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**An Outlying *Carlia* Population from Java and
Comments on Species Groups within the Genus *Carlia*
(Reptilia: Squamata: Scincidae)**

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An Outlying *Carlia* Population from Java and Comments on Species Groups within the Genus *Carlia* (Reptilia: Squamata: Scincidae)

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A population of *Carlia* occurs on Pulau Tindjil off the southwest tip of Java, distant from all other populations and species. A set of unique traits identifies the Tindjil *Carlia* as a new taxon; it is described herein. The new species has its closest affinities to populations (*C. peronii*, *C. spinauris*) living on Timor. Although the latter species has been considered a synonym of the former one, evidence is presented indicating that each name represents a unique species, a lowland and a montane one, respectively. Comparison of *Carlia* species is aided by the establishment of groups of presumed related species; these species groups are named and morphologically defined here.

KEY WORDS: Squamata, Scincidae, *Carlia peronii*, *Carlia spinauris*, Lesser Sunda Islands, Java, geographic variation, new species, intrageneric relationships, nomenclature.

Carlia, the four-fingered skink, is a moderately diverse genus of Australopapuan lizards. Australia has ~20 species, New Guinea and Papuan shelf islands have ~13 species, and across Lydekker's Line, Wallacea has six described species (Fig. 1). The contrast in diversity in numbers of species and their morphologies is striking on the east and west sides of the Line. The latter aspect is examined in more detail subsequently. In Wallacea, two of the six currently recognized species are the sole members of the *Carlia peronii* species group. This species group and others are defined later; however, the discovery of a population on Tindjil, an island off the southwest coast of Java instigated a re-evaluation of Wallacea *Carlia*. The Tindjil *Carlia* is a distant outlier from other Wallacea *Carlia* populations and has a unique morphology that declares it a different and undescribed species.

Before proceeding with its description, it is necessary to call attention to a nomenclature issue involving its presumed sister species living on Timor. The Timor population of *Carlia* has received two names: *Heteropus peronii* Duméril and Bibron, 1839 and *Lygosoma (Leiolopisma) spinauris* Smith, 1927. Although the assignment of a name to this population would seem simple, it is not because *H. peronii* is potentially a secondary homonym. This nomenclatural issue is addressed following the description of the Javan species. Evidence indicates that both taxa are valid, thus I use the types of both *H. peronii* Duméril and Bibron and *L. spinauris* Smith for comparison.

A second item requiring attention is the issue of species groups within the genus *Carlia*. Because this topic requires more than a paragraph to delineate the diverse morphologies of the ~40 species of *Carlia*, I note here only that the medium-sized *Carlia* of the Lesser Sundas with their ear-openings completely encircled with pointed lobules represent the *Carlia peronii* species group. I examine intrageneric relationships at the end of this article.

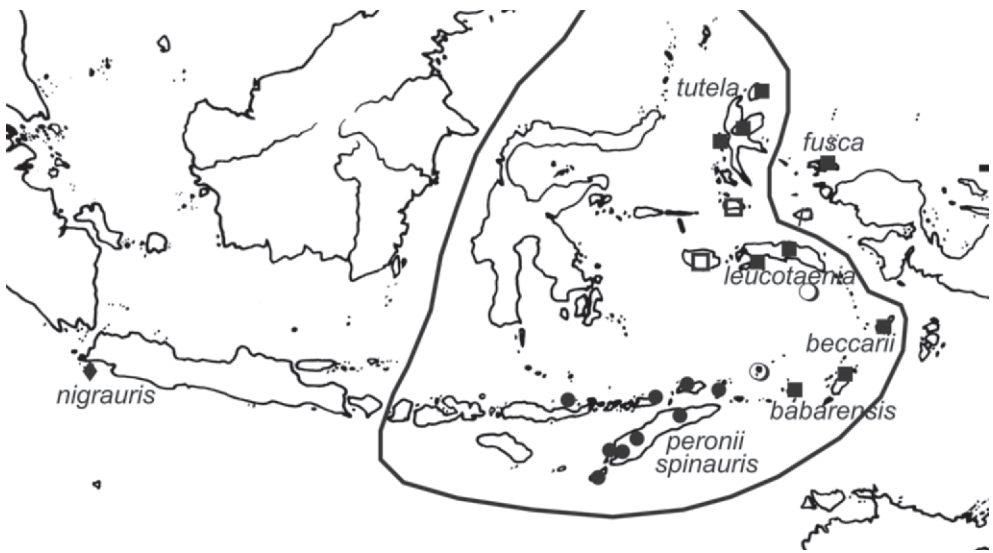


FIGURE 1. Occurrences of species of *Carlia* in Wallacea and Java. Plotting data are given in Appendix 3: Map resources. Wallacea enclosed in solid line. Symbols: diamond, type locality of *C. nigrauris*; circles, *C. peronii* species group members; squares, *C. fusca* species group members; solid symbol, species group assignment certain; open symbol, group assignment uncertain.

The geographic peculiarity of the Tindjil population is striking because of the absence of *Carlia* in the Lesser Sunda Islands west of Flores, and for Flores, *Carlia* is vouchered there only on the offshore island of Pulau Sukur (Fig. 1; Appendix, part 3). The gap from the main cluster of Wallacea *Carlia* is nearly 1800 km. The closest named populations are the Timor *C. peronii* and *C. spinauris*. The Tindjil population is not a member of either of these populations. Other *Carlia* populations occur on Roti, Alor, Wetar, Kisar, and Banda Ids. These populations similarly do not share the morphology of the Tindjil population; they may also represent undescribed species. These unnamed populations are compared also to the Tindjil population (see 'Comparison to other *Carlia*' below).

Carlia nigrauris Zug, sp. nov.

Figure 2.

TYPE MATERIAL.— HOLOTYPE: SMF 53916, adult male from Indonesia, Baten Province, Pulau Tindjil (6°58'S 105°45'E), collected by A.M.R. Wegner, 28 June 1955. PARATYPES. SMF 53915, 53917–53922, same locality, date, and collector as holotype; WAM R101496, R101498, Indonesia, Baten Province, Pulau Tindjil (6°58'S; 105°45'E), collected by M. Bangs, 1989; WAM 104927, same locality as preceding, collected by M. Bangs, 4 March 1990. Adult males — SMF 53915, 53917, WAM R101496, R104927, subadult male (immature) — WAM R101498; subadult females (immature) SMF 53919, 53921–53922, juvenile females — SMF 53918, 53920.

DIAGNOSIS.— *Carlia nigrauris* is a member of the *C. peronii* species group and differs from all other group members by the black color of the scales and skin of the ear openings and its perimeter in juveniles and adults. Additionally, *C. nigrauris* averages larger (adult males mean 56 mm SVL) than *C. peronii* and *C. spinauris* (~40 mm SVL) and males have a proportionately longer hindlimb (110% HindIL/TrunkL, 91 and 102% respectively). *C. nigrauris* averages more Dorsal (50), Midbody (33), and 4ToeLm (28) than *C. peronii* and *C. spinauris* (45, 29, 27 and 48, 30, 24, respectively).



FIGURE 2. The holotype of *Carlia nigrauris* sp. nov., dorsal aspect, preserved, SMF 53916. Bottom row. Dorsal and lateral views of the head of the holotype, respectively.

