Systematics of the *Carlia “fusca”* Lizards (Squamata: Scincidae) of New Guinea and Nearby Islands

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I wish to thank the staffs of the museums visited for their hospitality and assistance. These institutions are: AMNH American Museum of Natural History; AMS Australian Museum; BMNH The Natural History Museum (formerly British Museum of Natural History); BPBM Bernice P. Bishop Museum; BYU Monte L. Bean Life Science Museum, Brigham Young University; FMNH Field Museum of Natural History; IRSNB Institut Royal des Sciences Naturelles de Belgique; Laboratorium voor Algemene Dierkunde, Rijkuniversiteit Centrum Antwerp (all specimens now in IRSNB); MCZ Museum of Comparative Zoology; MNHN Muséum National d'Histoire Naturelle, Paris; NMW Naturhistorisches Museum, Wien; PNGM National Museum & Art Gallery-Papua New Guinea; QM Queensland Museum; RMNH Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie); SAM South Australian Museum, University of Adelaide; SMF Natur-Museum und Forschungs-Institut Senckenberg; WAM Western Australian Museum; ZMA Zoologische Museum, Universiteit van Amsterdam; ZMB Museum für Naturkunde, Universität Humboldt; ZMFK Zoologisches Forschunginstitut und Museum Alexander Koenig; ZSM Zoologisches Sammlung des Bayerischen Staates. Many of the preceding collections and others (MHNG Museum d'Histoire Naturelle, Genéve; MSB Museum of Southwestern Biology, University of New Mexico; NMBA Naturhistorisches Museum Basel; ZMUC Zoologisk Museum, Københavns Universitet) lent specimens. I also thank the staff of these collections for their assistance.

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ABSTRACT

On New Guinea and its surrounding islands, an assortment of *Carlia* with weakly tricarinate to smooth dorsal scales has been variously recognized as *C. fusca* or members of the *fusca* group. The *C. fusca* group has never been defined or characterized explicitly, nor has any other group of *Carlia*. A preliminary cladistic analysis of the Australian, New Guinean, and Sundan *Carlia* failed to identify species groups. This maximum parsimony analysis using a character set of predominantly scalation and body proportions yielded 1 putative clades with the other *Carlia* species branching before this clade. Additionally, the 2 *Lygisaurus* species are within the *Carlia* cluster and near the base. Removing body size and sexual dimorphism yielded a consensus tree with 2 small clades among a massive polytomy of all other taxa including the outgroups; the clades were: (*dogare*, *vivax*); (((*coensis, scirtetis*) *beccarii, luctuosa*) *longipes*, *rostralis*). The New Guinea "*fusca*" species were not linked as an unambiguous clade; nevertheless, the subsequent morphological analyses demonstrated a high similarity of the New Guinea species and their continued recognition as the *Carlia fusca* complex is recommended. This complex contains only the New Guinea and adjacent island species, *C. leucotaenia* and *C. tutela* of the Mollucas, *C. longipes* of Cape York and Torres Strait islands, and tentatively the Lesser Sundan species *C. babarensis* and *C. beccarii*. This complex is characterized, but it is not proposed as a formal taxonomic unit.

Quantitative analysis of meristic, morphometric, and color pattern characters of New Guinean *C. "fusca*" reveals at least 14 species in the New Guinea region. Names are available for the Babar and Tanimbar populations (*C. babarensis*)*;* the Kei islands (*C. beccarii*); southeastern Irian Jaya (IJ) and Aru (*C. diguliensis*); Waigeo, north coastal Vogelkop IJ (*C. fusca*); southeastern Papua New Guinea (PNG) (*C. luctuosa*); northeastern IJ and northwestern PNG (*C. pulla*); and Seram-Ambon (*C. leucotaenia*). Although interpopulational variation in scalation is slight, differences in juvenile and adult coloration and adult sizes suggest the recognition of the previous named species as well as several new species. The new species are *C. aenigma* from the eastern PNG Gulf lowlands, *C. ailanpalai* from the Admiralty Islands, *C. aramia* from the central PNG Gulf area to the Morehead plains and to mid elevations in the Fly drainage, *C. eothen* from the vicinity of Milne Bay and the eastern island groups, *C. mysi* of the PNG north coast from Adelbert Mtns. area east to Cape Vogel and the Bismarck Archipelago, and *C. tutela* of Halmahera and Morotai. Several areas (PNG highlands, IJ south-central coast, and Sepik drainage) have populations that potentially represent new species, but the present samples and analyses were inadequate for confirmation.

Current morphological data provide no reliable clues to assess interspecific relationships among the New Guinea "*fusca*" complex, hence this uncertainty does not allow a detailed biogeographical analysis. The distributions of the presently recognized taxa do not match closely those of any other clade of lizards, or any other group of reptiles, amphibians, or other New Guinea organisms. The oldest portion of New Guinea, the Australian craton, harbors the greatest number of *fusca* complex species but offers no direct clues to their isolation and subsequent speciation.

Unicolor populations occur in several areas, typically small island habitats. The Admiralty populations are recognized as a distinct species, *C. ailanpalai*, and the similarity of the Guam *Carlia* suggests that this population and those on nearby Micronesian islands derive from the Admiralties and the post-World War II transport of military supplies. The Kei, north coast IJ, and Halmahera unicolor populations cannot be assigned with surety to any of the recognized species. The Palau *Carlia* also appears to represent an accidental post-WWII introduction. Morphological evidence and to a lesser extent color pattern suggest that it derives from *C. tutela* populations of Halmahera and Morotai.

INTRODUCTION[1]

Carlia is an Australopapuan-Lesser Sundan genus of skinks, quickly recognized by only 4 digits on each forefoot. Two species groups of *Carlia* are generally recognized as occurring in New Guinea, although no one has formally partitioned the species of *Carlia* into species groups. The so-called *bicarinata*-group skinks are small (38–48 mm adult snout-vent length [SVL]; Ingram & Covacevich, 1989; Zug et al., 1982) with slender bodies and moderate length limbs, and a strongly bicarinate dorsal and lateral trunk scalation. The *fusca*-group skinks are generally larger (42–80 mm adult SVL) with more robust bodies and limbs, and possess weakly tricarinate to smooth trunk scalation.

Both groups are locally abundant in the Port Moresby area of New Guinea where they display a striking ecological segregation, which attracted my interest and closer inspection. *Carlia bicarinata* is xeric-adapted and lives in the eucalyptus savanna. *Carlia “fusca”* lives in open-canopied forest, along forest edges, and nonforested areas with dense herbaceous vegetation. In the lowlands of Papua New Guinea, *fusca*-group lizards occur broadly in similar habitats and are often locally the most abundant species of the lizard community. Although easily recognizable as *C. “fusca”*, the different populations show a variety of color patterns and body sizes. This variety attracted the attention of the 19th and early 20th century biologists who described several morphotypes as new species or varieties. These descriptions often introduced the new form with slight attention to their congeners, and their authors seldom attempted to determine the relationships of the species (morphotypes) or the geographic patterns of variation. However, the reports of Peters & Doria (1878) and Loveridge (1948) are notable exceptions.

In spite of the widespread occurrence and abundance of “*fusca*” skinks, the taxonomic identity of the numerous New Guinean morphotypes remains unknown or uncertain. The present study was initiated to investigate this aspect of *C.* “*fusca*” populations in New Guinea and is the major goal of this report. *C.* “*fusca*,” however, cannot be investigated in isolation from other Australopapuan *Carlia*; hence, I offer a preliminary phylogenetic analysis of all currently recognized species of *Carlia*. Both aspects of this study are based exclusively on external morphology, predominantly scalation.

CARLIA: AN ANALYSIS FOR SPECIES RELATIONSHIPS

Skinks of the present *Carlia* cluster of species have experienced various degrees of amalgamation and separation during the past 2 centuries, a common history for lygosomine skinks. Recognition of the distinctiveness of the species cluster began with Duméril’s and Bibron’s use (1839) of *Heteropus* Fitzinger, 1826 for *fusca* and *peronii*. *Heteropus* remained the genus for these species and others, presumably related, throughout much of the remainder of the 19th century. De Vis (1884) considered *Heteropus* a natural group with its chief diversity in Australia and provided a key to the Australian species and detailed descriptions to some species. The name *Heteropus* disappeared when Boulenger (1887) gathered all lygosomine skinks under *Lygosoma* Hardwicke & Gray, 1827. Boulenger’s *Lygosoma* retained groups of related species but relegated the nominal differentiation to a subgeneric level. In general, the resulting 11 subgenera were diagnosable. *Heteropus* skinks belonged to the subgenus *Leiolepisma*. Subsequently, *Heteropus* did not re-emerge for these skinks, because Duméril & Bibron had applied *Heteropus* incorrectly to *fusca* and *peronii* whereas Fitzinger (1826) had established the name originally for a new species of Arabian skink, which he apparently never described.

For the next 60 years, *Lygosoma* and less commonly *Leiolepisma* contained the *Carlia* species. *Carlia* Gray, 1845 formally reappeared in Mittleman’s generic reorganization (1952) of lygosomine skinks into putative phylogenetic groups. Although he did not explicitly propose hypotheses of relationships among the lygosomine genera, his arrangement and generic definitions were generally

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[1] I dedicate this study to Allen E. Greer in appreciation for his decades of research revealing the evolutionary relationships of skinks, his continual assistance of colleagues and students, and his friendship.

adopted. Subsequently, Greer (1974) provided more detailed generic definitions and suggested relationships among the lygosomines. He suggested the origin of *Carlia* from an ancestral *Lampropholis*. However, Greer did not give a list of *Carlia* species owing to his ongoing research. Later, he (Greer, 1989) stated that *Carlia*, *Lampropholis*, *Lygisaurus*, and *Saproscincus* were a natural subgroup within the *Pseudemoia* section of the Lygosominae. As a clade, these 4 taxa share unique hemipenial morphology.

Nearly concurrently with Mittleman's generic revision, Mitchell (1953) provided the first detailed review of the Australian species of the *Carlia*. He recognized 11 species and the importance of dorsal scale morphology as a diagnostic trait for the differentiation of species. In 1974, Greer suggested the possible existence of about 30 species. A year later, he (Greer, 1975) began an analysis of *Carlia* species with the examination and redescription of *Mocoa melanopogon*[2] Gray, 1845 and species previously synonymized with *melanopogon*. His study is critical because *Mocoa melanopogon* Gray (= *Carlia munda*) is the type species of *Carlia*. Greer observed that there was less intraspecific variation in dorsal scale morphology and auricular lobes than suggested by Mitchell's study. Further, he noted a high frequency of chromatic sexual dimorphism and a low interspecific variation in number of midbody scale rows and subdigital lamellae within species groups. The latter statement is the first explicit mention of species groups within *Carlia*. Although Greer mentioned groups, he did not name or define any. This absence of definition and species content of groups persists throughout subsequent studies of *Carlia*. The mention of species groups has centered largely on species sharing features of the species *bicarinata*, *fusca*, and *novaeguineae*. In part, the use of group names denotes the recognition of these taxa as polytypic units without an author's intent of examining species limits within the groups. Loveridge's (1948) subspecies for 3 New Guinean populations or morphs of *C. fusca* is the closest a systematist has come to defining a "species" group, i.e., the *fusca* group.

Greer (1976) examined the relationships of the Timor *Heteropus peronii* Duméril & Bibron, 1839 and *Lygosoma spinauris* Smith, 1927, noting that the latter was a synonym of the former. He also included a comparison of western Australian *Carlia* species with those of Timor to confirm that *C. peronii* did not come from Australia. Storrs (1974) provided an earlier review of NT and WA *Carlia*, recognizing 4 new species. He provided precise diagnoses for the western Australian taxa and *C. fusca* (now = *C. longipes*), also noting the latter's extralimital occurrence in northeastern Arnhem Land and Groote Eylandt. He further observed "the morphological gap between species of *Carlia* is much smaller than usual in congeneric lizards." He did not mention groups in his discussion of affinities. Covacevich & Ingram, in 1975 and subsequent publications, began to recognize the high diversity of Australian *Carlia* with the description of new species. Their studies culminated into 2 major revisions. In the first, Ingram & Covacevich (1988) transferred members of the "*novaeguineae* group" to the genus *Lygisaurus*. In the second (Ingram & Covacevich, 1989), they thoroughly reviewed the remaining Australian species of *Carlia*. This comprehensive study provides descriptions of each Australian species and a survey of the major diagnostic characters for *Carlia* species. They did not attempt a phylogenetic analysis or suggest species group partitioning other than noting that *C. longipes* was a member of the *C. fusca* complex. They did not define or delimit this complex; however, they observed that the ". . complex is not comprised of distinct forms that are largely allopatric as Loveridge (1948) thought . . ." Instead, they noted that sympatry of distinct populations occurs in some localities.

