supralabials; 53–58 longitudinal scale rows between parietals and tail base; and 19–21 lamellae under toe IV; *septentrionalis* Günther, 2000 (distribution: Indonesia: Papua Province; New Guinea), 24–26 midbody scale rows; seven supralabials; 18–22 lamellae under toe IV; and a cream vertebral stripe that broadens towards the tail, bordered by a dark line on each side; *subvittata* (Günther, 1873) (distribution: Indonesia: Sulawesi and Java; Philippines: Mindanao Island), SVL 47–56 mm; dorsal longitudinal stripes extend to the forearm region; 57–64 longitudinal scale rows between parietal and tail base; and 22 midbody scale rows; *surda* (Boulenger, 1900) (distribution: Peninsular Malaysia); supralabial IV and V contact orbit of eye; preanals subequal to ventral scales; and dorsum uniform brown; *venemai* (Brongersma, 1953; distribution: Indonesia: Papua Province; New Guinea), SVL 54.0–57.5 mm; external ear opening present; 2–3 pairs of nuchals; seven supralabials; 24 or 26 midbody scale rows; 59–60 longitudinal scale rows between parietals and base of tail; 19–21 lamellae under toe IV; and dorsum deep olive gray, the supraciliary region whitish, broadening posteriorly; *vittigera* (Boulenger, 1894; distribution: Peninsular Malaysia, Sumatra and Borneo), external ear opening present; 25 lamellae on toe IV; 28 midbody scale rows; and dorsal pattern comprising dark gray and bright yellow stripes (color photograph in Cox et al., 1998); *vulcania* Girard, 1856 (distribution: Philippines: Mindanao and Luzon islands), external ear opening present; seven supralabials; supralabial V in midorbital position; 32 midbody scale rows; 62 longitudinal scale rows between parietals and tail base; and 17 lamellae under toe IV; and *zamboangensis* (Brown and Alcala, 1963) (distribution: Philippines: Mindanao Island), SVL to 44.5 mm; external ear opening present; 24 midbody scale rows; 54 longitudinal scale rows between parietals and tail base; 20 lamellae under toe IV; and dorsum greenish with brown iridescence.

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APPENDIX 1

List of Comparative and Additional Material Examined

Lipinia inexpectata Das and Austin, 2007: MALAYSIA: Nanga Tekalit Camp on Sungei Mengiong, Kapit Division, Sarawak (FMNH 138539; 152400); Sandakan, Sandakan District, Sabah (BMNH 95.9.11.16); Sepagaya Forest Reserve, Sandakan District, Sabah (FMNH 63678); Sepilok, Sandakan District, Sabah (USNM 306415); Danum Valley, Lahad Datu District, Sabah (FMNH 230189; UMS 04399–04400); southeastern end of Dewhurst Bay, Kinabatangan District (FMNH 63678); KALIMANTAN: Pulau Nunukan, Kalimantan Timur Province (FMNH 72448).

Lipinia longiceps (Boulenger, 1895): PAPUA NEW GUINEA: Aitape (MCZ R.-48587).

Lipinia macrotympanum (Stoliczka, 1873): INDIA: Pulo Ulan (= Tiden), Little Nicobar Island, Andaman and Nicobar Islands (cited by Das, 1997; MCZ R–176760); Andaman Island, Andaman and Nicobar Islands (ZSI 5571, holotype of *Mocoa macrotympanum* Stoliczka, 1873).

Lipinia nitens (Peters, 1871): MALAYSIA: base of Gunung Pueh, Kuching Division, Sarawak (cited by Das and Greer, 2002; ZRC 2.4861); base of Gunung Matang, Kuching Division (illustrated in Das, 2004:61; ZRC 2.5746).

Lipinia noctua (Lesson, 1826): FIJI: Tubutkii (MCZ R–15013).

Lipinia pulchella Gray, 1845: PHILIPPINES: Zamboanga, Mindanao (MCZ R–26440).

Lipinia quadrivittata (Peters, 1867): INDONESIA: Salopa Waterfall, northwest of Poso, Sulawesi (ZRC 2.4652); PHILIPPINES: Sant Cotobato, Mindanao (CAS 61960–61).

Lipinia rabori (Brown and Alcala, 1956): PHILIPPINES: Maite River, Cuernos Negros Oriente (MCZ R–54393).

Lipinia semperi (Peters, 1867): PHILIPPINES: Agusan del Norte (MCZ R–20120).

Lipinia vittigera (Boulenger, 1894): MALAYSIA: Bukit Meraja, Bau, Kuching Division, Sarawak (SBC R.1); Kota Samarahan, Sarawak (FMNH 147561; 149371–74); Pulau Talang Talang Besar, Kuching Division (SM uncat. [two specimens]); Baram District, Miri Division, Sarawak (cited by de Rooij, 1915:232; BMNH 97.3.4.2); Danum Valley Field Centre, Lahad Datu District, Sabah (FMNH 241315–16; 241316; 246356–57); Jor Batang, Padang, Perak (ZRC 2.1637); Salang, Pulau Tioman, Pahang Samarahan Division, Sarawak (ZRC 2.4677); Labang Camp on Sungei Seran, Kapit Division, (ZRC 2.5151); The Gap Resthouse, Fraser's Hill, Selangor (ZRC 2.4622); SINGAPORE: Nee Soon (ZRC 2.4575); VIETNAM: Bau Sau, Nam Cat Tien, Dong Nai Province (ZRC 2.5474–78).