DESCRIPTION OF HOLOTYPE.— An adult male, 56.4 mm SVL, 64 mm tail length (regenerated, posterior ~third), 25.3 mm TrunkL, 27.4 mm HindLL, 12.8 mm HeadL, 10.3 mm JawW; 4.8 mm SnEye; 2.9 mm SnW; 1.5 mm PalpbD, and 1.6 mm EarD. Scalation right side for bilateral traits: large, flattened pentagonal rostral contacting posteriorly 1st supralabial and large square nasal on each side, and dorsomedially large pentagonal frontonasal; prefrontals large and widely separated on dorsal midline; large frontal and frontoparietal; moderately small triangular interparietal with well-developed parietal eye; pair of large rectangular parietals touching medially behind interparietal; each nasal pierced by large naris; anterior loreal bluntly triangular, higher than wide, and equal-sized to trapezoidal posterior loreal, wider than high; 2 preoculars, lower one largest and abutting large subocular, followed beneath eye and above supralabials by series of small, ovoid

suboculars, enlarging posteroventral and forming 7 distinct postoculars; above orbit 4 large supraoculars (Supoc), separated from eyelid by 8 supraciliaries (Supcil); upper eyelid immobile with 8 eyelid rim scales (Eyeld), lower eyelid mobile with 14 eyelid rim scales and with distinct transparent palpebral disc, width subequal horizontal ear-opening diameter; 4 temporal scales (Temp), anterior pair smaller than posterior pair; 7 supralabials (Suplab), 5th largest and beneath center of eye (BlwEye); large semicircular mental followed on each side by 6 infralabials (Inflab), first smallest; round ear-opening, encircled by ~14 acute auricular lobes, ones on anterodorsal and anterior border largest and sharply pointed (AuricN); 51 very weakly tricarinate dorsal scales (Dorsal), anteriormost bilateral pair enlarged as unkeeled nuchal scales; 33 scales rows around middle of trunk (Midbody), 21 smooth ventral lamellae on third finger (3FingL) and 28 smooth lamellae of fourth toe (4ToeL); preloacal scale only slightly larger than immediately anterior ventral scales; all ventral and ventrolateral scales smooth.

Coloration in preservative: Overall appearance is a medium brown lizard from tip of snout onto tail with a white underside. Closer inspection reveals top of head with coppery sheen, laterally head lighter and most scales with posterior edge irregularly bordered with dark brown, edging most distinct on supra- and infralabials; chin and throat bluish ivory with fine reticulation of black lines within scales. Dorsally neck onto tail, scales brown with narrow, diffuse, darker brown edges, forming broad vague middorsal stripe; darker brown dorsolaterally on neck and entire sides of trunk and tail. Ear opening walls and narrow external perimeter black, strikingly so against light brown background grading into the ivory white of the venter. Dorsally, fore- and hindlimbs share the brown of the body with a few dark brown to black specks; ventrally, limbs are white.

DESCRIPTION.— Mensural data based on five adult males (mean±1SD), meristic data on 11 juveniles and adults (median±1SD). A moderately large *Carlia* ranging in adult size from 54 to 58 mm SVL (55.6±1.72) with 21.8–25.8 mm TrunkL (24.1±1.57), 21.0–23.2 mm SnForel (22.4±1.22), and 25.5–27.4 HindIL (26.4±0.76); 12.3–13.7 mm HeadL (13.0±0.58), 8.3–10.3 mm JawW (9.2±0.02), 4.8–5.2 mm SnEye (5.0±0.21), 2.8–3.0 mm SnW (2.9±0.10), 1.5–1.8 mm PalpbD (1.6±0.13), and 1.5–1.8 mm EarD (1.7±0.11). Head and nuchal scales smooth; interparietal always present*; 4 Supoc, 7 Supcil, 8–10 Eyeld (9±0.71), 7 Suplab, 5th BlwEye, and 6 Inflab on each side. Ear opening circular to oblong-vertical, perimeter and upper inner wall with numerous acute auricular lobes, 1–8 (6±2.2) enlarged lobes on anterodorsal and anterior border (AuricN). Trunk scales weakly tricarinate dorsally and laterally, 42–50 Dorsal (50±1.4), 32–35 Midbody (33±0.98). Subdigital lamellae smooth, 18–22 3FingLm (20±1.2) and 26–33 4ToeLm (28±1.9). Without adult females, there is no means to determine whether *C. nigrauris* displays sexually dimorphic in any preceding traits. [*The SMF series of Tindjil *Carlia* was first reported by Mertens in his report (1957a) on the herpetofauna of extreme western Java. The series consisted of 21 juveniles and adults. He reported one individual with interparietal entirely fused with frontoparietal and partially fused in two others. Midbodys were 32–38 and 4ToeLm 26–32 (means 35.1 and 29.4, respectively; my calculations). Mertens recognized that the Tindjil population was distinct but was reluctant to describe them owing to the inadequacy of existing knowledge about ‘*fuscum*-Formen’ [= *Carlia*]. Mertens also presented some generalized color notes on the preserved specimens.]

Coloration is summarized in the subsequent Intraspecific Variations section.

DISTRIBUTION.— Known presently only from Pulau Tindjil [Tinjin, an alternate spelling] lying just off the southwest coast of Java (Fig. 1).

ETYMOLOGY.— The specific name derives from the Latin *nigra* (feminine) for black and *auris* (f.) for ear in reference to the color of the wall of the ear-openings and the external perimeter of adjacent head scales.

INTRASPECIFIC VARIATION.— In preservative, the colors of all life stages are muted and likely

the striped appearance of juveniles and subadult females is brighter and bolder in life and the brown of adults males has an iridescent sheen. Data on living individuals are not available.

The two SMF adult male paratypes do not differ strikingly from the holotype; both show the overall brown on the top of the head and remainder of trunk and tail. Ventrolaterally, their heads have the variegated light and dark pattern and the black walls and perimeter of the ear-openings make them appear larger than they are. The venters are ivory white with dark gray edging on posterior chin and anterior throat scales yielding a dusky longitudinal striping on throat. The largely regenerated tail of SMF 53915 appears orangish brown, particularly ventrally. The largest subadult female (WAM R101498) of the type series was too dehydrated to yield reliable coloration, similarly for the two adult WAM males.

The smallest paratypes (SMF 53918, 53920; both ~39 mm SVL) are juvenile females. Both are boldly striped although each in a somewhat different pattern. They share a broad middorsal stripe from the rear of the neck to the sacral area. This light stripe is bordered laterally by darker brown extending to the ventrolateral surface of the trunk, gradually becoming lighter toward the venter. In SMF 53918 (Fig. 3), the middorsal stripe is continuous with the coppery green top of the head and the dusky greenish brown of the sacral area and anterior half of the tail. On the neck and trunk, the stripe is glossy green muted by pairs of diffuse brown bars on each stripe scale. Laterally on neck, trunk and base of tail, the background color is dark brown and nearly black immediately adjacent to the middorsal stripe. On closer inspection, the lateral brown background is speckled with flecks (usually about half of a scale) of lighter brown or green; the green flecks are more numerous than the brown ones. The loreal and temporal areas of the head are predominantly brown; the upper and lower lips are green and brown barred. The black of the ear is confined to the internal walls. The venter is bluish ivory with the same dark scale marking as on the chin and throat scales of the adults. Fore- and hindlimbs are two-toned dorsally with the proximal portion dark brown matching the dorsolateral trunk color, distal half and foot medium brown; some lighter flecks. Ventrally, limbs are whitish like the trunk venter.

In SMF 53920, the middorsal stripe is slightly narrower than in the former juvenile and is beige from shoulder to sacrum, where the stripe disappears by merging with the parasagittal stripes into the dusky tan dorsal surface of the tail. Anteriorly from mid-neck, the dorsal surface is light brown to the tip of the snout. The middorsal stripe on rear of neck and trunk is narrowly edged with dark brown; a broad coppery brown stripe lies parasagittally on each side. Dorsolaterally the surface is dark brown from behind the eye to the base of the tail. The dark brown gradually lightens ventrolaterally as it merges into the bluish ivory venter. The sides of the head and ear-openings are as in the other juvenile. Limbs are also similar to the former juvenile.

The three SMF females are similar-sized (44–47 mm SVL) subadults (slightly enlarged ovarian follicles, oviducts strap-like). All three retain the juvenile coloration, most similar to SMF



FIGURE 3. The dorsal coloration of juvenile and subadult female *Carlia nigrauris*, preserved. From left to right: SMF 53918, 53929, 53921, 53922.

53920, but the middorsal and parasagittal light stripes are narrower owing to the expansion of the dark brown border between them. The side of head, neck, and trunk are as in the juveniles. The black surface is confined to the walls of the ear-opening. The venters are bluish ivory with diffuse dark striping on chin and anterior neck.