Characters and Taxa

Earlier studies suggested either the existence of groups of related species or have provided characters that suggest relationships among the species of *Carlia*. From these studies and my comparison of taxa, I selected 21 characters for an analysis of relationships. Some of the seemingly most diagnostic characters include adult body size, nature of keeling of dorsal trunk scales, and several aspects of cephalic morphology and scalation. The characters, their abbreviated names, and their coding in brackets are:

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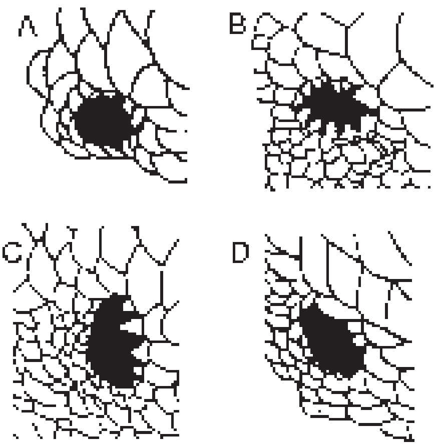
[2] *Mocoa melanopogon* Gray, 1845 became a junior homonym of *Lygosoma melanopogon* Duméril & Bibron, 1839 when Boulenger (1887) included all lygosomine species in the genus *Lygosoma*. The nomenclatural code states (Article 59.3; 1999 International Code of Zoological Nomenclature, 4th edition): a junior secondary homonym replaced prior to 1961 is permanently invalid unless the substitute is not in use and the relevant taxa are no longer congeneric.

Scalation-cephalic. Interparietal scale (Interp): separate or rarely fused with frontoparietal (<5%) [0]; occasionally fused, 5–50% [1]; typically fused, >50% [2]. Prefrontal contact (PrefrC): separate or rarely touching one another (<5%) [0]; occasionally in contact, 5–50% of sample with contact [1]; frequently in contact, >50% [2]. Supraciliary scales, number (Supcil): 8 [0]; 7 [1]; 6 [2]. Auricular scales or lobes position (AuricP): on anterior edge and occasionally extending onto dorsoposterior border [0]; around entire circumference [1]. Auricular scales, shape (AuricS) (Figure 1): pointed [0]; rounded [1]. Auricular scales, number (AuricN), mode: 0 [0]; 1–2 [1]; 3–4 [2]; >4 [3].
Morphology-cephalic. Palpebral disk, size (PalpbS): small, <1 /2 orbital diameter [0]; large, ≥1 /2 [1]. External ear, shape (EarS) (Figure 2): circular [0]; oblong, diagonal axis [1]; oblong, vertical axis [2]; oblong, horizontal axis [3].
Scalation-body. Nuchal keeling (NucK): smooth to striated [0]; weakly keeled [1]; strongly keeled [2]. Dorsal trunk scale keeling (DorsK) (Figure 3): smooth to striated [0]; weakly keeled [1]; strongly keeled [2]. Dorsal trunk scale keels, number (DorsKN): none [0]; bicarinate [1]; tricarinate [2]. (Figure 3) Dorsal scale rows, number (Dorsal), mean: few ≤42 [0]; standard 43–49 [1]; moderate 50–55 [2]; many 56–60 [3]; great many >60 [4]. Midbody scale rows, number (Midbody), mean: few <24 [0]; standard 24–32 [1]; moderate 33–40 [2]; many >40. Third finger subdigital lamellae, number (3FingL), mean: few <16 [0]; standard 16–22 [1]; many >22 [2]; fourth finger in pentadactyl taxa. Fourth toe subdigital lamellae, number (4ToeL), mean: few <20 [0]; standard 20–28 [1]; many >28 [2]. Subterminal lamellae of forefoot digits (FfLClf): without cleft [0]; with cleft [1].
Size & Shape. Adult snout-vent length (SVL), mean: small ≤36 mm [0]; moderate 38–46 mm [1]; large 48–57 mm [2]; big ≥58 mm [3]. Relative trunk length (Trk/SV), mean: short <48% [0]; moderate 48–52% [1]; large >52% [2]. Relative hindlimb length (Hndl/SV), mean: very short ≤32%; short 32–42% [1]; moderate 43–52% [2]; large >52% [3]. Sexual dimorphism (SexDi) in SVL: absent [0]; female smaller than male [1]; female larger than male [2]. Forefoot digit, number (FftDig): 5 digits [0]; 4 digits [1].

For any character displaying sexual dimorphism, i.e., female and male sample means statistically significant difference at the 95% confidence level, the mean value for the female sample is substituted for the total sample mean.

1



2

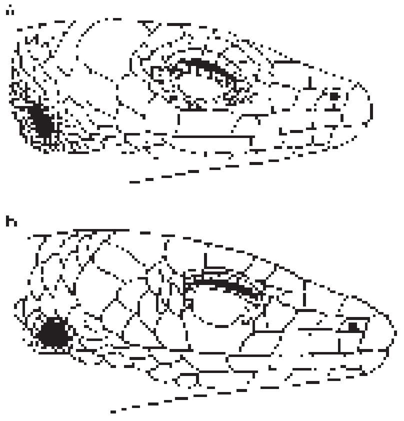


Figure 1. Shape of the external ear in members of the genus *Carlia*. **A**, round; **B**, oblong horizontal; **C**, oblong vertical; **D**, oblong diagonal. The illustrations derive from *Carlia munda* (Fig. 24), *Carlia bicarinata* (Fig. 5), *Carlia longipes* (Fig. 21), *Carlia dogare* (Fig. 11), respectively, of Ingram & Covacevich (1989); anterior is to the right. **Figure 2**. Relative size of palpebral disks in members of the genus *Carlia*. **A**, small disk (< 0.5 × area of lower eyelid) and **B**, large disk (> 0.5 × area of eyelid), from top to bottom. The illustrations derive from *Carlia coensis* (Fig. 8) and *Carlia munda* (Fig. 24), respectively, of Ingram & Covacevich (1989)..

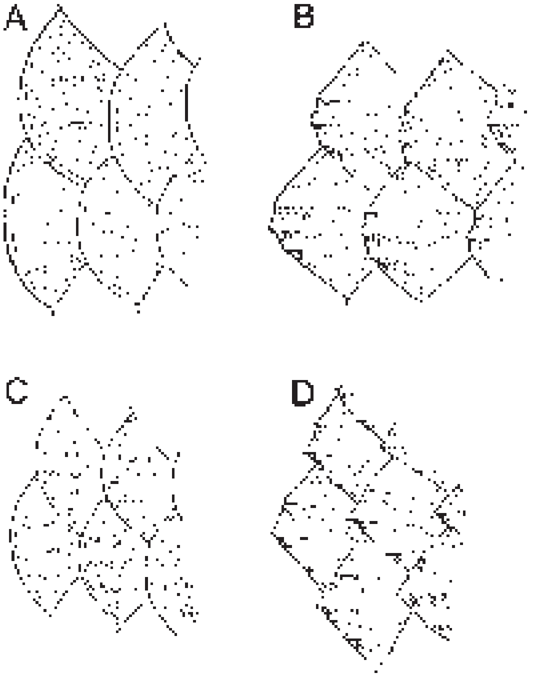


Figure 3. Surface morphology of dorsal trunk in members of the genus *Carlia*. **A**, weakly tricarinate or striated (*Carlia mundivensis*); **B**, strongly tricarinate – hexagonal (*Carlia pectoralis*). **C**, weakly tricarinate – ridges pimpled (*Carlia coensis*); **D**, strongly tricarinate – tricuspidate or quadrangular (*Carlia triacantha*). The illustrations derive from Figure 3 of Mitchell (1953).

Further definitions for some preceding characters are available in the Materials & Methods of the subsequent New Guinean *Carlia "fusca"* section. For analysis, the preceding characters are coded variously: binary characters, 0, 1; multiple-state characters, 0, 1, 2, etc. Multistate character coding followed two rules: for characters with a narrow range, each state was assigned a value from 0 upward sequentially; for characters with wide ranges, states were gap-coded and assigned a value from 0 upward sequentially. The characters are summarized in Table 1 (means for continuous characters) and in Table 2 (coded for phylogenetic analysis).

Thirty species of *Carlia* are included in the analysis and 4 outgroup taxa, *Saproscincus mustelinus*, *Lampropholis delicata*, *Lygisaurus curtus* and *Lygisaurus novaeguineae* (see Appendix Table A for specimens examined). The Australian *Carlia* species are those recognized by Ingram & Covacevich (1989) and the more recently described *C. parrhasius* (Couper et al., 1994). Each species was characterized by the examination of small samples (usually *n* = 10–12) of adults (see Appendix: Table A) and reference to the descriptions in Ingram's & Covacevich's monograph (1989) or the original description of the new species. The extralimital Australian species derive from a preliminary analysis of the NG data sets; only the most strikingly different morphotypes with available names are included for NG taxa.

Relationships were determined with PAUP 4.0b7 (Swofford, 2000). PAUP offers many options for assessing phylogenetic relationships among operational taxonomic units (OTU), but owing to the limits of the current data set to external and largely scalation characters, I choose to present only results from a few potential options: 1) all taxa/OTUs and all characters via a heuristic

Table 1. **Taxon-character matrix for *Carlia* species analysis**.

Taxon	Geog	FftDig	Interp	PrefrC	Supcil	AuricP	AuricS	AuricN	PalpbS	EarS	NucK	DorsK	DorsKN	Dorsal	Midbody	3FingL	4ToeL	FfLClf	SVL	SexDi	TrkSV	HndlSV
Saproscincus	au	5	0	0	7	•	•	0	1	0	0	0	0	58	22	12	17	0	54	2	56	29
Lampropholis	au	5	0	0	8	•	•	0	0	2	0	0	0	55	26	16	23	0	39	0	53	34
Lygisaurus c	ng	4	0	?	6	0	1	1	1	0	0	0	0	44	26	18	26	?	36	?	51	36
Lygisaurus n	ng	4	0	0	8	0	1	1	1	0	0	0	0	42	26	17	22	1	34	0	48	32
amax	au	4	0	1	7	0	0	2	1	0	?	2	2	39	33	18	22	0	35	0	43	4
babarensis	mo	4	0	0	8	1	0	5	0	1	0	1	3	48	31	21	30	0	45	1	47	49
beccarii	mo	4	0	0	8	0	0	4	1	2	0	1	3	54	38	24	32	?	64	1	44	53
bicarinata	ng	4	0	0	7	1	0	5	1	0	0	2	2	47	31	20	29	1	42	0	49	49
coensis	au	4	0	0	8	0	1	4	0	2	0	1	3	61	37	25	32	0	61	?	43	54
diguliensis	ng	4	0	0	8	0	0	2	1	1	0	1	3	47	32	20	29	1	50	0	46	56
dogare	au	4	0	0	6	0	1	2	1	2	0	2	2	50	31	21	27	0	45	?	47	50
fusca	ng	4	0	0	8	0	0	3	0	2	0	1	3	48	32	21	29	1	53	1	47	49
gracilis	au	4	0	0	6	•	•	0	0	3	1	2	3	45	28	16	21	0	36	0	47	43
jarnoldae	au	4	0	0	7	0	1	1	1	3	0	2	3	45	31	17	22	0	42	0	48	46
johnstonei	au	4	0	0	8	1	0	6	1	0	0	2	2	45	35	18	23	0	42	0	45	42
leucotaenia	mo	4	1	0	8	0	0	4	1	1	0	0	3	48	31	21	29	0	44	1	50	48
longipes	au	4	0	0	8	0	0	4	0	2	0	1	3	51	36	22	30	0	62	0	48	49
luctuosa	ng	4	1	0	8	0	0	4	1	2	0	1	3	50	38	23	33	1	66	1	48	50
munda	au	4	0	1	6	•	•	0	1	3	0	0	3	45	30	18	23	0	40	0	46	43
mundivensis	au	4	0	1	8	0	0	4	1	2	0	2	3	53	38	17	22	0	54	0	48	46
parrhasius	au	4	0	0	8	1	0	5	1	0	0	0	0	48	29	19	26	0	32	?	44	36
pectoralis	au	4	0	0	7	0	1	2	1	2	0	2	3	47	31	20	26	1	43	0	48	47
peronii	su	4	0	0	7	1	0	4	1	0	0	2	3	47	30	17	24	0	39	0	48	41
pulla	ng	4	0	0	8	0	0	3	1	2	0	1	3	48	34	22	29	1	56	1	44	48
rhomboidalis	au	4	2	0	8	0	1	2	0	0	0	0	0	47	33	19	27	1	51	0	48	45
rimula	au	4	0	0	8	1	0	8	0	2	0	0	0	51	31	20	28	0	36	?	50	39
rostralis	au	4	0	0	8	0	0	3	0	2	0	0	3	48	35	22	30	0	59	0	45	52
rufilatus	au	4	0	1	7	•	•	0	0	3	0	2	3	45	29	19	25	0	39	0	45	45
schmeltzi	au	4	0	0	8	0	0	2	0	2	0	2	3	46	35	18	25	0	57	0	47	42
scirtetis	au	4	0	0	8	1	0	10	0	2	0	1	3	67	45	25	33	0	62	0	45	60
storri	ng	4	0	0	8	1	0	5	1	1	2	2	2	46	31	22	29	1	41	0	50	48
tetradactyla	au	4	0	1	8	0	1	1	0	1	0	0	0	50	31	16	22	0	53	0	49	39
triacantha	au	4	0	2	7	0	0	2	1	1	0	2	3	41	32	19	24	0	45	0	43	47
vivax	au	4	0	0	6	0	1	1	1	1	2	2	2	48	32	16	24	0	42	0	48	46

The integer of continuous characters equals the mean of the sample rounded to the nearest whole number. Characters are defined in the text. The size and composition of the taxonomic samples (OTUs) are in the Appendix Table A. “•”, character not present; “?”, data unavailable at time of analysis.