APPENDIX 2

Two hundred ninety-three base-pair DNA sequences from the mitochondrial *cytb* gene for *Lipinia inexpectata* (from the type series), *Lipinia quadrivittata* (topotype material from Mindanao; CCA 1268–70), and three other congeneric species (*Lipinia noctua* (SAMA R47838) from Papua New Guinea, *Lipinia leptosoma* (SAMA R47903 and R47904) from Palau, and *Lipinia pulchella* (TNHC 53979) from the Philippines, and the outgroup *Sphenomorphus leptofasciatus* (SAMA R4195) from New Guinea. A dot indicated the same base as found in the top reference outgroup sequence SAMA R4195.

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SAMA R4195    TCTCTTCTAGGCCTCTGCCTAATCGCACAGGTACTCACAGGATTATTCCT
TNHC 51595    .....A......A.G........T.T...A...GCA..C..CC.T.....
CCA1269       ..CT.GT.......T.....T...ATG..A..CT.A..C..CC....T..
CCA1268       ..CT.GT.......T.....T...ATG..A..CT.A..C..CC....T..
CCA1270       ..CT.GT.......T.....T...ATG..A..CT.A..C..CC....T..
ZRC ID7190    ..CT.G..C.....T.........A..A.A..C..A..CA.CC.......
ZRC ID7191    ..CT.G..C.....T.........A..A.A..C..A..CA.CC.......
SAMA R47903   ..C.....T...........C..T.....A...A..T.C..CC.G.....
SAMA R47904   ..C.....T...........C..T.....A...A..T.C..CC.G.....
TNHC 53979    ..C.....C..A..A........TAT...A...T.A.....C........

SAMA R4195    TGCAATACATTACACAGCAGACATCTCCTCAGCCTTTTCATCCGTCGCCC
TNHC 51595    G..C..G...................T..C...........AA.T....
CCA1269       .........C...........G.......C.....C......A.T....
CCA1268       .........C...........G.......C.....C......A.T....
CCA1270       .........C...........G.......C.....C......A.T....
ZRC ID7190    C........C.........TG.T.....C.....C......A.....
ZRC ID7191    C........C.........TG.T.....C.....C......A.....
SAMA R47903   G........C..........T.......C.....C.............
SAMA R47904   G........C..........T.......C.....C.............
TNHC 53979    A..C.....C.................T..T..C.....A..A..G.

SAMA R4195    ATATCTGCCGCGACGTTCAACACGGTTGACTAATCCGAAACCTACATGCC
TNHC 51595    .C........A...................T.....C.....C.....T
CCA1269       ..........T.....C........C.....C.................A
CCA1268       ..........T.....C........C.....C................AA
CCA1270       ..........T.....C........C.....C.................A
ZRC ID7190    .C........T..T.....G..T..C.............T.G..C...
ZRC ID7191    .C........T..T.....G..T..C.............T.G..C...
SAMA R47903   .C..T.....A.........T.T..C................G..C...
SAMA R47904   .C..T.....A.........T.T..C................G..C...
TNHC 53979    .C..T..T..A.....C..T....C.....C..G.........T......

SAMA R4195    AACGGCGCCTCTATATTCTTTATTTGCCTTTACCTACACGTCGGACGGGG
TNHC 51595    ............T.G.....C..C.....A..TA.....A....G.....
CCA1269       .....G......G.......C..C.....C.....C...A.........
CCA1268       .....G......G.......C..C.....C.....C...A.........
CCA1270       .....G......G.......C..C.....C.....C...A.........
ZRC ID7190    .....G.....C..G..T...........G.....T...A....G.....
ZRC ID7191    .....G.....C..G..T...........G.....T...A....G.....
SAMA R47903   .....G.....A.........C........G.T...T..TA.......C..
SAMA R47904   .....A.....A.........C........G.T...T..A.......C..
TNHC 53979    ........A..C.........G.C..T..C.......TA....C..A..

SAMA R4195    ACTTTATTATGGCTCCTACATATACAAAGAGACATGAAATATCGGCGTTG
TNHC 51595    C.....C..C..A.......G.......A.........C..T..T..A.
CCA1269       C..G..C..C.....G.....G.TT.....A........C..T..T..AA
CCA1268       C..G..C..C.....G.....G.TT.....A........C..T..T..AA
CCA1270       C..G..C..C.....G.....G.TT.....A........C..T..T..AA
ZRC ID7190    CT.A..C.................TT.....A........C.....G..AA
ZRC ID7191    CT.A..C.................TT.....A........C.....G..AA
SAMA R47903   .T.A..C..C..........G.T.....A..C.....C.....G..C.
SAMA R47904   .T.A..C..C..........G.T.....A..C.....C.....G..C.
TNHC 53979    G..G..C..C........T..........A........C.....G..G.

SAMA R4195    TCCTTCTACTACTTGTAATAGCAACCGCCTTTGTAGGCTACGT
TNHC 51595    .G..G..T.....A...........T..A..C.....G..T..
CCA1269       ....CT.T..C..C........G..A.....C..G.......
CCA1268       ....CT.T..C..C........G..A.....C..G.......
CCA1270       ....CT.T..C..C........G..A.....C..G.......
ZRC ID7190    C.T.GT.C..C..C...........G.....C..G.......
ZRC ID7191    C.T.GT.C..C..C...........G.G...C..G.......
SAMA R47903   ....AT.C..C..A.....G.....A..T..C..T.......
SAMA R47904   ....AT.C..C..A.....G.....A..T..C..T.......
TNHC 53979    .GT.G..C.....G..T...........T..C..C..A..T..
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