COMPARISON TO OTHER *CARLIA*.— This comparison examines only geographically adjacent taxa and populations, i.e., Wallacea and islands of the New Guinea shelf adjacent to Lydekker's Line. Comparison to more distant taxa and populations is available in the subsequent discussion of species groups within the genus *Carlia*.

Currently, there are six named populations of *Carlia* within Wallacea (Fig.1): *C. babarensis* (Babar and Tanimbar); *C. beccarii* (Kai); *C. leucotaenia* (Ambon and Seram); *C. peronii* (Timor); *C. spinauris* (Timor); and *C. tutela* (Halmahera, Morotai, Ternate). Unassigned *Carlia peronii* group populations are vouchered by adequate samples from several other Wallacea islands (Alor, Kisar, Roti, Pulau Sukur, Banda) to permit comparison with *C. nigrauris*. These unassigned populations might represent new species or representatives of *C. peronii* or *C. spinauris*; however, that analysis requires more recently collected specimens with color notes and/or images of vouchered living specimens. Recent and ongoing fieldwork in Timor-Leste likely will provide an opportunity for such a detailed analysis by those fieldworkers.

Wallacea species (*C. babarensis*, *C. beccarii*, *C. leucotaenia*, *C. tutela*) have been assigned to the *C. fusca* species group (Zug 2004). Even though ear-shape can be altered in preservation, its oblong oblique or vertical orientation in the *fusca*-group taxa is strikingly different from the usual circular ear-opening of the *peronii*-group taxa. Additionally the rim of the latter group is completely encircled with acute auricular lobes, distinctly pointed on anterior and anterodorsal edge, contrasting with the blunter lobes confined to the anterior and anterodorsal border in the *fusca*-group taxa. These four *fusca*-group taxa bracket, but do not overlap, adult male SVL with *C. nigrauris* (54–58 mm): *C. babarensis* 45–51 mm; *C. beccarii* 65–80 mm; *C. leucotaenia* 43–53 mm; *C. tutela* 41–54 mm. All five taxa share similar body proportions, although hindlimbs of *C. beccarii* are longer than in the other taxa, i.e., 50–59% HindL/SVL to 39–54% for others. Not as striking, trunk length of *C. nigrauris* (40–45% TrunkL/SVL) lies in the lower half of the range of the *fusca*-group members (39–51%).

Among the *peronii*-group, *C. nigrauris* is the largest member with all other populations distinctly smaller (Table 1). The largest males in the Kisar and Banda samples are 47 mm SVL. The Timor-WAM and Banda samples show size dimorphism between adult females and males; these two samples and the Alor one (not size dimorphic) are the only ones with adequate numbers of females and males to test for dimorphism. Aside from the overall size difference between *C. nigrauris* and its *peronii*-group relatives, body proportions are generally similar (comparison confined to males). Among adults, *C. nigrauris*, Alor males, Kisar males, and Banda females and males have proportionately longer hindlimbs. Among *Carlia* and other skinks, females regularly have longer trunks than males; this dimorphism is evident in the larger *peronii*-group samples, but statistically significant only in the Banda sample.

In scalation, *C. nigrauris* is a typical *fusca*- and *peronii*-group taxon, that is scalation traits are little different (ranges overlap) among the species. The exception is the auricular lobe trait. I note here the low variability of scalation traits in all samples, even in the combined juvenile and adult samples. Coefficients of variation (*v*) range between 3 and 9% for mensural traits (adult only samples) and 3–9% for the scalation and proportions in both adult-only and combined juvenile-adult samples.

Among the *peronii*-group samples, Dorsal, 3FingLm, 4ToeLm, and DorsKN (Table 2) offer the greatest intersample difference and potential evidence of possible regional differentiation. In

TABLE 1. Summary of variation in select mensural characters in adult samples of the *Carlia peronii* species group. Mean \pm 1 standard deviation, range, and statistically significant dimorphism * (Student's t $p \leq 0.05$); sample size in brackets; species assignment in parentheses.

Locality		SVL	TrunkL/SVL	HindIL/Trunkl	HeadL/SVL	EarD/Headl
Java-Tindjil (<i>nigrauris</i>)	[5 ♂]	55.6 \pm 1.72 54.3–58.3	0.43 \pm 0.019 0.40–0.45	1.10 \pm 0.062 1.03–1.18	0.23 \pm 0.008 0.23–0.25	0.13 \pm 0.005 0.12–0.14
Timor						
<i>H. peronii</i> D&B (MNH 3037)	[1 ?]	32.3	0.45	1.02	0.24	0.13
<i>L. spinauris</i> Smith (BMNH 1946.8.17.58)	[1 ♂]	41.3	0.46	0.91	0.2	0.17
Timor-WAM	[11 ♂]	39.1 \pm 1.82* 34.6–40.8	0.45 \pm 0.021 0.43–0.50	0.96 \pm 0.066* 0.86–1.05	0.23 \pm 0.007* 0.21–0.24	0.14 \pm 0.017 0.11–0.17
	[11 ♀]	37.0 \pm 1.57* 34.7–39.9	0.47 \pm 0.027 0.43–0.51	0.85 \pm 0.063* 0.78–0.98	0.21 \pm 0.006* 0.21–0.22	0.14 \pm 0.016 0.12–0.17
Roti (unassigned)	[1 ♂] [4 ♀]	41 38.0 \pm 1.10 36.4–38.0	0.43 0.45 \pm 0.025 0.42–0.48	1.12 0.87 \pm 0.031 0.84–0.90	0.22 0.21 \pm 0.007 0.21–0.22	0.11 0.12 \pm 0.007 0.11–0.13
Alor (unassigned)	[7 ♂] [8 ♀]	43.2 \pm 1.74 42.1 \pm 1.17 39.4–43.0	0.43 \pm 0.028 0.47 \pm 0.034 0.42–0.51	1.06 \pm 0.084* 0.89 \pm 0.088* 0.73–1.06	0.23 \pm 0.006* 0.22 \pm 0.006* 0.21–0.22	0.13 \pm 0.011 0.14 \pm 0.011 0.11–0.15
Kisar (unassigned)	[7 ♂] [2 ♀]	46.0 \pm 1.88 40.0 \pm 0.07 39.9–40.0	0.45 \pm 0.012 0.49 \pm 0.026 0.47–0.50	1.04 \pm 0.082 0.95 \pm 0.085 0.89–1.05	0.23 \pm 0.008 0.22 \pm 0.009 0.21–0.23	0.13 \pm 0.005 0.13 \pm 0.005 0.12–0.13
Other outliers						
Pulau Sukur (unassigned)	[2 ♂] [3 ♀]	40.7 \pm 0.50 39.7 \pm 0.65 39.1–40.4	0.50 \pm 0.020 0.52 \pm 0.019 0.50–0.54	0.93 \pm 0.079 0.84 \pm 0.053 0.78–0.87	0.22 \pm 0.015 0.22 \pm 0.011 0.21–0.23	0.15 \pm 0.015 0.16 \pm 0.007 0.16–0.17
Banda Ids. (unassigned)	[7 ♂] [6 ♀]	44.8 \pm 1.45* 42.9 \pm 1.58* 41.5–45.8	0.42 \pm 0.013* 0.46 \pm 1.380* 0.43–0.50	1.17 \pm 0.043* 1.01 \pm 1.604* 0.97–1.06	0.24 \pm 0.005* 0.23 \pm 0.001* 0.22–0.23	0.13 \pm 0.009 0.12 \pm 0.378 0.10–0.14

Dorsal, the overall range is 45 to 55 scale rows with Alor possessing the highest average (53) and Timor-WAM the lowest (47). 3FingLm ranges 15 to 22; most samples average 17 or 18, but *C. nigrauris* (20) and Banda (21) have distinctly higher means. A similar pattern occurs for 4ToeLm with 23 and 24 the most frequent means, and *C. nigrauris* and Banda adult males with means of 29. All *peronii*-group samples show striations or weak keeling on dorsal trunk scales. The most common DorsKN is tricarinate. Some individuals of Timor-WAM, Roti, and Alor have a mix of bicarinate and tricarinate scales on the dorsal and upper lateral trunk; tricarinate scales are the

TABLE 2. Summary of variation in select meristic characters in samples of the *Carlia peronii* species group. Median \pm 1 standard deviation, range, and statistically significant dimorphism* (Student's t $p \leq 0.05$); sample size in brackets; species assignment in parentheses.