Table 2. **Taxon-coded character matrix for *Carlia* species analysis**.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Saproscincus	0	0	0	1	•	•	0	1	0	0	0	0	3	0	0	0	0	2	2	2	0
Lampropholis	0	0	0	0	•	•	0	0	2	0	0	0	2	1	1	1	0	1	0	2	1
Lygisaurus c	1	0	?	2	0	1	1	1	0	0	0	0	1	1	1	1	?	0	?	1	1
Lygisaurus n	1	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	1	0	0	1	0
amax	1	0	1	1	0	0	1	1	0	?	2	1	0	2	1	1	0	0	0	0	2
babarensis	1	0	0	0	1	0	3	0	1	0	1	2	1	1	1	2	0	1	1	0	2
beccarii	1	0	0	0	0	0	2	1	2	0	1	2	2	2	2	2	?	3	1	0	3
bicarinata	1	0	0	1	1	0	3	1	0	0	2	1	1	1	1	2	1	1	0	1	2
coensis	1	0	0	0	0	1	2	0	2	0	1	2	4	2	2	2	0	3	?	0	3
diguliensis	1	0	0	0	0	0	1	1	1	0	1	2	1	1	1	2	1	2	0	0	3
dogare	1	0	0	2	0	1	1	1	2	0	2	1	2	1	1	1	0	1	?	0	2
fusca	1	0	0	0	0	0	2	0	2	0	1	2	1	1	1	2	1	2	1	0	2
gracilis	1	0	0	2	•	•	0	0	3	1	2	2	1	1	1	1	0	0	0	0	2
jarnoldae	1	0	0	1	0	1	1	1	3	0	2	2	1	1	1	1	0	1	0	1	2
johnstonei	1	0	0	0	1	0	3	1	0	0	2	1	1	2	1	1	0	1	0	0	1
leucotaenia	1	1	0	0	0	0	2	1	1	0	0	2	1	1	1	2	0	1	1	1	2
longipes	1	0	0	0	0	0	2	0	2	0	1	2	2	2	1	2	0	3	0	1	2
luctuosa	1	1	0	0	0	0	2	1	2	0	1	2	2	2	2	2	1	3	1	1	2
munda	1	0	1	2	•	•	0	1	3	0	0	2	1	1	1	1	0	1	0	0	2
mundivensis	1	0	1	0	0	0	2	1	2	0	2	2	2	2	1	1	0	2	0	1	2
parrhasius	1	0	0	0	1	0	3	1	0	0	0	0	1	1	1	1	0	0	?	0	1
pectoralis	1	0	0	1	0	1	1	1	2	0	2	2	1	1	1	1	1	1	0	1	2
peronii	1	0	0	1	1	0	2	1	0	0	2	2	1	1	1	1	0	1	0	1	1
pulla	1	0	0	0	0	0	2	1	2	0	1	2	1	2	1	2	1	2	1	0	2
rhomboidalis	1	2	0	0	0	1	1	0	0	0	0	0	1	2	1	1	1	2	0	1	2
rimula	1	0	0	0	1	0	3	0	2	0	0	0	2	1	1	1	0	0	?	1	1
rostralis	1	0	0	0	0	0	2	0	2	0	0	2	1	2	1	2	0	2	0	0	2
rufilatus	1	0	1	1	•	•	0	0	3	0	2	2	1	1	1	1	0	1	0	0	2
schmeltzi	1	0	1	0	0	0	1	0	2	0	2	2	1	2	1	1	0	2	0	0	1
scirtetis	1	0	0	0	1	0	3	0	2	0	1	2	4	3	2	2	0	3	0	0	3
storri	1	0	0	0	1	0	3	1	1	2	2	1	1	1	1	2	1	1	0	1	2
tetradactyla	1	0	1	0	0	1	1	0	1	0	0	0	2	1	1	1	0	2	0	1	1
triacantha	1	0	2	1	0	0	1	1	1	0	2	2	0	1	1	1	0	1	0	0	2
vivax	1	0	1	2	0	1	1	1	1	2	2	1	2	1	1	1	0	1	0	1	2

Characters and coding are defined in the text. The size and composition of the taxonomic samples (OTUs) are in the Appendix Table A. Characters are arranged as in Table 2: 1 = FftDig; 2 = Interp; et seq.

search using the maximum parsimony model without rooting the tree; and 2) all taxa and 19 characters, excluding SVL and SexDi via the preceding search and model algorithm. In all analyses, characters are of equal weight and entered randomly. The 4 outgroup taxa were not identified as outgroup OTUs in any analysis. Owing to low consistency indices, my discussion of potential relationships is limited to the results of consensus trees. Even with these restrictions, the low values for all the PAUP analyses warn against over-interpretation of the potential clades depicted in the consensus trees of the various analyses.

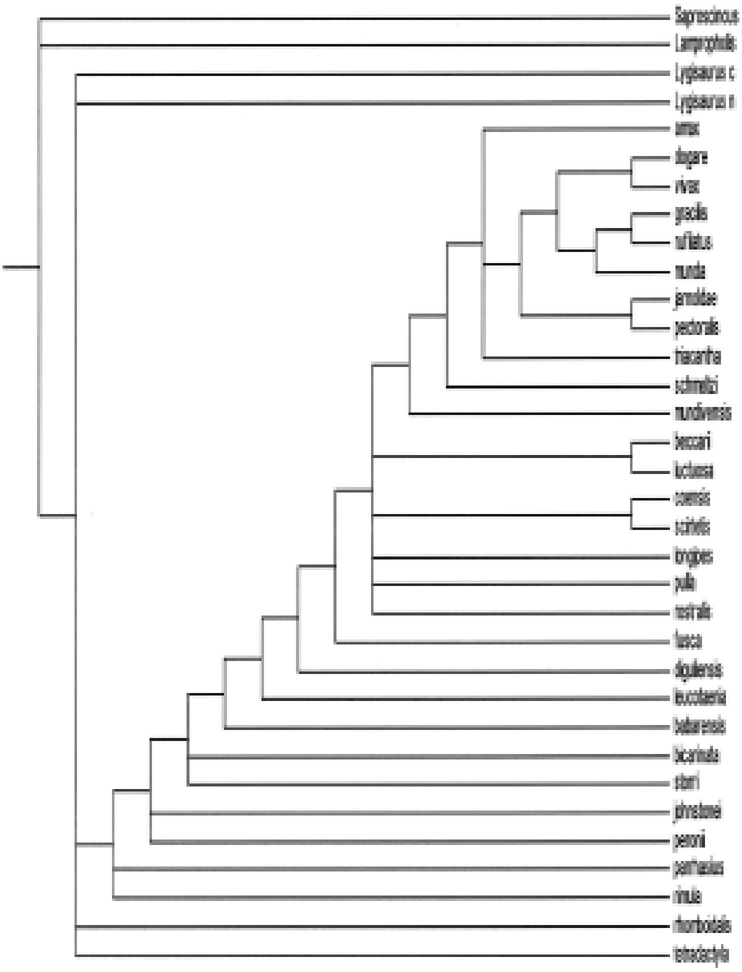


Figure 4. Potential phylogenetic relationships of members of the genus *Carlia*. This strict consensus tree derives from 1273 maximum parsimony trees of length 123 (CI = 0.36, HI = 0.64, Rescaled consistency index = 0.22), generated from the total matrix of 21 characters, states unordered (Table 2).

PHYLOGENETIC ANALYSIS

The analysis of the full character set with characters defined as ordered yields 137 trees with a minimum branch length of 137 and with characters unordered 1273 trees with minimum branch length of 123 (Fig. 4). The consistency indices (CI), homoplasy indices (HI), and retention indices (RI) are similar 32 36%, 68 64%, 64 61%, respectively, ordered vs. unordered analyses. The ordered and unordered character sets provide some similarities: 1) the outgroup *Saproscincus* and *Lampropholis* arise as independent and basal branches with a clade comprised of all the remaining OTUs; 2) the two *Lygisaurus* species branch independently from one another and near the base of the tree; 3) most *Carlia* species branch independently in a stepwise fashion with the exception of a single clade comprised of *amax*, *dogare*, *gracilis*, *jarnoldae*, *munda*, *mundivensis*, *pectoralis*, *rufilatus*, *schmeltzi*, *triacantha*, and *vivax*, although the branching sequences are not the same for the characters ordered and unordered; 4) shared sister taxa are (*beccarii*, *luctuosa*), (*coensis, scirtetis*), (*dogare*, *vivax*), (*jarnoldae*, *pectoralis*), and ((*gracilis*, *rufilatus*) *munda*); 5) *rhomboidalis* and *tetradactyla* are basal branchings.

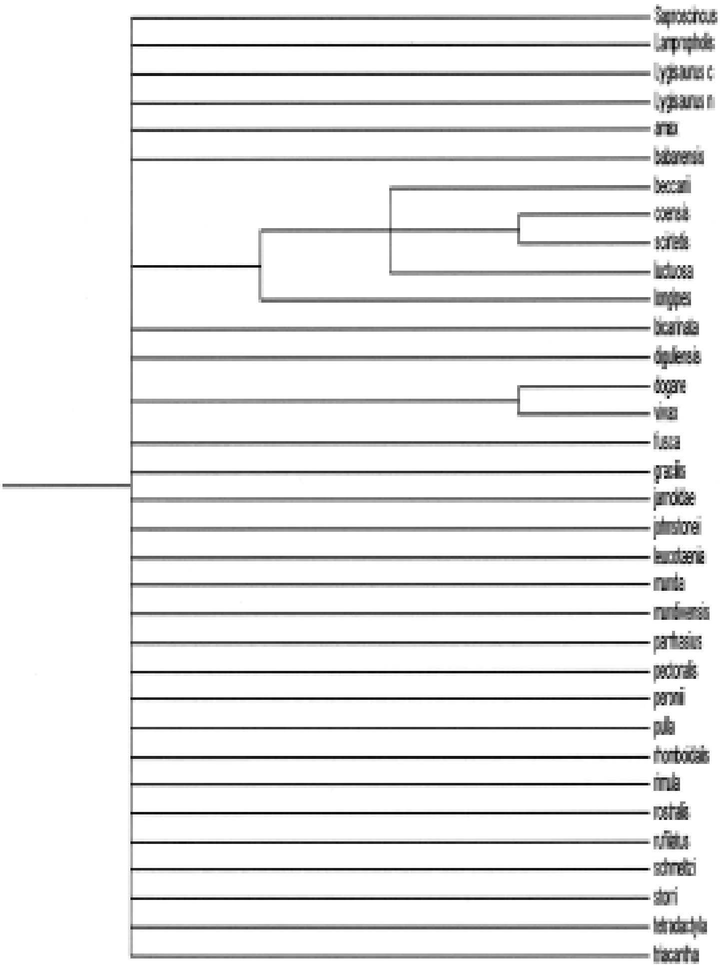


Figure 5. Potential phylogenetic relationships of members of the genus *Carlia*. This strict consensus tree derives from 1363 maximum parsimony trees of length 109 (CI = 0.37, HI = 0.63, RCI = 23), generated from the *Carlia* matrix (Table 2) with body size and sexual dimorphism characters excluded, character states unordered.

Because size (SVL) and sex dimorphism (SexDi) can vary among adjacent populations of the same species, they were excluded from the final analysis, which also used character states as unordered. Unordered states implies no evolutionary direction, and no direction was assumed in the initial development of states. PAUP identifies 1363 trees with minimum length of 109, 37% CI, 63% HI, and 63% RI from the 19-character analysis. Stepwise branching in a strict consensus tree (Fig. 5) from this analysis is nearly nonexistent. Most *Carlia* species and the outgroup taxa arise from a single basal polytomy. Only two clades occur: 1) *beccarii*, *coensis*, *longipes*, *luctuosa*, *rostralis*, and *scirtetis*; 2) *dogare* and *gracilis*. The latter pair is an obvious sister group, and within the former group, (*coensis*, *scirtetis*) is the only sister pair. For both 19 and 21 character-set analyses, the 50% majority-rule consensus yields trees with more pairing and stepwise branching; however, I believe little is gained by emphasizing the presumptive relationships suggested by this consensus tree.