Locality		Dorsal	Midbody	3FingLm	4ToeLm	DorsKN
Tindjil	[5 ♂]	49 \pm 1.58	33 \pm 0.55	20.5 \pm 0.96	29 \pm 2.07	3 \pm 0.0
(<i>nigrauris</i>)		47–51	33–34	20–22	28–33	
	[11 juv & ad]	50 \pm 1.37	33 \pm 0.98	20 \pm 1.20	28 \pm 1.91	3 \pm 0.0
		47–51	32–35	18–22	26–33	
Timor						
(<i>peronii</i>)	[?]	45	29	19	27	2
(<i>spinauris</i>)	[1 ♂]	48	30	19	24	3
Timor -WAM	[11 ♂]	47 \pm 1.3	31 \pm 0.79	17 \pm 1.22	23 \pm 1.83	3 \pm 0.47
		45–49	30–32	15–19	19–25	2–3
	[11 ♀]	48 \pm 0.82	30 \pm 1.43	17 \pm 1.44	24 \pm 1.29	3 \pm 0.41
		46–48	28–32	15–20	21–25	2–3
Roti	[8 ♀]	51	33	17	24	2
(unassigned)		46–51	32–34	15–20	22–26	2–3
	[8 juv & ad]	49.5 \pm 1.60	32 \pm 0.76	17.5 \pm 1.60	23.5 \pm 1.28	2 \pm 0.46
		46–51	32–34	15–20	22–26	2–3
Alor	[7 ♂]	51 \pm 1.35*	34 \pm 1.38	18 \pm 0.98	24 \pm 1.95	3 \pm 0.0
(unassigned)		49–51	1–35	15–20	22–27	
	[8 ♀]	53 \pm 1.13*	33.5 \pm 1.17	17 \pm 1.20	23.5 \pm 2.39	3 \pm 0.35
		51–55	32–35	16–20	21–27	2–3
Kisar	[7 ♂]	50 \pm 1.35	33 \pm 0.79	18 \pm 1.16	25 \pm 1.13	3 \pm 0.0
(unassigned)		48–52	31–33	16–19	24–27	
	[9 juv & ad]	50 \pm 1.74	33 \pm 1.23	18 \pm 1.05	26 \pm 1.27	3 \pm 0.0
		48–54	30–34	16–19	24–28	
other outliers						
Pulau Sukur	[2 ♂]	50 \pm 1.41	33 \pm 0.0	18.5 \pm 0.71	25 \pm 2.83	3 \pm 0.0
(unassigned)		49–51	–	18–19	23–27	
	[11 juv & ad]	51 \pm 1.0	33 \pm 0.75	18 \pm 0.93	24.5 \pm 1.43	3 \pm 0.0
		49–53	32–34	17–20	22–27	
Banda Ids.	[7 ♂]	46 \pm 0.95*	33 \pm 1.51	21 \pm 0.54	29 \pm 1.38	0 \pm 1.60
(unassigned)		45–48	30–34	21–22	26–30	0–3
	[6 ♀]	48.5 \pm 0.98*	32.5 \pm 0.82	21 \pm 1.17	28.5 \pm 0.55	1.5 \pm 1.64
		47–49	32–34	19–22	28–29	0–3

most abundant, and infrequently bicarinate scales dominate. Individual Banda *Carlia* has smooth or weakly tricarinate dorsal scales.

Greer (1976) described the coloration of the *H. peronii* holotype as having a narrow light dorso-lateral stripe from ear to end of trunk, a narrow midlateral light stripe from ear to at least mid-trunk, and the two light stripes enclosed a broader dark brown stripe with a few tiny light spots on each side, and dorsally olive brown with a scattering of small brown spots on the edges of some

dorsal scales. My notes on the type agree with Greer's description of lateral coloration and additionally a narrow dark middorsal stripe. Smith's description (1927) of *C. spinauris* is brief: dorsum dark brown with indistinct light dorsolateral stripe bordered below with black (width of the black is not given), and venter is white with throat black spotted. A specimen (RMNH 7941) from Semau (island opposite Kupang) had a "fusca" brown dorsum with slight peppering of dark brown, dorsolateral light stripe continuous from eye to anterior quarter of trunk, no midlateral light stripe and dusky brown sides from ear to inguen. Alor juveniles and adults have a brown dorsum from snout onto tail with black speckling (dark scale edges) on trunk, moderately broad dorsolateral light (tan) stripe from snout onto tail (ontogenetically disappears from snout to eye, then eye to ear, and become more diffuse but still distinct on neck and trunk in adults); laterally brown, dark brown from eye to trunk just behind forelimb, thereafter brown same as dorsum; laterally temporal area and neck spotted with white; venter ivory and throat with narrow black stripping. Color slides (R. How) were available for a living specimen each from Wetar (WAM R117553, adult male) and Kisar (WAM R117487, adult male). The Wetar male was brown from head to base of tail, brassy anteriorly becoming lighter, somewhat coppery on posterior half of trunk; laterally head brown, supra- and infralabials white with black edges, brown and white mottling continues on neck to axilla; side of trunk golden beige with band of bright orange from shoulder to hindlimb, lighter on posterior half and side of tail orangish; sides of throat with dark and light striping. Inside of ear-opening appeared dark. The Kisar male similarly colored although less bright laterally on trunk and lateral trunk band a subdued coppery orange; dorsolaterally neck unicolor dark brown and more diffused dark and light mottling below, white spot behind ear. None of these colorations match the pattern of *C. nigrauris*. Timor *C. peronii* and *C. spinauris*, and the Alor population display a distinct dorsolateral light stripe from ear to inguen. The Wetar and Kisar populations lack the dorsolateral light stripe (at least in adult males) and any indication of dark brown on sides of trunk.

NATURAL HISTORY.—Mertens (1957a) included no natural history information. Notes with some WAM specimens mentioned that they were found on ground as is typical for *Carlia*.

TIMOR *CARLIA* — NOMENCLATURAL REVIEW

Duméril and Bibron (1839) described *Heteronotus peronii* from a specimen with the locality data of "Ile de France" [= Mauritius], an erroneous locality. The description is adequate to recognize the specimen as a four-fingered skink. When Boulenger (1887) published his catalog of lizards, he reassigned *H. peronii* D&B and a multitude of other skinks to the genus *Lygosoma*. He specifically included three of De Vis's Queensland taxa (*Myophila vivax* DV 1884, *Heteropus lateralis* DV 1885, *H. blackmanni* DV 1885) as synonyms of *H. peronii*. It is not known whether Boulenger examined the type of *H. peronii* D&B. Boulenger also assigned *Seps peronii* Fitzinger 1826 (an unrelated Australian reduced-limbed taxon) to *Lygosoma* thereby creating a homonymy with *Lygosoma peronii* (D&B) as a secondary homonym. Boulenger did not address this homonymy; indeed, he presented two *Lygosoma peronii* species accounts in his Catalog (i.e., *Lygosoma peronii* (D&B) account #82, page 286 and *Lygosoma peronii* (Fitzinger) #134, page 326). The Strickland nomenclatural code was in effect when Boulenger published his Catalog, and that code recognized the necessity of replacing secondary/junior homonyms with a new name. Boulenger offered no replacement name for *H. peronii* D&B, nor has anyone else since its creation as a homonym.

De Rooij (1915) did not list any four-fingered *Lygosoma* from Timor. This absence re-enforced the persistence of D&B's incorrect type-locality for *H. peronii* and de Rooij's acceptance of *L. peronii* (D&B) as a member of the Australian herpetofauna and outside the area of her treatise.

In 1927, Malcolm Smith described the four-fingered skinks that he had collected in the moun-

tains of Timor as *Lygosoma (Leiolopisma) spinauris* Smith 1927. Because he had no reason to suspect that *L. peronii* (D&B) derived from Timor, he was unaware that a Timor population had a scientific name.

In 1952, Mittleman resurrected *Carlia* Gray for the four-fingered Australopapuan skinks and *Hemiergis* Wagler for the group of reduced-limbed (four digits or fewer on fore- and hindlimbs) Australian skinks. Mittleman also included a list of species for all his resurrected genera, and specifically noted in the introduction to this list that he considered all listed species to be “distinguishable racial entity.” (Mittleman 1952:21.) This action removed the homonymy and re-established *Carlia peronii* (D&B) and *Hemiergis peronii* (Fitzinger) as valid and separate taxa.

In 1953, Mitchell reviewed the status of the four-fingered skinks of Australia. He continued the use of *Leiolopisma*, because either he was unaware of Mittleman’s generic reorganization or his manuscript was in press when Mittleman’s synopsis appeared. Because *L. peronii* (D&B) was assumed to be an Australian *Carlia* and related to or synonymous with *L. vivax* (De Vis), he called attention to the situation by stating “[*peronii*] suppressed as a homonym in the genus *Lygosoma*.” (Mitchell 1953:85.) His action was appropriate and potentially suppressed the use of *peronii*, because the nomenclatural code then in effect and the subsequent edition defined a secondary homonym as an identical species group name established for different nominal taxa subsequently brought together in the same generic name group. The younger name is the secondary homonym and invalid.

In 1976, Greer examined the type of *Heteropus peronii* D&B and recognized that it was most similar to *Carlia spinauris* (Smith). Following a detailed morphological comparison of *H. peronii* with Smith’s type specimens of *L. spinauris*, he concluded that the latter was a synonym of the former. He did not address the issue of the *peronii* homonymy. Under the nomenclatural code then in effect, he could have declared *H. peronii* D&B invalid owing to Boulenger’s 1887 creation of a secondary homonym. Instead, he accepted the name as a senior synonym for the Timor *Carlia*, and further demonstrated that D&B’s ‘Ile de France’ type locality was incorrect and reassigned the type-locality to Timor. He examined the itinerary of Peron and suggested that the MNHN type likely derived from “the principal harbor and town of Timor” [= Kupang] and not from Semau [island opposite Kupang]. If we accept this origin [and there is no compelling reason to reject it], this origin of the holotype of *H. peronii* D&B has important ramifications for the assignment of names to Timor populations.

Mittleman’s resurrection of *Carlia* and Greer’s failure (intentional or otherwise) to address the *peronii* homonymy create a potential nomenclature quagmire if we follow the “letter of the” Code that was in force when Mitchell noted the homonymy. Mitchell, however, did not propose a replacement name, and his nomenclature comment occurred a year after Mittleman eliminated the homonymy by resurrection of *Carlia*. Further, the actions of Mittleman and Greer re-established the regular use of the name *Carlia peronii* (D&B) in the herpetological literature. The absence of a previous examination and the resolution of this nomenclatural matter allow me to propose the validity of *Carlia peronii* (Duméril and Bibron) under Article 59.2 of the present Code (1999, ICZN, 4th ed.).

As noted earlier, I consider both *C. peronii* (D&B) and *C. spinauris* (Smith) as valid Timor species, the former a lowland species and the latter a montane one, based on the type localities of their holotypes. The situation is potentially more complex if Hinrich Kaiser’s assessment (*in litt.*, December 2009) of four species in Timor-Leste is correct; however, both named species derive from west Timor, and one of his challenges will be to determine whether one or both western Timor *Carlia* also occur in Timor-Leste.

TIMOR *CARLIA* — MORPHOLOGY OF *C. PERONII*

The Timor-WAM sample derives from Kokabis (10°11'S 123°46'E), a small village ~25 km east of Kupang in an undulating and largely agricultural landscape (Google Earth, 28 Jan. 2010 image), and one Kupang specimen. This sample offers an opportunity to characterize *Carlia peronii* as a population instead of as a single immature individual. This characterization is based on an assumption of the accuracy of the type locality of *H. peronii* D&B. As noted in the preceding nomenclatural review, *H. peronii* D&B and *L. spinauris* Smith are available and represent different populations owing to their type localities. The former derives from a lowland locality, i.e., vicinity of Kupang, the major port of Timor and the only Timor location visited by Peron (Greer 1976). The holotype of *L. spinauris* was personally collected by M. Smith and his wife at Lelogama, which he (Smith 1927) describes as wooded hilly area (750 m elevation). Thus south (or west) Timor appears to have two species of *peronii*-group *Carlia*, an upland and a lowland one. Of the Timor samples available, I have analyzed only the WAM specimens; the following characterization of *Carlia peronii* (D&B) is based on that sample.

Carlia peronii is a moderately small skink, ranging in adult size from 35 to 41 mm SVL (♂ 39.1±1.82, 34.6–40.8; ♀ 37.0±1.57, 34.7–39.9) with 15.0–19.9 mm TrunkL (♂ 17.7±0.95, 16.1–19.3; ♀ 17.4±1.46, 15.0–19.9), and 14.7–18.1 HindLL; (♂ 17.0±0.88, 15.7–18.1; ♀ 14.7±0.95, 13.0–15.7); 7.4–9.3 mm HeadL (♂ 8.9±0.44, 7.9–9.3; ♀ 7.9±0.32, 7.4–8.4), 1.0–1.3 mm PalpbD (♂ 1.2±0.1.0–1.3; ♀ 1.1±0.10, 1.0–1.3), and 0.9–1.4 mm EarD (♂ 1.2±0.13, 1.0–1.4; ♀ 1.1±0.11, 0.9–1.3). Body proportions Timor-WAM in Table 1, scalation in Table 2. Head and nuchal scales smooth; interparietal always present; prefrontal large but separated by rostral and frontonasal in contact, 4 Supoc, 7 Supcil (rarely 6 or 8), 7–10 Eyeld (9±0.91), 7 (rarely 6) Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening circular or nearly so, perimeter and upper inner wall with numerous acute auricular lobes, 1–9 (5±2.2) enlarged lobes on anterodorsal and anterior border (AuricN). Trunk scales weakly tricarinate and/or bicarinate dorsally and laterally (65% tri, 27% mixed, 8% bi), 45–49 Dorsal (47.5±1.10), 28–32 Midbody (30.5±1.13). Subdigital lamellae smooth, 15–20 3FingLm (17±1.31) and 19–25 4ToeLm (23.5±1.59), some digits with pre-penultimate and penultimate lamellae creased (may reflect specimen dehydration rather than real state. Adult sample sexually dimorphic (Student's t $p \leq 0.05$) in SVL, HindLL, HeadL, PalpbD, HindLL/SVL, HindLL/TrunkL, HeadL/SVL, and Supcil. Aside from Supcil, 4ToeLm and shape of ear-opening, the preceding characterization matches Greer's (1976) redescription of the holotype of *H. peronii* D&B. My lower by one 4ToeLm likely represents a difference in defining the first proximal lamella; the first one for me is the first lamella wider than long and in contact with dorsal digit scales. Ear-opening shape is strongly dependent upon condition at time of preservation; any dorsoventral compression or bending of the head will alter the original condition.