The two sister-pairs revealed by both 19- and 21-character sets suggest real phylogenetic affinities. Both *C. coensis* and *C. scirtetis* are rock-living skinks of Cape York, and each has a small geographic range. Among the characters examined, they uniquely share >60 Dorsal; HndlSV >50% with *C. beccarii* and *C. diguliensis*; and mean SVL >60 mm with *C. beccarii*, *C. longipes*, and *C. luctuosa*. The other members of the six-membered clade are not united in a clade in the 21-character analysis. The second sister-pair, *C. dogare* and *C. vivax*, has no uniquely shared characters. They are moderately small, bicarinate-scaled lizard of tropical Queensland with *C. dogare* allopatrically enclosed in the distribution of *C. vivax.*

While this phylogenetic study was in its initial analytical stages, Stuart-Fox examined the phylogenetic relationships of *Carlia* using mtDNA data as an honours thesis (1998). Her results (Stuart-Fox et al., 2002) similarly showed poor resolution of phylogenetic affinities, although the mtDNA results suggest several clades and about a dozen sister pairs. Unfortunately, our taxon sampling is sufficiently dissimilar to hinder ready comparison of proposed relationships. The Stuart-Fox species sample lacked *C. scirtetis*, so an independent test of my data's strongest sister pair is not possible. *C. dogare* and *C. vivax* are not paired in her strict consensus tree although linked in a polytomous clade. Stuart-Fox interpreted the poor resolution (polytomy) as representing a burst of rapid diversification in the Miocene. My data and analyses neither conflict nor support her interpretation. They only encourage re-examination with broader character set and the polarization of character states.

NEW GUINEA *CARLIA "FUSCA"*

Heteropus fusca Duméril and Bibron was described in 1839 from the islands of Waigeo and Rawack, lying northeast of the Vogelkop Peninsula of New Guinea. Similar appearing brown *Carlia* occur throughout New Guinea and eastward to Seram-Halmahera, westward to Bougainville-Louisiade Archipelago and southward into northern Australia. Three outlier populations (Guam, Yap and Palau) exist. As noted earlier, none of the Australian *Carlia* populations represent *fusca* sensu stricto (Ingram & Covacevich, 1989). The following analysis examines the nonAustralian populations, commonly labeled *C. fusca*, to determine whether they represent a single polytypic species or several species.

Materials and Methods

The analysis of intra- and interpopulational variation in and among the New Guinean *fusca*-group relies on a different set of characters and a different sampling regime than the *Carlia* phylogenetic analysis. For this study, I attempted to create geographically restricted samples of about 20 adult specimens. Most geographically restricted samples represent specimens collected within a 5 km radius; a few, e.g., Milne Bay (#28) or Kai(67), encompass areas of upward to about 50 km radius. I assume that the samples adequately delimit character variation at each locality and also encompass the full range of morphologies through the examination of many localities (Fig. 6). Where possible, the samples include an equal number of adult males and females. A few samples contain 40+ individuals to test the preceding assumption that the smaller samples adequately encompassed local and

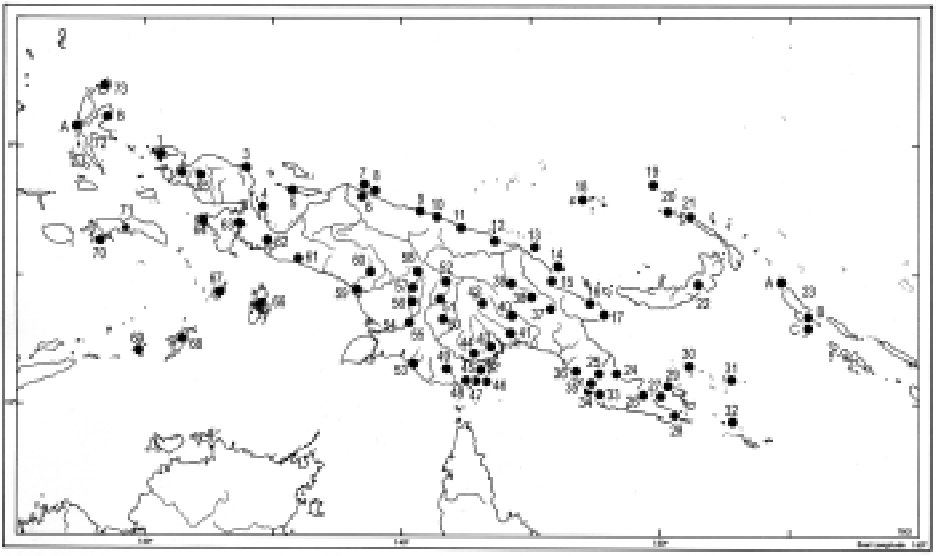


Figure 6. The distribution of the sample localities for the analysis of geographic variation in *Carlia* "*fusca*." The numbered localities are identified in the Appendix Table B.

sexual variation. These larger samples also permit tests of the homogeneity of several morphologically distinct populations with recently and uniformly preserved specimens. A worldwide museum search yielded 70+ sample localities (Fig. 6), 35 of which had 20 or more specimens, 22 of 10–19 specimens, and 21 of <10 specimens. The sample compositions and the sources of the specimens are detailed in Appendix Table B. All locality-samples are compared statistically. My criterion for a "statistically useful" sample is a sample of 3 or more adults of each sex, of 8 or more adults, or of 10 or more specimens (see Sample Size in Results). Although larger samples are desirable, that option was not always possible, and even smaller ones are included for comparison of types or to obtain a broader geographic coverage.

Characters Examined

Three sets of characters were examined and recorded: 1) mensural characters are straight line measurements of body segments to the nearest 0.1 mm with dial calipers; 2) meristic characters are scalation features of head, body and limbs, recorded from right side on paired features; 3) color patterns concern the shapes, number and distribution of markings and their various colors from alcoholic specimens. Sex and reproductive state (maturity) were determined by dissection and examination of the gonads. Mature females possess vitellogenic follicles >1.5 mm, oviducal eggs/embryos, or stretched but empty oviducts; mature males have enlarged testes and epididymides. Determination of maturity for female is more reliable for the lizards in transition owing to the discreteness of virginal versus nonvirginal oviducts in females compared to the recognition of "enlarged" testes in males.

Mensural characters.— Snout-vent length (SVL): distance from the tip of the snout to the posterior edge of precloacal scales. When specimens are neatly positioned during initial preservation, this feature can be measured with high accuracy. Measurement error is greater when a contorted preserved specimen must be straightened to obtain SVL. Trunk length (TrunkL): distance from the posterior edge of the forelimb insertion (axilla) to the anterior edge of the hindlimb insertion

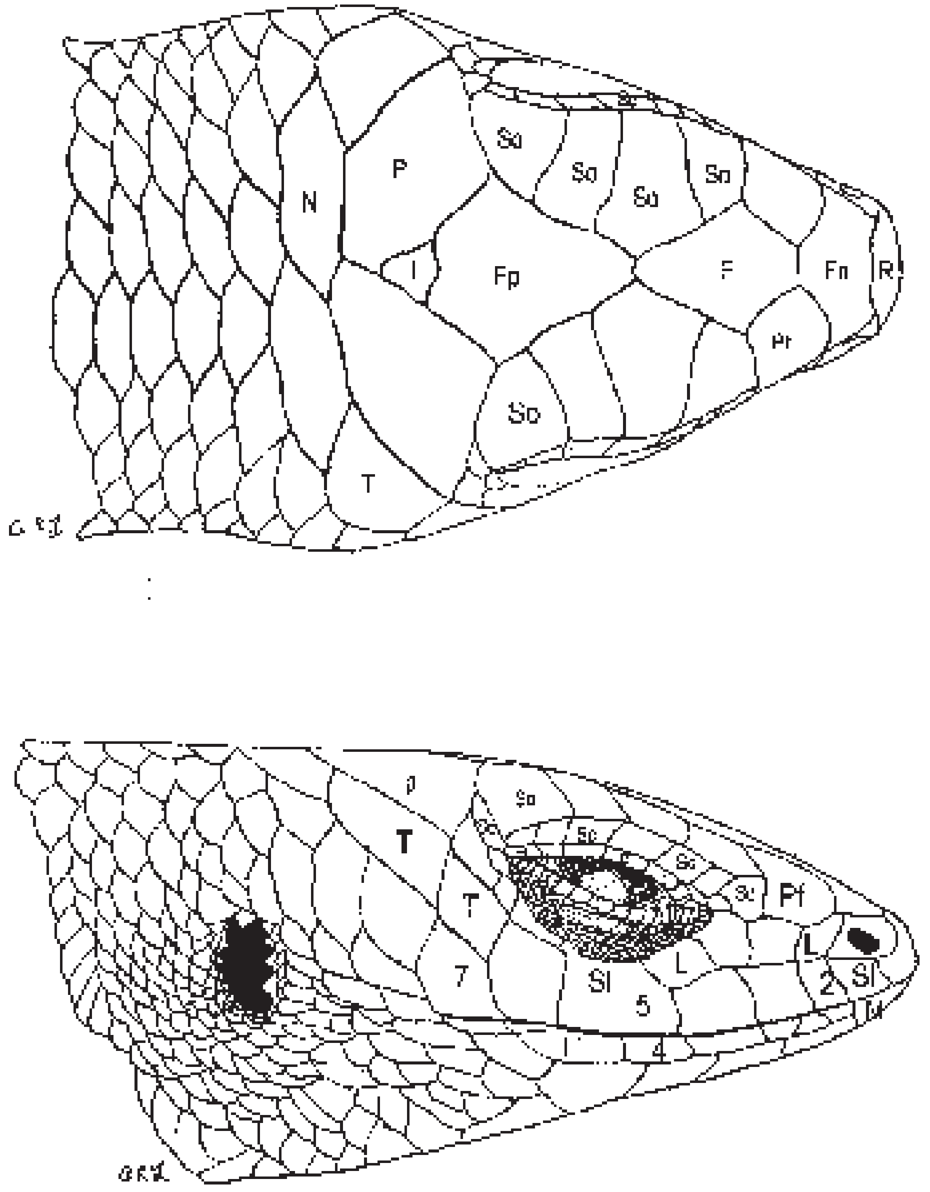


Figure 7. Schematic depiction of head scalation in *Carlia “fusca”* skinks, dorsal and lateral views. Some supra- and infralabials are numbered to identify position of scales in sequence. Abbreviations: e, eyelid scales; F, frontal; Fn, frontonasal; Fp, frontoparietal; I, interparietal; Il, infralabials; L, loreals; M, mental; N, nuchal; P, parietals; Pf, prefrontals; R, rostral; Sc, supraciliaries; Sl, supralabials; So, supraoculars; T, temporals.

(inguen). Hindlimb length (HndlL): distance along the posterior margin of the straightened hindlimb from its insertion to the tip of the fourth toe. These latter 2 lengths are subject to considerable measurement error in poorly preserved/positioned specimens, owing to the contorted nature of such specimens and the artificial limb position produced in attempts to straighten the body and limb for measurement. Hence, these values and their ratios potentially have a higher variance owing to measurement error. Head length (HeadL): distance from the tip of the snout to the anterior edge of the ear opening, measured parallel to the side of the head. Palpebral diameter (PalpbD): maximum diameter along the anteroposterior axis of the transparent scaleless area of the lower eyelid. Ear diameter (EarD): maximum diameter (usually along dorsoventral axis) of the ear opening. 5 proportions from these measurements allow the recognition of shape differences: TrunkL/SVL; HndlL/SVL; TrunkL/HndlL; HeadL/SVL; PalpbD of EarD.

Meristic characters.— Scalation features were defined to increase the consistency and accuracy of the counts made discontinuously over a long time period. The goal was to avoid differences in procedure that can occur as perception changes. Since the definitions depend upon strict topography, the scale terminology herein does not always match that of other authors studying skinks. Interparietal scale (Interp): separate or fused to an adjacent scale, usually the frontoparietal. Supraocular scales, number (Supoc): large scales lying between the frontal-frontoparietal scales on the midline and the brow ridge of small scales above the eye (Fig. 7). Supraciliary scales, number (Supcil): scales forming the dorsal margin (brow ridge) of the orbit, extending from the loreals to the parietal scales; only the supraciliaries touching the supraoculars are counted. Eyelid scales, number (Eyeld): row of scales on the outer (ventral) edge of the upper eyelid. Temporal scales, number (Temp): number of scales intersected by an imaginary vertical line drawn dorsally from the suture between the last 2 supralabials to the parietal; this count always includes the primary temporal and either a postocular and/or secondary temporal scale. Loreal scales, number (Lor): enlarged scales touching the supralabial scales and lying between the nasal scale (pierced by the naris) and the granular scales of lower eyelid; the count includes the anterior and posterior loreal scales and one or more preoculars (presuboculars). Supralabial scales, number (Suplab): upper lip scales from rostral scale to posterior corner of the mouth. Supralabial scale below orbit (BlwEye): enlarged scale beneath middle of eye. Infralabial scales, number (Inflab): lower lip scales from mental to scale with its posterior border lying beneath last supralabial. Auricular lobes, number (AuricN): enlarged and protruding scales on the anterior border of the ear opening. Dorsal body scales, number (Dorsal): rows of scales on dorsal midline of body from the posterior edge of the hindlimb insertion anteriorad to the parietal scales; the slightly enlarged nuchal scales are counted as dorsal scales. Midbody scale rows, number (Midbody): scale rows around the circumference of the body midway between the fore- and hindlimbs. Subdigital lamellae, number: enlarged scales on the ventral surface of the third finger (3FingL) of the forefoot and the fourth toe (4ToeL) of the hindfoot (Fig. 8); the first (proximal-most) subdigital lamella at the base of the digit is the first scale wider than long and touching a supradigital scale on at least one side of the digit. Keeling of body scales (DorsKN): degree and type of keeling on the dorsal, lateral, and ventral body scales. Precloacal scales size (Precl): scales on anterior lip of the cloacal opening, equal or larger than the ventral scales of the pelvic area.

Color pattern.— Coloration is the most subjective of the characters examined, particularly so since color and pattern were recorded from preserved specimens. Color pattern is emphasized over actual color, which is modified by the type and manner of preservation and time in preservatives. Special attention was paid to the shape, arrangement, and position of stripes, bands, spots, and other marks on the head, neck, supra-axilla (shoulder), back and sides of trunk, and venter. I recorded patterns by sketches and brief verbal descriptions; these are condensed in the Results section into a semitelegraphic format. Colors mentioned herein are those of preserved specimens, unless stated otherwise. The analysis of color pattern is qualitative, emphasizing the geographic distribution of the numerous patterns observed. My goal has been to determine whether the color pattern distributions are concordant with mensural and meristic character distributions.

General analytical protocol.— All statistical analyses were performed with SYSTAT version

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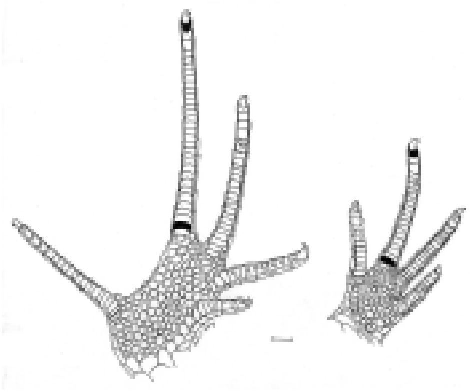

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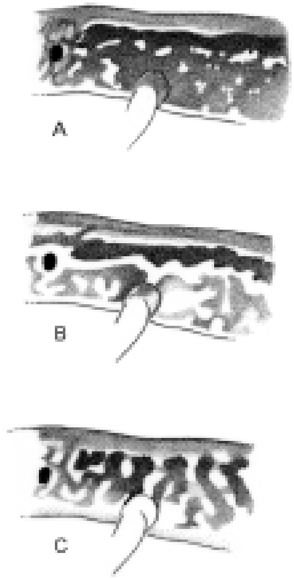

Figure 8. Schematic depiction of right hindfoot and forefoot scalation in a *Carlia "fusca"* skink *C. luctuosa*. Note clefts in distal lamellae; first and last lamellae counted on the fourth toe and third finger are shaded. **Figure 9**. Schematic depiction of juvenile shoulder pattern in *Carlia "fusca"* skinks. Type A *Carlia aenigma* (USNM 232063), type B *Carlia aramia* (USNM 232043), and type C *Carlia luctuosa* (USNM 232196).

9 (1999, SPSS Inc.). As noted above, specimens were pooled to create small, discrete geographic samples. Each sample was examined by basic statistics, e.g., means, medians, standard deviations, to determine local variation of each character and to determine which characters displayed sexual dimorphism by Students' *t* test with pooled variance. The within-character variation (as measured by the coefficient of variation) of several larger samples provided a means to test the relative accuracy of the means and range of samples containing <10 individuals.

Multivariate techniques (PC, principal component analysis; DA, discriminant function analysis) are used to examine the similarity and potential relationships among samples (populations). These tests are performed separately for mensural characters of adult females and males, and for the total sample for scalation characters owing to the occurrence of sexual dimorphism in the former and rarely in the latter. Additionally, scalation and proportions are examined directly and measurements are natural logarithm transformed; analyses are also performed separately for the 3 character sets to permit maximum resolution and to avoid conflict among different value types. PC assists in determining the characters with the most information content and to suggest possible differentiation among individuals within and between samples. DA serves to test the levels of differentiation among samples.

Character Analysis: Results

Sample Size and Variation

How adequately does a sample of twenty or fewer adults predict the character-parameters of populations of *Carlia "fusca"*? None of my samples is sufficiently large to provide a statistically convincing test; nevertheless, several lines of evidence offer corroborative support for the adequacy of a sample size of 20 adults and even smaller samples in some instances.

Seven samples have over 30 adult specimens of equal or nearly equal numbers of females and males: New Ireland [locality #21]; Inawi [36]; Aru [66]; Kai II [67B]; Ambon [70]; Palau [96]; and Guam [99]. Of these, only the Inawi sample unquestionably represents a single population or deme; it derives from a 3 hour sampling bout of all lizards in a quadrate roughly 100x100 m adjacent to Inawi village. The other samples are geographically broader but still geographically restricted. The strong similarity in character means of most characters from these distant localities demonstrates the high level of uniformity or low character variation of "*fusca*" populations. This uniformity is examined later in the geographic patterns section; however, this uniformity persists even in smaller samples and deviations indicate inadequate sample size, biased sampling or incorrect data-recording.

The coefficient of variation (*V*, expressed as a percentage) offers another means of examining uniformity within and between samples. *V* is a sample size-free statistic because it is the standard deviation of a character divided by its mean (Simpson, 1960). This aspect allows a comparison of variation both between different characters within a sample and the same character in different samples. Equivalent *V*s indicate equivalent ranges of variation relative to the numerical size of the mean; 0 = no variation, <12 "normal" intrapopulational variation, and >12 one or more datum-outliers.

For example among the above 7 samples, *V* ranges from 0–15.8 for all scalation characters except AuricN (*V* = 20–39) and Interp (0–96), and 2.4–13.6 for the mensural characters. Supoc is invariant, hence *V* = 0. Dorsal (1.8–3.6), and Midbody (2.7–4.2) are low with a narrow range; the others have broader ranges of 3 to 8, e.g., Supcil (2.0–9.3), Suplab (2.2–5.6), Eyeld (7.0–12.4) or 4ToeL (4.5–7.3). Kerfoot (1970) showed that these *V* values and ranges are typical of Dorsals among lizard families and likely reflect some functional correlate. Simpson (1960) noted that most mensural data from mammals commonly have a *V* range of 4–10 and 5–6 as the average. This observation matches the mensural data for the 7 samples, e.g., SVL (3.9–6.1), HeadL (3.6–6.4), EarD (9.0–13.6). The point of this discourse on *V* is that this statistic can be used to evaluate the reliability of the statistics from the smaller samples. If their *V*s lie within the ranges of those from the 7 larger samples and are <12, the character means, etc. are reasonable estimates of the population parameters. This interpretation is re-enforced by the *V*s of AuricN, Interp, and EarD. Higher values are driven either by low frequency of one presence-absence character state (Interp) or widely variable states with infrequent outliers (AuricN) or measurement error (EarD). Thus, in the following character analyses, character statistics from smaller samples are identified as questionable only when their *V*s are outside the range of those of the large samples.

Sample size has a different effect on the accuracy of determining the presence-absence of sexual dimorphism. Inequality of female and male samples can either inflate or deflate the differences between the means owing to the nonrandomness of specimen availability. A single statistical measure is not available to serve as a "rule of thumb" for decision on the accuracy of sexual-dimorphism determination. I have relied on SYSTAT's pooled-variance adjusted Students *t* at $p \leq 0.05$ to accept or reject the occurrence of sexual dimorphism of a character. This criterion ensure confidence with $n \geq 10$ of each sex, but less so when samples are smaller and especially if unequal. I note my uncertainty in such cases.

BODY SIZE AND PROPORTIONS

Size at sexual maturity.— Species of *Carlia* range from 32 to 66 mm average adult SVL (Table 1). The range of mean adult SVL is less for females (43.7–65.8 mm; males, 46.1–73.1 mm) of the New Guinean populations of "*fusca*" (Table 3). Nearly half of the samples (Table 4) are sexually dimorphic in body size with females always smaller than males. Maturity occurs at a smaller SVL than the mean body size and is recognized easily in females because changes in ovarian follicle morphology are observed easily; hence, the minimum adult SVL of females is more accurate. Testicular maturation is less obvious so minimum adult male SVL is less accurate, and the following comments are confined to females.

The Central Province samples (#33–36) contain the largest females of the "*fusca*" samples with a maximum 75.4 mm SVL, which is only slightly less than the male maximum 77.7 mm for

Table 3. **Summary of selected characters for the major *Carlia “fusca”* localities**.

	Snout-vent Length								Sample
Locality	female	male	Head/SV	Hndl/SV	Dorsal	Midbody	3FingL	4ToeL	Size
01	52.7	56.3*	0.23	0.50	48.5	32.0	21.3	29.2	21(12, 7)
03	49.6	51.7	0.22*	0.46*	48.5	33.4	20.5	28.7	19(10, 6)
06	50.7	53.8*	0.22*	0.46*	48.5	34.2	20.0	28.1	20(8, 12)
09	55.4	60.3*	0.23	0.49*	48.1	33.6	21.8	28.8	22(11, 9)
10	58.2	61.6*	0.21*	0.44*	47.3*	34.9	21.4	29.6	24(12, 12)
11	49.8	48.5	0.22*	0.48*	49.0*	33.6	21.6	28.9	8(5, 3)
12	56.4	56.0	0.22*	0.47	46.9*	32.8*	21.1*	28.1	9(4, 3)
14	59.3	54.3	0.22*	0.45*	47.8	33.2	21.3	28.2	20(10, 10)
15	53.8	56.2	0.22*	0.46*	47.8*	33.6	21.0	29.0*	33(23, 3)
17	54.1	55.9	0.22*	0.48	48.7	34.2	21.8	29.9	20(11, 9)
18	52.7	54.4	0.21*	0.48*	48.5	32.4*	21.3	29.5	32(15, 17)
20	47.4	52.0	0.23	0.48	49.1	31.7	21.2	29.3	9(3, 6)
21	49.0	51.4*	0.22*	0.46*	47.1	31.3	20.1	27.9	41(20, 17)
22	49.7	52.4	0.24*	0.45	48.3	32.6	20.7*	28.2	29(14, 12)
23	48.4	49.9	0.23*	0.48	49.0	32.3	20.5	27.4	19(8, 9)
24	50.7	52.0	0.23	0.47*	48.3	32.7*	21.6	30.0	13(6, 3)
25	52.6	55.8	0.22	0.48	49.9	33.5	21.6	28.9	8(5, 1)
27	51.6	54.5*	0.22*	0.47*	48.6	32.6*	20.7	27.6	20(12, 8)
30	56.0	60.3	0.21*	0.47*	48.6	33.9	19.9	28.0	18(6, 10)
31	55.8	61.6*	0.22*	0.48	48.7	35.6	22.3	30.7	12(4, 6)
32	54.9	52.2	0.22*	0.50	48.4	35.0	22.2	29.6	11(4, 3)
33	63.2	68.8*	0.21	0.51	50.2	37.3	22.2	31.5	12(8, 4)
34	65.7	72.4	0.23*	0.52	48.6	37.5	23.3	33.5	11(3, 4)
35	56.0	63.7*	0.22*	0.53	48.4*	36.9	21.9	31.1	30(11, 13)
36	65.8	70.0*	0.22*	0.48*	49.8*	38.0*	23.3*	33.0*	40(19, 21)
37	50.3	53.2	0.23	0.47	48.0	31.7	20.3	27.3	10(5,2)
38	54.8	57.6*	0.22*	0.48	48.0	34.3*	20.1*	27.0	36(16, 18)
39	53.3	58.6*	0.22*	0.47	47.0	32.9	20.4	27.6	25(14, 8)
40	52.7	54.6	0.23	0.48	48.0*	34.0	22.0	28.0	21(15, 6)
42	50.7	49.0	0.23*	0.48*	46.0	33.6	21.2	28.4	12(6, 6)
43A	46.0	46.5	0.22*	0.45*	46.1	31.6	19.5	26.2	17(10, 7)
43B	51.2	53.4	0.23*	0.51	47.1*	34.5	22.7	31.1	15(7, 8)
44	48.5	46.8	0.22*	0.45*	49.0*	33.4	21.4	28.7	26(12, 14)
45	48.1	49.8	0.23*	0.47	46.6	33.1	21.9*	28.3*	21(11, 10)
46	53.1	55.1	0.23	0.44*	47.9	34.5	20.0	27.2	20(10, 7)
47	47.9	45.7	0.22	0.47	47.7	32.3	19.6	27.2	9(7, 1)
48	49.8	51.2	0.22*	0.47	46.7*	32.1*	19.6	26.4	12(6, 6)
49	46.0	46.4	0.22*	0.44	47.4	32.2	20.0	26.3	11(6, 5)
50	47.5	49.0	0.23*	0.49	46.8	33.3	20.5	28.1	20(11, 9)
51	48.8	50.4	0.25	0.50	46.9	34.4	21.7	30.5	10(4, 1)
53	48.6	51.1*	0.22*	0.46*	47.5*	31.5	19.8	26.5	17(8, 9)
54	49.5	51.5	0.23*	0.57	48.3	33.4	21.7	29.2	17(10, 5)
55	47.8	50.0	0.23	0.50	46.2	32.4	20.5	28.1	14(3, 2)
56	51.7	50.8	0.23*	0.49*	46.6	33.6	21.1	28.2	18(15, 3)
57	50.2	51.1	0.23	0.56	47.4	33.0	22.2*	29.6	12(2, 7)
58	50.4	50.8	0.23	0.48*	46.6	32.2	19.3	25.5	20(10, 10)
59	47.6	55.3*	0.23	0.48	45.8	33.6	19.7	27.1	19(8, 8)
62	49.8	50.0	0.23*	0.48*	46.7*	33.4*	21.8	29.0	20(10, 10)
63	49.5	53.5*	0.22*	0.45	47.9	33.3*	20.0	27.2	18(9, 9)
65	48.6	50.9*	0.22*	0.46*	47.7	33.0*	21.4	28.4	30(13, 17)
66	49.1	51.3*	0.23*	0.48*	45.4*	32.9*	21.8*	29.3*	43(23, 20)
67A	64.1	73.1*	0.22*	0.53*	54.4	38.5	23.6	32.3	28(10, 11)
67B	48.3	48.5	0.23*	0.49	47.7	32.2	22.1	30.3	35(15, 14)
68	44.6	49.1*	0.22*	0.49	47.7	31.3	20.4	29.7*	20(8, 7)
70	43.7	47.5*	0.22*	0.49	47.5*	31.5	21.0	28.8	41(14, 16)
71	48.0	48.9	0.21*	0.48	47.7	31.4	21.2	28.3	21(11, 5)
72A	46.1	46.5	0.22*	0.46*	47.9	32.3	19.9	26.6	20(6, 14)
73	45.7	46.1	0.22*	0.46*	48.3	32.4	21.9	29.7	29(16, 13)
96	47.9	50.0*	0.22*	0.46*	47.4	32.2	19.8*	26.9	39(18, 18)
99	52.7	52.8	0.22*	0.48*	49.5	33.0	21.1*	29.5*	37(15, 16)