Greer (1976) noted that the *H. peronii* holotype had a narrow light dorsolateral stripe from ear to end of trunk and a narrow midlateral light stripe from ear to at least mid trunk; the two light stripes enclosed a dark brown stripe with a few tiny light spots. These data on coloration can be expanded by an examination of the frequency of striping. My wife and I recorded a set of five pattern traits in a large sample of adult Timor-WAM specimens ($n = 37$, 18 ♂ 19 ♀): 1) chin-throat scales — no black edges, little to moderate black edging, most scales black edged; 2) dorsolateral light stripe on neck — absent or present; 3) lateral light stripe on neck — absent or present; 4) dorsolateral light stripe on trunk — absent or present; 5) lateral light stripe on trunk — absent or present. Only one female lacked black-edged scales on the throat, 13 females (68%) had moderate amount of edging, and five had most scales black edged. In contrast, 15 males (83%) had most

scales black edged and only three with moderate edging. Sexual dimorphism also occurred in levels of the dorsolateral and lateral light striping. All females retained neck and trunk dorsolateral stripes, and all females possessed lateral stripes on the neck and 16 (84%) had lateral stripes on the trunk. All males had a dorsolateral stripe on the neck but only three (17%) retained the dorsolateral stripe on the trunk. Most males (83%) had the lateral stripe on the neck, but none had a lateral trunk stripe. Males and females had similar frequencies of DorsKN; most individuals were tricarinate (67% ♂ 68% ♀); a few individuals of each sex were mixed bi- and tricarinate; and two females and one male were bicarinate.

CARLIA MORPHOLOGY — SPECIES GROUPS

The last quarter of the 20th century saw the Australopapuan four-fingered skinks *Carlia* going from a relatively obscure and low diversity group with 12 species (Mitchell 1953) to nearly 40 species now and others await description. First, Storr (1974) reviewed the populations of Western Australia and the Northern Territory, recognizing four new species and two existing ones. On the opposite side of the continent, Covacevich and Ingram in a series of research articles, ending with their 1989 review (Ingram and Covacevich 1989) added five new taxa, recognizing a total of 21 Australian species (including three species recently transferred to *Liburnascincus*). Zug's review (2004) of the New Guinean *Carlia fusca* resulted in a fissure of this taxon into 19 species, including six new ones and eight resurrected ones; further four differentiated populations were not described. With this increase in diversity, interest in their interspecific relationships grew, and Stuart-Fox (1998; and subsequently Stuart-Fox et al. 2002) performed a phylogenetic analysis with mtDNA. Unfortunately, the results (strict consensus of best MP and ML tree) showed poor resolution of species relationship with the majority (16 of 19) of the taxa arising from a midlevel polytomy. A few taxa were linked: (*C. "fusca," C. longipes*); (*rhomboidalis*, southern *rubrigularis*); (*rostralis*, *vivax*); (*johnstonei*, *triacantha*); (*munda*, *rufilatus*); and at lower levels, all *Lygisaurus* including *C. parrhasius*, (*gracilis* (*bicarinata*, *pectoralis*)), and (*coensis*, *mundivensis*).

Zug (2004) attempted a phylogenetic analysis with a set of 21 external morphological characters; his results also yielded a largely unresolved tree. Three species pairs and one triplet suggested some relationships: (*dogare*, *vivax*); (*jarnoldae*, *pectoralis*); (*coensis*, *scirtetis*); (*munda* (*gracilis*, *rufilata*)). More recently, Dolman and Hugall (2008) increased the molecular data, eliminating the polytomy and obtained a number of well-supported clusters (clades) of taxa. Critically, their data showed a single basal dichotomy between the long-limbed, rock-dwelling 'Carlia' (*coensis* (*mundivensis*, *scirtetis*)) and all other 'Carlia.' This latter group also showed a sister group relationship to the *Lygisaurus-Carlia* clade. They resurrected *Liburnascincus* for the rock-dwelling taxa and re-established *Lygisaurus*. The branching within *Carlia* is reasonably robust and yields numerous clades. Donnellan and colleagues (2009) examined relationships within the Australian populations of the *Carlia fusca* complex (= species group) with a molecular, karyotypic, and morphological data set. Although they emphasized the *fusca* group population relationships, they also included an assortment of other 'Carlia' and confirmed that *Liburnascincus* and *Lygisaurus* were valid clades. Further their data revealed that the Australian *fusca* group member *Carlia longipes* contained at least three recognizable species and supported the phylogenetic unity of the *fusca* species group.

I find it useful to identify species groups within *Carlia* to examine the origin, divergence, and biogeography of the various species. Dolman's and Hugall's Maximum Parsimony tree (2008: fig. 2) provides putative clades on which to construct group content and definitions. Their MP tree contains three major clades (*Liburnascincus* (*Lygisaurus* *Carlia*)). Bootstrap support for the sister

group bifurcation of *Liburnascincus* and the other two genera and for the linkage of *Liburnascincus coensis*, *L. mundivensis*, and *L. scirtetis* is 100%. Bootstrap support for the *Lygisaurus* and *Carlia* is less strong but still significant (70%). The monophyly of the 17 Australian and three New Guinea *Carlia* of their data set is quite robust (97%). Subsequent bifurcations within *Carlia* are weakly supported until near the crown-group level. The two strongest supported clades are the *fusca* group (*longipes*, *mysi*, and an undescribed S Highlands PNG population) and the *rhomboidalis* group (*rhomboidalis*, *rubrigularis*). Other clades are less robust (bootstrap values <50%); nonetheless, the MP clades suggest the following groups: *vivax* group (*vivax* (*dogare*, *rostralis*)); *tetradactyla* group (*amax*, *tetradactyla*); *triacantha* group (*rufilatus* (*johnstonei*, *triacantha*)); *munda* group (*munda*, *pectoralis*); *bicarinata* group (*storri* (*bicarinata*, *schmeltzii*)); *gracilis* group (*gracilis*, *jarnoldae*). Definitions for these species groups are available in Appendix 4.

Placement of some *Carlia* species within groups rests solely on morphology, because these taxa have not been included in molecular phylogenetic analysis. Dolman and Hugall (2008) sampled broadly among the Australian species and only *C. rimula* was missing from their analysis.

Carlia rimula is a small skink (mean ~32 mm SVL, max. 39 mm) from east-central Cape York Peninsula and the smallest of the currently recognized *Carlia*. Its character states are a broad mix of those defining the species group, therefore they do not allow a convincing assignment to any of the species groups, not even to those groups containing members of strikingly divergent morphologies. Is *C. rimula*, like *C. parrhasius*, incorrectly placed in *Carlia* or will it prove to be a basal divergence like the *gracilis* group?

Among the species groups, the *tetradactyla* and the *vivax* groups have morphologically divergent members. Does this divergence question the sister relationship proposed by the MP tree? The *tetradactyla* group has the lowest bootstrap support (9%; Dolman and Hugall 2008: fig. 2), suggesting that additional molecular characters could alter the placement of *C. amax* and *C. tetradactyla*. The bootstrap support (44%) for the *vivax* group is modest, and in spite of divergent SVLs, trunk-scale keeling and other shared morphologies

TABLE 3. Geographic arrangement and species group assignment of the currently recognized species of genus *Carlia*.