The locality numbers are identified in Appendix Table B. All values are means; an * indicates a significant differences between adult females and males. All means, except SVL, Head/SV and Hndl/SV, are for the total sample; the exceptions are ratios that are sexually dimorphic and then the value is the adult female mean; otherwise the mean is for total sample. Sample size is total sample and in parentheses, numbers of adult females and males.

these samples. The minimum mature SVL is 53.6–59.5 mm for the Central Prov. females. The smallest females are from small Sundan islands (#68, 70) and have minimum adult SVLs of 41.1 and 39.0 mm, respectively. For most other populations, the minimum mature female size centers around 50 mm SVL (46–54 mm).

Table 4. Frequency of sexual dimorphism among the characters in all locality samples of *Carlia* "*fusca*".

Frequency	Characters
no dimorphism	Interp, Supoc, Supcil, Temp, Suplab, BlwEye, Inflab, DorsKN
1–5%	Eyeld, Lor, AuricN, Precl
9–16%	Midbody, 3FingL, 4ToeL, PalpbD/SVL
20–32%	TrunkL, Dorsal, TrunkL/SVL
40–50%	SVL, PalpbD, EarD, HndlL/SVL, TrunkL/HndlL
75–82%	HeadL, HndlL, HeadL/SVL

Sexual dimorphism.—Fifty-five samples have 3 or more adult females and males each. Only one sample (locality #20) has no characters displaying sexual dimorphism, i.e., *p* £ 0.05 for pooled variance *t*. A few other samples (#17, 24, 49, 50, 54) have 3 or fewer dimorphic characters. These exceptions to dimorphism are emphasized owing to the uncertainty of correctly identifying dimorphism in small samples or samples with strongly unequal numbers of females and males.

Sexual dimorphism is strikingly apparent in a few populations with distinctly larger males (e.g., #33–36) or with male breeding coloration (see later section); however, for other populations, the statistical identification of sexual dimorphism may reflect sampling and measurement errors. Frequency of occurrence of dimorphism among characters (Table 4) and number of dimorphic characters in each sample (Table 5) offer one method of correctly identifying sexually dimorphic populations. Among the characters, Dorsal is the only aspect of scalation with a moderately high occurrence (24%, Table 4) and, to my mind, the only scalation character that is truly dimorphic between the sexes. Any character with a frequency <10% is suspect, and suspicion seems appropriate for those <20% dimorphic characters in small or unequal samples. This suspicion, thus, largely eliminates scalation as displaying sexual dimorphism. The exception, Dorsal, is dimorphically paired with TrunkL (27%) in 9 of its 13 dimorphic occurrences, therefore is likely a true dimorphism.

Table 5. Distribution and frequency of occurrence among sexually dimorphic characters. An asterisk denotes a sample with SVL dimorphism (see Table 3).

Number of sexually dimorphic characters	Sample localities of occurrence
0	20
1	24, 32
2	49
3	11, 17, 33*, 34, 40, 50, 54, 67B
4	3, 12, 23, 30, 45, 56
5	31*, 42, 43B, 46, 58
≥6	1*, 6*, 9*, 10* 14, 15, 18, 21, 22, 27*, 28, 29, 35*, 36*, 38*, 39*, 43A, 44, 48, 53*, 59*, 62, 63*, 65, 66*, 67A*, 68*, 70*, 71, 72A, 73, 96*, 99

HeadL is dimorphic in most samples (82%); HeadL/SVL (82%) is equally widespread although the dimorphic pairing of these 2 characters is not totally concordant (HeadL:HeadL/SVL – no:no, locality #20, 24, 33, 43, 58; no:yes, #17, 32, 40, 44, 56, 66; yes:no, #1 ,3, 9, 46, 59). HndlL dimorphism is also widespread (75%), and although HndlL/SVL is less prevalent (49%), it occurs in a significant proportion of the populations. SVL dimorphism (40%) is also less common, nevertheless it is an attribute of many populations. This size dimorphism is always males larger than females. The difference (statistically significant) in length, is 3–4 mm in most samples (Table 3), and that for HeadL is almost always less than 1.2 mm. HndlL dimorphism occurs in 75% of the samples and usually is about 2 mm different with larger hindlimbs in males. This aspect and the low *V* (4–9) of HndlL surprised me because of my concern about the accuracy of measuring hindlimbs. As an explanation, I can suggest only a nonbiased measurement error and further that HndlL dimorphism is real.

In summary, sexual differences in size and body proportions are a common attribute of "*fusca*" populations, although difference in overall body size (SVL) of females and males occurs in <50% of the population. Dimorphism is most common in HeadL and HndlL and their proportions.

HEAD SCALATION

Interparietal and prefrontals.— Interp records the presence or absence of the interparietal scale. The interparietal is normally present. Of the 77 samples examined, 55 (71%) have all members with an interparietal. In the other samples, the incidence of no interparietal is low, typically <15% of sample with interparietal absent. Only one sample (#36) has a high incidence (48%) of absence; yet, its neighboring Central Province samples (#33–35) have 93–100% of sample with an interparietal. An interparietal is absent when it is fused to the posteromedial edge of the frontoparietal.

Prefrontals are usually separated on the midline by the frontal abutting the rostral. Most samples (>90%) contain no specimens with the prefrontals contacting on the midline. The incidence of contact within samples is always low (<10%) and usually no more than point contact at the midline.

Supraoculars, supraciliaries, and eyelid scales.— There are typically 4 enlarged supraoculars (Supoc) scales on each side. Occasionally one supraocular is clefted (usually one side only), creating 5, rarely 6 supraoculars. Four supraoculars is the median value in all samples, and 69 (80%) samples are invariant. The incidence of 5 or 6 scales in the other samples is always low.

The number of supraciliaries (Supcil) is typically 8 but with a range of 6 to 10 supraciliary scales. Seven and 9 supraciliaries are common variants, and these variants are likely to occur once or twice in any moderate to large sample. The other variants are uncommon, although in the Menapi sample (#25), all specimens have 6 supraciliaries on each side.

Eyelid scales (Eyeld) are the most variable of this triplet. The range across all samples is 3 to 15 scales (usually from 8–12); 9 or 10 scales is the median value for 62 samples (80%), 3 samples with 8, and 8 samples with 11 scales.

Temporals and loreals.— Because of their definitions (see Materials and Methods), the temporal (Temp) and loreal (Lor) characters differ from those of other authors. Two temporal scales on each side are nearly universal in "*fusca*" skinks; very rarely does one or 3 temporals occur.

Lor also has low variation, 4 scales (median in 30% of samples) – an anterior and a posterior loreal and 2 preoculars or 5 scales (70%) – a single preocular between the posterior loreal and the eye (although 3 preoculars occur, stacked vertically). The anterior loreal is typically higher than long and somewhat smaller than the posterior loreal, which is longer than high.

Labials.— The typical condition is 7 supralabial scales, exclusively so in 44 samples (57%) and the median value for all samples. Occasionally, 6 or 8 supralabials result from the fusion or division of one of the anterior supralabial scales. The incidence of these states in a sample is low to moderate, rarely exceeding 15% occurrence. Because of low variation in total number of supralabials, the large fifth supralabial beneath the eye is the most common state, median for 60% of the samples. BlwEye becomes the fourth or sixth supralabial with the fusion or division, respectively, of an anterior labial. The Wewak sample (#10) is the only variant population with as many as 10 supralabials, but the sample size is too small to determine whether this results from a few deviant individuals or is typical of the Wewak population.

Typically, there are 6 infralabial scales, occasionally 5 or 7 and rarely 8. Seven infralabials is produced usually by the division of the fifth infralabial scale and 5 infralabials by the fusion of the first and second or second and third infralabial scales. Six infralabials is the median for all but one sample and the exclusive state for 19 samples (25%).

Auricular lobes and ear shape.—Ingram & Covacevich (1989) and other researchers have used the shape of the ear opening, and the number and location of the auricular lobes to differentiate populations of *Carlia.* The New Guinean "*fusca*" have ellipsoidal to oblong ear opening, commonly with a slight posteriorad inclination from bottom to top. Although, I used diagonal versus vertical ears as an invariant character in the preceding cladistic analysis, I find it difficult to precisely determine this state in many preserved specimens and believe that the vertical and diagonal conditions are not separate states, at least not within the New Guinean populations. In "*fusca*" populations, the ear diameter is subequal to the transparent palpebral disk of the lower eyelid. The PalpbD/EarD ratio ranges from 0.40 to 2.00 and is much narrower in most samples; mean and median values typically are within the 0.96 to 1.02 range.

Enlarged scales or lobes (AuricN) are confined largely to the anterior edge of the ear. They are typically blunt-triangular, and 1 or 2 lobes are 2–3 × larger than adjacent lobes. AuricN varies from 0 to 7 throughout all samples. Three (60%) or 4 (19%) lobes are the median number for most samples; the median is never more than 5 or less than 2.

BODY AND LIMB SCALATION

Dorsal and midbody scale rows.— Within all samples, the dorsal scale rows vary from 42 to 60; however, the range is much narrower in individual samples, usually ≤ 6. The means and medians range between 47 and 49 for the majority of samples (>80%) (Table 3) with a range of 45 to 54 for all medians. Three samples have a median of 45, 3 of 46, 5 of 50, and one of 54.

The number of scale rows around midbody (Midbody) shows a similar uniformity across the 77 samples. Midbody ranges 28 to 42, but the range of medians (and means, Table 3) is much narrower, 32 to 38 (30 samples of 32, 14 of 33, 23 of 34, 3 of 35, 2 of 36, 2 of 37, 3 of 38 scale rows).

Keeling.— Tricarinate dorsal scales characterize New Guinean "*fusca*" samples, yet no "*fusca*" skink is heavily keeled and many individuals are smooth. The dorsal and lateral body scales of most adult "*fusca*" are striated or weakly keeled with 3 very low or pimply ridges (Fig. 3). More than half the samples have a few individuals recorded as smooth/striated or very weakly to weakly keeled.

Precloacal scales.— The scales forming the anterior lip of the vent (cloacal opening) are not specialized in shape or orientation. These precloacal scales are enlarged in more than half of the specimens in the majority (>85%) of the samples. However, they are enlarged only slightly; that is, the precloacal scales are typically much less than 2 × the area of the pubic scales immediately anterior to them

Subdigital lamellae.— Lamellar number reflect either the relative length of a finger/toe or the relative width (thinness) of the lamellae. In New Guinean "*fusca,*" both third finger (3FingL) and fourth toe lamellae (4ToeL) are moderately broad (Fig. 8) and have low variation among the samples. For all specimens, 3FingL ranges from 17 to 28, 4ToeL from 23 to 38. The range of sample medians is 19–23 and 26–33, respectively (see Table 3 for means). The dominant sample medians are 20 to 22 for 3FingL (86% of samples) and 28 to 30 for 4ToeL (66%).

EVALUATION OF QUANTITATIVE CHARACTERS

Four samples were selected to determine the characters with the highest information content for sample (population) differentiation: Ambon (locality #70; Appendix Table B); Inawi (36); Kundiawa (38); and Palau (96). Each sample contains more than 30 adults and a nearly equal number of females and males, and each sample was analyzed separately. Principal component analysis (PC) of sixteen scalation characters, excluding keeling, in all adults reveals 6 characters of potential value (component value >0.600) for individual and sample differentiation: Eyeld; AuricN; Dorsal; Midbody; 3FingL; 4ToeL. In all 4 samples, Toe4 has the highest loading for the first component in all 4 samples; AuricN, Dorsal, and 3FingL rank second in their influence on this component in one or more analyses. Midbody, Dorsal, and 3FingL had the highest loading for the second component. The first 2 components account for 79%, 61%, 51%, and 67%, respectively, of the variation in the 4 samples. Because of the regular occurrence of these 6 scalation traits in all 4 analyses and in their loading on both or one of the first 2 components, they are the ones emphasized in the analysis of geographic variation.

PC allows a similar selection of the mensural and proportional characters; however, these analyses were performed separately on males and females owing to the high frequency of sexual dimorphism in these characters. For log-transformed body measurements, female SVL, HeadL, and HndlL have the highest loading on the first component and with SVL, TrunkL and HndlL next in contribution to loading. The second component in females has PalpbD and TrunkL with the greatest loading and PalpbD and EarD next in loading. For male, SVL and HeadL are either first or second in loading value in all samples, and similarly for PalpbD and EarD for second component. In both male and female samples, 2 samples have no second-component eigenvalue <0.9 (thus the second component is not significant). Body proportions show also a slight divergence on character loading. TrunkL/HndlL has the highest loading component in females and males in all samples; HndlL/SVL is second highest in all male and one female samples, and TrunkL/SVL in 3 female samples. For males, PalpbD/EarD and TrunkL/SVL have the highest loading on the second component, HndlL/SVL and TrunkL/SVL for females. These results suggested the use of all mensural characters and all proportions but HeadL/SVL; however, subsequent interpopulational comparison revealed proportions as low discriminators and their examination was abandoned.

The preceding sample and "critical" characters permit the identity of a benchmark for discriminant function analysis (DA). Initial DA suggested the Wilk's *L* (lambda) as a potential measure to assess the accuracy of discrimination between and among samples; however, *L* appears to be strongly influenced by unequal sample sizes, and even accurate classifications might have an intermediate *L* value. Thus, I use a classification of $\geq$90% as a arbitrary indicator of genetic differentiation and speciation, and I attempt to assess the strength of this classification by additional interpopulational comparisons rather than by a single statistical measure of intra- and intersample variance, such as the Wilk's *L*.

COLOR PATTERN

Verbal depictions of color pattern are always inadequate. They are even less satisfactory when the description is condensed for brevity; nonetheless, I use a semi-telegraphic style in the following descriptions to summarize the great variety of patterns displayed by "*fusca*" skinks and to permit comparison among the localities. For descriptive purposes, I treat the skink's body as a rectangular box: dorsum, the top; lateral, the sides; venter, the bottom; the edges between these surfaces are the dorsolateral and ventrolateral surfaces. A stripe is a longitudinal strip of contrasting color of 0.5 to 1.5 scales wide; a line ≤0.5 scale wide; a band ≥ 2.0 scales wide. Spots are contrasting areas of color occupying one or more scales; flecks, less than a scale in area, usually much smaller and often on a scale edge.

The color is that of preserved specimens unless stated otherwise. Again for conciseness, I limit color labels to: tan (= beige to light brown), brown (medium shades), dark brown (dark chocolate to nearly black), and black (intense melanism) for dorsal and lateral surface coloration; white (white to beige) for light and black (brown to black) for dark colored flecks, spots, lines, and stripes; and cream (yellowish to light beige), ivory (white, often shiny), and dusky (gray) for ventral color. In life, many "*fusca*" skinks are iridescent, esp. dorsally on head, neck and occasionally on the anterolateral trunk even in preserved specimens; this condition is labeled coppery. In some populations, sexually active males develop areas of bright coloration ranging from light to dark shades of yellow through red and orange to gold (see *C. gracilis* and *C. longipes* in Cogger, 1992); these colors are described as yellow, orange or gold, also noting iridescence if evident.

Patterns are identified by species epithet for those descriptions based on type and topotypic specimens, or by locality sample name when no taxonomic name is available. The distribution or occurrence is listed by sample number or by locality name when specimens are not part of a major or minor sample. Note, a sample may include more than one pattern type, hence such a sample is listed in more than one pattern group. The "HISTORY AND DECISIONS" section following this "CHARACTER ANALYSIS" section identifies and provides the history for the available names of the *Carlia* populations.

Color descriptions are segregated into juvenile and adult states. Juvenile patterns may be a key characteristic for recognizing phylogenetic relationships among populations owing to their seemingly conservative retention in populations with either different or convergent adult patterns. However, whether a widespread pattern is apomorphic or plesiomorphic remains untested; further, young juveniles are not represented in many samples, likely a sampling bias. The juvenile pattern "fades" as the individual approaches maturity (see discussion in adult Aru pattern) and is lost sooner or changes completely in males. Females in many populations retain a reduced juvenile pattern into adulthood and presumably, the most uniformly colored females in these populations are older. In some instances, sexual dimorphism may be the source for the observations of assumed sympatry of "*fusca*" skinks, but it has not produced multiple names for any New Guinea populations with the exception of *C. luctuosa*. In combination, the ontogenetic shift of pattern and coloration and the sexual dimorphism produce multiple patterns at a single location although this diversity is typically dominated by a single adult pattern or 2 if a population is dimorphic. Patterns are labeled with lower case geographic names or nonitalicized species names.

Juvenile. — Early observations suggested juvenile shoulder patterns as a diagnostic trait. While this "diagnosticity" now seems questionable, the 3 presumed states (Fig. 9) are useful for descriptive purposes. Descriptions arranged clockwise from locality #1 as in Appendix Table D.

FUSCA: Dorsum brown with white single-scale spots, most numerous from mid-trunk to base of tail; head and nape coppery. Laterally, dorsolateral white stripe from above eye to mid-neck, faded thereafter and not visible after mid-trunk; dark brown band from ear to inguen, faded posteriorly, containing scattered white spots and flecks; occasionally indistinct white midlateral stripe on neck; shoulder pattern not matching A, B or C (Fig. 10A). Venter immaculate cream to ivory. Occurrence — #1, possibly #2 (only faded juvenile available), #3.

TRICARINATUS: No juveniles available. Occurrence — #5.

TOEM: Dorsum brown with black scale-edge flecks, occasionally aligned in short lines; head and nape coppery. Laterally, dorsolateral white to tan stripe from above posterior corner of eye to anterior trunk, faded thereafter or disappearing thereafter; dark brown band from ear onto tail base, often faded posteriorly, containing scattered white spots and black flecks; white midlateral stripe from eye or ear to anterior or mid trunk; tan on neck and trunk below midlateral stripe; shoulder pattern B-like. Venter immaculate ivory. Occurrence — #6.

JAMNANUM: No juveniles available. Occurrence — #8.

PULLA: Dorsum from nearly uniform brown (Humboldt Bay) to strongly striped (Vanimo) in shades of brown, midline brown band from mid-neck onto tail bordered on each side by lighter brown stripe disappearing at tail base, light stripes in turn bordered by brown stripe/bands that merge with midline band and form median band extending down tail. Laterally, broken dorsolateral white stripe from canthus over eye to and onto tail, usually continuous on head to above ear and always continuous and broader on tail; dark brown band from loreals to and onto tail, broad on neck and trunk (Fig. 10B) extending from dorsolateral stripe to ventrolateral edge of trunk; midlateral white stripe from beneath eye through temporals, interrupted and reappearing over ear, then a series of short broken stripe/spots to inguen; second series of white spots below midlateral stripe/spots on neck and sides; shoulder pattern A or C. Venter immaculate cream to ivory. Occurrence — #9, 10, 17 [slight differences], Sermowai.

WEWAK: Pulla pattern with slight differences. Dorsum, indistinct pulla striping with middorsal dark brown line from mid-neck onto tail base. Laterally, variable length dorsolateral white stripe; dark brown band on trunk with numerous white diagonal elongate spots and flecks; few white spots rather than midlateral stripe on neck. Occurrence — #12, 16.

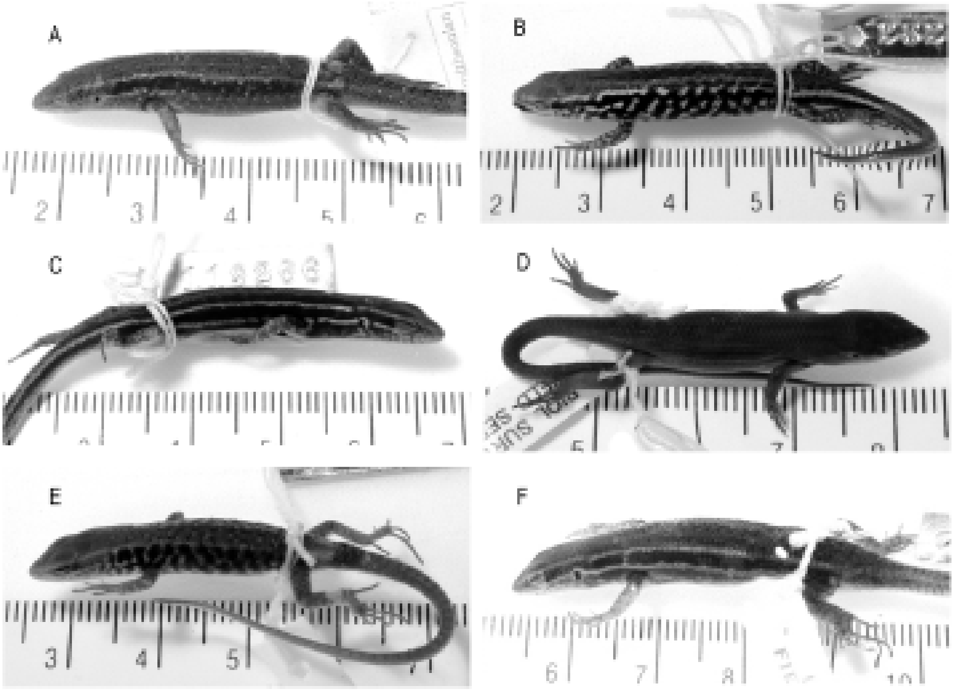

Figure 10. A sampling of juvenile color patterns. **A**, *Carlia fusca* (Toem, USNM 119312; 34.4 mm SVL); **B**, *Carlia pulla* (Vanimo, USNM 232094; 34.1 mm SVL); **C**, *Carlia mysi* (Finschhafen, USNM 119266; 35.7 mm SVL); **D**, *Carlia ailanpalai* (Guam, USNM 532916; 31.3 mm SVL); **E**, *Carlia luctuosa* (east of Port Moresby, USNM 232197; 32.4 mm SVL); F, *Carlia aramia* (Aramia R., USNM 213235; 38.9 mm SVL).

MADANG: Indistinct pulla pattern dorsally and laterally. Dorsolateral white stripe faint from tympanum to midtrunk; faint spotting in dark lateral band; midlateral stripe not evident; shoulder pattern, indistinct A or C. Occurrence — #14, 15, Kranket I., Manam I. Yabob, Tomab.

FINSCHHAFEN: Pulla pattern with exception of continuous dorsolateral white stripe (Fig. 10C) occasionally faded in ear region, continuous dark lateral band, and continuous midlateral white stripe, occasionally as a series of spots on trunk below lateral band. Occurrence — #15, 17, 26, short snout #65.

MANUS: Guam pattern (Fig. 10D); dorsum and sides nearly uniform with some dark edged scales. Occurrence — #18.