Australian Taxa [20]	
<i>Carlia amax</i>	<i>tetradactyla</i> species group
<i>Carlia dogare</i>	<i>vivax</i> species group
<i>Carlia gracilis</i>	<i>gracilis</i> species group
<i>Carlia jarnoldae</i>	<i>gracilis</i> species group
<i>Carlia johnstonei</i>	<i>triacantha</i> species group
<i>Carlia longipes</i>	<i>fusca</i> species group
<i>Carlia munda</i>	<i>munda</i> species group
<i>Carlia pectoralis</i>	<i>munda</i> species group
<i>Carlia quinquecarinata</i>	<i>fusca</i> species group
<i>Carlia rhomboidalis</i>	<i>rhomboidalis</i> species group
<i>Carlia rimula</i>	not assigned
<i>Carlia rostralis</i>	<i>vivax</i> species group
<i>Carlia rubrigularis</i>	<i>rhomboidalis</i> species group
<i>Carlia rufilatus</i>	<i>triacantha</i> species group
<i>Carlia schmeltzii</i>	<i>bicarinata</i> species group
<i>Carlia sexdentata</i>	<i>fusca</i> species group
<i>Carlia storri</i>	<i>bicarinata</i> species group
<i>Carlia tetradactyla</i>	<i>tetradactyla</i> species group
<i>Carlia triacantha</i>	<i>triacantha</i> species group
<i>Carlia vivax</i>	<i>vivax</i> species group
New Guinea Taxa [13]	
<i>Carlia aenigma</i>	<i>fusca</i> species group
<i>Carlia ailanpalai</i>	<i>fusca</i> species group
<i>Carlia aramia</i>	<i>fusca</i> species group
<i>Carlia bicarinata</i>	<i>bicarinata</i> species group
<i>Carlia bomberai</i>	<i>fusca</i> species group
<i>Carlia caesius</i>	<i>fusca</i> species group
<i>Carlia diguliensis</i>	<i>fusca</i> species group
<i>Carlia eothen</i>	<i>fusca</i> species group
<i>Carlia fusca</i>	<i>fusca</i> species group
<i>Carlia luctuosa</i>	<i>fusca</i> species group
<i>Carlia mysii</i>	<i>fusca</i> species group
<i>Carlia pulla</i>	<i>fusca</i> species group
<i>Carlia storri</i>	<i>bicarinata</i> species group
Wallacea Taxa [7]	
<i>Carlia babarensis</i>	<i>fusca</i> species group
<i>Carlia beccarii</i>	<i>fusca</i> species group
<i>Carlia leucotaenia</i>	<i>fusca</i> species group
<i>Carlia nigrauris</i>	<i>peronii</i> species group
<i>Carlia peronii</i>	<i>peronii</i> species group
<i>Carlia tutela</i>	<i>fusca</i> species group
<i>Carlia spinauris</i>	<i>peronii</i> species group

increase the likelihood of sister-group relationships. The three taxa also share a tropical Queensland distribution.

The *fusca* group has the highest diversity with at least 14 species, most (11) occurring in New Guinea and its adjacent islands, although the north Queensland populations likely harbor more species (Donnellan et al., 2009). This group has a broad size range (44–72 mm mean SVL) and diverse coloration, yet the other character states are surprisingly uniform. This morphological uniformity and the high bootstrap support (100%) emphasize the phyletic unity of the group. The uniformity also supports a single ancestor origin for the colonization and subsequent differentiation in New Guinea.

The *peronii* group likely has a single ancestor origin as well. My preceding insular-population analysis suggest the likelihood of greater species diversity in the Moluccas, but it also supports the similarity of the insular populations and the high probability of their membership in a single clade. Morphologically, the *peronii* group seems most similar to the *gracilis* group. The geographic closeness to northwestern Australia offers a likely source for dispersal and colonization by an ancestral member of the *gracilis* group. The origin of *C. nigrauris* remains enigmatic. The coastal habitats of the Greater Sunda Islands have been well surveyed, and no *Carlia* have been discovered. This absence and the greatest morphological divergence of *C. nigrauris* argue for a longer divergence from other group members or a separate origin from a *gracilis* group ancestor. Its survival on a small island is also enigmatic.

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Appendix

1. MATERIALS AND METHODS

This study relies on the character set and definitions used in a review of morphological variation and differentiation of the *Carlia fusca* complex of New Guinea (Zug 2004). The set contains six mensural and 19 scalation characters. Sex and maturity determined by examination of gonads. All statistical analyses used SYSTAT 11 for statistical analysis, and sexual dimorphism between adult females and males relied on Student’s *t* tests and $p \leq 0.05$ differences among pooled variance samples. Characters and their abbreviations are available in Zug (2004).

2. SPECIMENS EXAMINED (HOLOTYPES HIGHLIGHTED IN **BOLD**)

Carlia nigrauris: Java, Pulau Tindjil SMF 53915, 53916, 53917-922, WAM R101496, R101498, R104927.

Carlia peronii: ‘Ile de France’ MNHN 3037 [locality corrected to Timor by Greer; proposed as vicinity of Kubang, Timor, herein]; Timor, Kokabis WAM R107308, R107312, R107319-320, R107328-340, R107343, R107345, R107355; Samoa [= Semau] RMNH 30414, Soë BMNH 1946.8.10.81 [not seen]. Color statistics — Kokabis WAM R107306-307, R107309-311, R107314-318, R107321, R107323-331, R107333-342, R107344, R107346-349, Kupang WAM R107304.

Carlia spinauris: Timor, Lelogama BMNH 1946.8.16.32, 1946.8.17.58, Djamplong BMNH 1946.8.10.81.

Carlia peronii species group (specific identity not assigned): Flores, Pulau Sukur ZMA 15316A-K; Alor, Apui WAM R107932, R107934, R107937-939, R107941, R107958, R107960, R107965-967, R107974-976, R107978, R107981-982, R107991, R107999; Banda, Bandaneira WAM R109401-402, R109413-414, R109416-417, R109419, R109421-422, R109424-427; Kisar, Nomaha WAM R117421-422, R117424, R117427-430, R117487, Wonreil WAM R117441; Roti, Oeseli WAM R105829, R105836-837, R105839-843; Timor [no additional data] RMNH 7032, 7943, 30412-413; Wetar [no additional data] RMNH 5533, Ilpokil WAM R117509, R117553. Color notes – Semau RMNH 7941; Wetar WAM R117553 (color slide); Kisar WAM R117487 (color slide).

Carlia fusca species group: Timor [no additional data] RMNH 30414, ZMB 4981A-B, ZMDanm [specimens in ZMA collection] 47918-920.

3. MAP RESOURCES FOR FIGURE 1

Southern tier of islands

Java-Tindjil. *Carlia nigrauris*: Mertens 1957a; see preceding Specimens Examined section.

Java-main island. No *Carlia* reported: Barbour 1912; de Rooij 1915; Brongersma 1930, 1931; Mertens 1957a; Crampton et al. 1990; Manthey and Grossmann 1997.

Bali. No *Carlia* species reported: Barbour 1912; Mertens 1930, 1936, 1957b; Brongersma 1931; McKay 2006.

- Lombok. No *Carlia* species reported: Barbour 1912; Boulenger 1897; Mertens 1930.
Sumbawa. No *Carlia* species reported: Mertens 1930.
Komodo. No *Carlia* species reported: Dunn 1927; Darevsky 1964; Auffenberg 1980;
Sumba. No *Carlia* species reported: Boulenger 1897; Barbour 1912; Forcart 1949.
Flores. No *Carlia* species reported: Boulenger 1897; Barbour 1912; Mertens 1930.
Pulau Sukur [= Pulau Sukun]. *Lygosoma fuscum*: de Rooij 1915; *Carlia* sp: see preceding Specimens examined.
Solar. No data available.
Alor. *Carlia* sp: see preceding Specimens Examined section.
Roti. *Carlia* sp: see preceding Specimens Examined section.
Wetar. *Carlia* sp: see preceding Specimens Examined section.
Romang. No data available.
Damar. *Lygosoma fuscum*: de Rooij 1915.
Semau. *Carlia peronii*: see preceding Specimens Examined section.
Timor. *Carlia peronii*: Duméril and Bibron 1837, corrected to Timor (Greer, 1976); see preceding Specimens examined. *Carlia spinauris*: Smith 1927; see preceding Specimens Examined section.
Moa. No data available.
Sermata. No data available.
Leti. No data available.
Babar. *Carlia babarensis*: Zug 2004.
Tanimbar. *Carlia babarensis*: Zug 2004.

Northern tier of islands

- Sulawesi. No *Carlia* species reported: Brongersma 1931.
Kepulauan Banggai. No data available.
Ternate. *Lygosoma fuscum*: de Rooij 1915. *Carlia tutela* : Zug 2004. No *Carlia* species reported: Brongersma 1931.
Morotai. *Carlia tutela* : Zug 2004.
Halmahera. *Lygosoma fuscum*: de Rooij 1915. *Carlia tutela* : Zug 2004. No *Carlia* species reported: Brongersma 1931.
Sanana. No *Carlia* species reported: Kopstein, 1926.
Bacan. No data available.
Obi. No data available.
Misool. *Lygosoma fuscum*: de Rooij 1915.
Buru. No *Carlia* species reported: Barbour 1912. *Lygosoma fuscum*: Kopstein, 1926.
Seram. *Leiolopisma fuscum*: Barbour 1912. *Lygosoma fuscum*: de Rooij 1915. *Carlia leucotaenia*: Zug 2004.
Ambon. *Leiolopisma fuscum*: Barbour 1912. *Lygosoma fuscum*: de Rooij 1915. *Carlia leucotaenia*: Zug 2004.
Haruku. *Lygosoma fuscum*: Kopstein 1926.
Saparua. *Lygosoma fuscum*: de Rooij 1915.
Banda Ids. *Lygosoma fuscum*: Kopstein 1926. *Carlia* sp: see preceding Specimens Examined section.
Kepulauan Goram. *Lygosoma fuscum*: de Rooij 1915.
Kai. *Lygosoma beccarii*: Barbour 1912; de Rooij 1915. *Carlia beccarii*: Zug 2004.

4. *CARLIA* SPECIES GROUPS

Morphological and distributional data derive from Ingram and Covacevich (1989) and Zug (2004); the reported states are means for mensural traits and medians for meristic traits.

***bicarinata* group**

Definition. Dorsal and lateral trunk scales of adults strongly bicarinate, occasionally tricarinate or mixed (*schmeltzii*); 41–42 and 57 (*schmeltzii*) mm SVL, 42–49% HindlL/SVL, 21–23% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 7 (*bicarinata*) or 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, about half of lower eyelid area; ear-opening oblong vertical with few blunt AuricL on anterior border; 46–47 Dorsal, 31–35 Midbody, 18–22 3FingLm, 25–29 4ToeLm.

Geography. Subtropical Queensland through Cape York Peninsula, Fly River Plains and Port Moresby area New Guinea.

Sister group. *fusca* group.

Species content. *bicarinata*, *schmeltzii*, *storri*.

***fusca* group**

Definition. Dorsal and lateral trunk scales of adults smooth to weakly tricarinate; 44–72 mm SVL, 44–56% HindlL/SVL, 21–24% HeadL/SVL; prefrontals seldom in contact, interparietal rarely fused, 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less of lower eyelid area; ear-opening round to oblong vertical with few weakly pointed AuricL on anterior border; 46–50 Dorsal, 31–38 Midbody, 20–24 3FingLm, 26–34 4ToeLm.

Geography. Northern tropical Queensland through Cape York Peninsula, broadly throughout New Guinea and adjacent islands, and eastern Wallacea from Morotai to Kai and Tanimbar islands.

Sister group. *bicarinata* group.

Species content. *fusca*, *longipes*, *mysi*, *quinquecarinata* and others (Table 3).

***gracilis* group**

Definition. Dorsal and lateral trunk scales of adults moderately tricarinate; 36–42 mm SVL, 43–46% HindlL/SVL, 21–24% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 6 or 7 Supcil, 7 Suplab, 5 BlwEye; PalpbD small to modest, usually less half of lower eyelid area; small ear-opening circular to oblong horizontal with 1–2 weakly pointed AuricL on anterior border; 44–46 Dorsal, 28–31 Midbody, 16–17 3FingLm, 21–22 4ToeLm.

Geography. Northern Western Australia and Northern Territory, and southern Cape York Peninsula through northern tropical Queensland.

Sister group. Clade containing all other species groups.

Species content. *gracilis*, *jarnoldae*.

***munda* group**

Definition. Dorsal and lateral trunk scales of adults weakly (*munda*) to strongly tricarinate; 40–43 mm SVL, 43–47% HindlL/SVL, 23% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 6 (*munda*) or 7 Supcil, 7 Suplab, 5 BlwEye; PalpbD large, more half of lower eyelid area; ear-opening circular to oblong vertical with 0–2 blunt AuricL on anterior border; 45–47 Dorsal, 30–31 Midbody, 18–20 3FingLm, 23–26 4ToeLm.

Geography. Northwestern Western Australia across northern Australia to subtropical Queensland.

Sister group. *triacantha* group.

Species content. *munda*, *pectoralis*.

***peronii* group**

Definition. Dorsal and lateral trunk scales of adults weakly tricarinate, uncommonly mixed bi- and tricarinate; 37–46 and 57 (*nigrauris*) mm SVL, 40–47% HindIL/SVL, 21–23% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 7 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less than half of lower eyelid area; ear-opening circular with numerous acute lobes around perimeter; 46–53 Dorsal, 32–34 Midbody, 17–21 3FingLm, 23–29 4ToeLm.

Geography. Pulau Tindjil, Java, and Lesser Sunda Islands from Flores through Timor and its adjacent islands.

Sister group. Uncertain.

Species content. *nigrauris*, *peronii*, *spinauris*.

***rhomboidalis* group**

Definition. Dorsal and lateral trunk scales of adults smooth to weakly tricarinate; 41–44 mm SVL, 45% HindIL/SVL, 22% HeadL/SVL; prefrontals seldom in contact, interparietal fused to frontoparietal, 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD small, less than half of lower eyelid area; ear-opening oblong diagonal with 1–2 large AuricL on anterior border; 47 Dorsal, 32–33 Midbody, 19 3FingLm, 27–29 4ToeLm.

Geography. Northern and southern tropical Queensland.

Sister group. Clade containing *tetradactyla* and *vivax* groups

Species content. *rhomboidalis*, *rubrigularis*.

***tetradactyla* group**

Definition. Dorsal and lateral trunk scales of adults smooth to weakly tricarinate (*tetradactyla*) or strongly bicarinate (*amax*); 35 (*amax*) and 45 mm SVL, 39 (*tetradactyla*) and 48% HindIL/SVL, 22 (*tetradactyla*) and 25% HeadL/SVL; prefrontals in contact, interparietal separate, 7 (*vivax*) or 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less than half of lower eyelid area; ear-opening oblong diagonal or vertical with few blunt AuricL on anterior border; 39 (*amax*) and 50 Dorsal, 31–33 Midbody, 16–18 3FingLm, 22 4ToeLm.

Geography. Northern Western Australia to Northern Territory (*amax*) and subtropical Queensland to eastern Victoria (*tetradactyla*).

Sister group. *vivax* group.

Species content. *amax*, *tetradactyla*.

***triacantha* group**

Definition. Dorsal and lateral trunk scales of adults strongly bicarinate (*johnstonei*) or tricarinate; 43–45 mm SVL, 39 (*triacantha*) and 42–45% HindIL/SVL, 23% HeadL/SVL; prefrontals usually in contact or rarely so (*johnstonei*), interparietal separate, 7 (*rufilatus*) or 8 Supcil, 7 Suplab, 5 BlwEye; PalpbD small, less than half of lower eyelid area; ear-opening oblong vertical with few blunt AuricL on anterior border; 45–50 Dorsal, 29–32 Midbody, 18–19 3FingLm, 22–25 4ToeLm.

Geography. Northern Western Australia and Northern Territory.

Sister group. *munda* group.

Species content. *johnstonei*, *rufilatus*, *triacantha*.

***vivax* group**

Definition. Dorsal and lateral trunk scales of adults strongly bicarinate to weakly tricarinate (*rostralis*); 42–45 (*dogare*, *vivax*) and 59 (*rostralis*) mm SVL, 46–52% HindIL/SVL, 22% HeadL/SVL; prefrontals seldom in contact, interparietal separate, 6 or 8 (*rostralis*) Supcil, 7 Suplab, 5 BlwEye; PalpbD modest, half or less than half of lower eyelid area; ear-opening oblong vertical with few blunt AuricL on anterior border; 48–50 Dorsal, 31–35 Midbody, 16 (*vivax*) and 21–22 3FingLm, 24 (*vivax*) and 27–30 4ToeLm.

Geography. Cape York to subtropical Queensland.

Sister group. *tetradactyla* group.

Species content. *dogare*, *rostralis*, *vivax*.