NEW IRELAND: Dorsum seemingly uniform. Laterally pulla pattern with midlateral white stripe continuous ear to mid-trunk. Occurrence — #21, 23A.

NEW BRITAIN: Dorsum seemingly uniform. Laterally pulla pattern with midlateral white stripe indistinct replaced with scattered white spots on trunk. Occurrence — #22, 23C, 31.

BOUGAINVILLE: Two pulla-like patterns, as above for New Ireland and New Britain. Occurrence — 23.

KOKODA: Dorsum indistinct pulla pattern. Laterally, white dorsolateral stripe from canthus onto tail; lateral brown band from eye onto base of tail, uniformly dark throughout length; white midlateral stripe from below eye onto base of tail; moderate dark brown below stripe on neck and trunk to ventrolateral edge, white spots only on neck; shoulder pattern B. Venter immaculate cream to ivory. Occurrence — #24, 25, 26, 27, 29, 70.

MILNE BAY: K.B. MISSION. Six-striped. Dorsum with bold pulla pattern with white parasagittal stripes. Laterally, white dorsolateral stripe from canthus onto tail; lateral brown band from eye onto base of tail, uniformly dark throughout length; white midlateral stripe from below eye onto base of tail; moderate dark brown below stripe on neck and trunk to ventrolateral edge, white spots only on neck. Venter immaculate ivory. Occurrence — #28.

MILNE BAY: ALLATAI. Faded pulla pattern. Occurrence — #28, 30.

TROBRIAND: Dorsum nearly uniform. Laterally, dorsolateral stripe usually continuous eye to inguen; white midlateral stripe complete on neck, broken into spots from shoulder to inguen; dark lateral from eye to inguen; shoulder pattern A. Venter immaculate ivory. Occurrence — #30.

LOUISIADE: Faded pulla pattern. Dorsum indistinctly striped to nearly uniform. Laterally neck and trunk stripes broken into fewer and smaller white spots. Occurrence — #31, 32.

LUCTUOSA: Dorsum, head and neck uniform brown with scattered white single-scale spots and black flecks from shoulder onto tail. Laterally, dorsolateral faint tan stripe on canthus above eye to temporals, faded posteriad of ear; white midlateral stripe from below eye to ear or slightly beyond, no stripe thereafter (Fig. 10E); lateral brown band from eye to neck, dark brown band from ear to inguen; lateral dark area broad occupying entire side and containing numerous white spots and bars, spots typically along dorsolateral edge and series of diagonal bars from mid- to ventrolateral area; shoulder pattern C. Venter immaculate cream to ivory. Occurrence — #33-36, Tapini (USNM).

KIKORI: Dorsum brown, uniform to indistinctly dark lined and flecked, occasional white single scale spots posteriorly. Laterally, dorsolateral white stripe from above eye to neck, interrupted, then continues on neck to anterior trunk, faded or absent thereafter; dark brown band from ear to inguen, distinct throughout length, darkest in shoulder region, and extending to ventrolateral edge of trunk; series of midlateral white spots from behind of eye to inguen; shoulder pattern A. Venter immaculate dusky. Occurrence — #37, 38, 40, 41, 42, 43.

EMETI I: Balimo pattern. Dorsum with some dark edged scales forming indistinct lines. Dorsolateral white stripe from behind eye to axilla, faded on posterior half of trunk; lateral brown band distinct; midlateral white stripe from below eye to inguen, distinct throughout; shoulder pattern B. Venter light. Occurrence — #43A.

EMETI II: Kikori pattern. Midlateral series of white spots and dashes on trunk; shoulder pattern A or absent. Venter dusky; gray from chin to belly, creamy over vent and thighs, dusky beneath tail. Occurrence — #43B.

BALIMO: Dorsum brown, uniform to indistinctly striped in pulla-like manner; head and nape unicolor to coppery. Laterally, dorsolateral white stripe from above eye to mid-trunk, faded thereafter or no stripe present on neck and trunk; dark brown band from ear to inguen, distinct throughout length (Fig. 10F); white midlateral stripe from beneath middle of eye, over ear to inguen, usually distinct throughout length, occasionally faded from mid-trunk onward, or no midlateral stripe and only a few spots; shoulder pattern A or B with midlateral stripe present. Venter immaculate cream to ivory. Occurrence — #43A, 44.

ORIOMO: Balimo pattern with uniform to lightly dark flecked dorsum, and commonly with a continuous dorsolateral white stripe from eye to inguen. Occurrence — #45, 49.

DARU: Less bold kikori pattern. Dark brown lateral band confined to dorsal half of sides; midlateral series of white spots faded or absent. Venter dusky. Occurrence — #44, 46, 47.

MAKA: Dorsum uniform brown, occasionally with dark flecking. Laterally, dorsolateral white stripe from above eye to posterior trunk; dark brown band from ear to inguen; white midlateral stripe from before eye to inguen; shoulder pattern B. Venter dusky. Occurrence — #50, 51.

DIGULIENSIS: Dorsum brown with white or tan single-scale spots, most numerous from mid-trunk to base of tail; head and nape coppery. Laterally, dorsolateral white stripe from above eye to mid-neck, faded thereafter or as widely spaced white spots; dark brown band from ear to inguen; midlateral white stripe from below eye to beyond ear, thereafter series of widely spaced white spots and flecks, occasionally as stripe on mid-trunk; shoulder pattern A. Venter immaculate cream to ivory. Occurrence — #54, 55, 56, 57, 58, 66.

AGATS: Dorsum brown or dark scale-edges forming longitudinal lines. Laterally, dorsolateral white stripe from above eye to anterior trunk, faded thereafter or as widely spaced white spots; dark brown band from ear to inguen; midlateral white stripe from below eye to midbody, fading and breaking into series of white spots thereafter; and flecks; shoulder pattern B. Venter immaculate cream to ivory. Occurrence — #59, Bayum, 63.

GARIAU: Dorsum brown, uniform to indistinctly lined by dark scale-edges and occasional single scale light spots. Laterally, dorsolateral white stripe from above eye to anterior trunk, fading and narrowing to inguen; dark brown band from ear to inguen; white midlateral stripe from eye to just beyond ear, series of white spots and dashes to inguen; shoulder pattern A. Venter immaculate cream to ivory. Occurrence — #62.

AYAMARU: Two patterns, dorsum of both faded pulla pattern with dark middorsal line. 1) <normal snout> Laterally, pulla dorsolateral and midlateral white stripes and dark brown band, fewer spots and bars on trunk; shoulder pattern A. 2) <short snout> Laterally, dorsolateral white stripe from above eye to inguen; reddish brown band from eye to inguen containing scattered white spots and flecks; white midlateral stripe from beneath eye to anterior trunk, a series of small white spots thereafter; shoulder pattern B. Venter immaculate ivory. Occurrence — #65

BECCARII/KAI I: Dorsum brown, uniform or speckled with black scale edges. Laterally, no dorsolateral or midlateral white stripes; lateral band from eye to behind ear brown mottled with cream, black band from mid-neck to inguen, bordered above and below by some white flecking; shoulder pattern not A, B or C. Venter immaculate ivory. Occurrence — #67A.

KAI II: Guam-like pattern with no stripes or band laterally. Occurrence — #67B.

BABARENSIS: Dorsum brown to dark brown; head and nape brown mottled with dark flecks and trunk dark brown with light and dark flecks, densest anteriorly and disappearing posteriorly. Laterally, dorsolateral white stripe from above ear to just beyond axilla; dark brown to black band from behind ear to just beyond axilla, brown before and after; no midlateral stripe; shoulder pattern not A, B or C. Venter immaculate ivory. Occurrence — #68, 69.

LEUCOTAENIA: Kokoda-like pattern. Dorsum brown nearly uniform. Laterally, distinct dorsolateral and midlateral white stripes and dark brown band from eye to base of tail, generally uniformly light below midlateral stripe; shoulder pattern B. Venter immaculate cream to ivory. Occurrence — #70, 71.

HALMAHERA: Two patterns, dorsum of both uniform brown or with some dark flecking posteriorly. 1) Laterally, dorsolateral and midlateral white stripes and dark brown band; shoulder pattern B. 2) Laterally, uniform brown; ventrolaterally neck with dark oblique lines; shoulder pattern not A, B or C. Venter immaculate ivory. Occurrence — #72A.

MOROTAI: Dorsum brown with black flecks posteriorly. Laterally, dorsolateral cream stripe from eye to axilla, faded thereafter; dark brown band from eye to inguen; white midlateral stripe from eye to mid-trunk; shoulder pattern B. Venter immaculate cream and ivory. Occurrence — #73.

PALAU: Dorsum brown with numerous white single-scale spots and black flecks, from shoulder to base of tail; head and nape coppery. Laterally, dorsolateral tan stripe from posterior corner of eye to mid-neck, faded and diffuse thereafter; dark brown band from eye to inguen, but lighter scale centers creating diffuse appearance, and confined to dorsal half of neck and trunk; no white midlateral stripe on neck or trunk; ventral half of neck and trunk tan, grading to ivory venter; shoulder pattern not A, B or C. Venter immaculate ivory. Occurrence — #96.

YAP: No juveniles. Occurrence — #98.

GUAM: Dorsum and sides brown, either nearly uniform brown ground-color or sides of each scale edged in black and scale alignment yields numerous lines from middle of neck to base of tail or center of each scale lighter brown than edges yielding a suffuse striping; head and nape coppery. Laterally, no dorsolateral white stripe (occasionally a vague hint of one), no lateral dark band, and no midlateral stripe on neck or trunk; shoulder largely uniform (Fig. 10D). Venter immaculate ivory, occasionally slightly dusky. Occurrence — #99.

Adult. — Adult color pattern tends to reproduce a faded version of the juvenile pattern with males displaying an earlier and greater loss of stripes and bands than females, although presumably

Table 6. **Ontogenetic change of the lateral white stripes in Aru *Carlia***. Juvenile condition has a bright dorsolateral stripe from eye to axilla and a bright midlateral stripe from upper lip to ear. The integers are the number of individuals possessing a specific state.

	Dorsolateral Stripe				Midlateral Stripe			
	bright	distinct	indistinct	absent	bright	distinct	indistinct	absent
juveniles	4				4			
females		8	8	1		4	5	8
males		8	4					12

older females match the uniform pattern of males in some populations. A recent collected sample from Aru demonstrates this ontogenetic shift (Table 6). Juvenile patterns among "*fusca*" populations regularly show bright white or cream marks against a contrasting background. As in these Aru skinks, the contrast between the light stripes and darker background declines. The stripes fade, and melanin appears to replace the lighter pigments entirely or in part, as is shown by the disappearance of the midlateral stripe in the mature males (Table 6).

The following descriptions are organized sequentially as those of the juveniles, and if coloration is sexually dimorphic, the female coloration is presented first.

FUSCA: Adults monomorphic. Dorsum and sides largely uniform brown; occasionally with a few white, single-scaled spots or narrow brown lines. Dorsolateral white stripe, if present, faded and confined largely to neck and axilla; lateral brown band similarly uncommon, faded, and darkest on neck to axilla; midlateral stripe absent. Venter cream to ivory. Occurrence — #1, 2, 3.

ROON: Adults monomorphic. Uniform brown fusca pattern with dark longitudinal lines more evident on dorsum and sides. One individual with distinct, but faded, dorsolateral light stripe from ear to inguen. Venter cream to ivory. Occurrence — #4.

TRICARINATUS: Single specimen, neotype. Dorsum largely uniform brown, with scattered dark flecks, forming dark brown middorsal line between shoulders. Dorsolateral white stripe from ear to midtrunk; lateral brown band from eye to midtrunk; no midlateral stripe. Venter cream. Occurrence — #5.

TOEM: Adults monomorphic. Dorsum brown with white single-scale, black edged spots, most numerous from mid-trunk to base of tail. Laterally, dorsolateral white stripe from above eye to axilla, faded and narrower thereafter containing series of light spots; dark brown band from ear to midtrunk; no white midlateral stripe on neck or trunk. "Older" individuals nearly uniform brown dorsally and laterally. Venter immaculate cream to ivory. Occurrence — #6.

WAKDE: Adults monomorphic. Dorsum uniform tan from head to tail base. Laterally, faint brown band from behind ear to inguen; no dorsolateral or midlateral stripes. Venter cream to ivory. Occurrence — #7.

JAMNANUM: Single specimen, holotype, poorly preserved and brittle. Dorsum and sides uniform dark brown. Venter dusky tan. Occurrence — #8.

PULLA: Adults somewhat dimorphic. Females, faded juvenile pattern with dorsolateral stripe, lateral dark band, and midlateral spots most evident on neck to axilla and in inguen area; dorsal stripes faded but evident. Males nearly uniform brown dorsally and laterally. Both sexes with distinct dorsolateral stripes on tail. Venter cream to ivory. Occurrence — #9, 10, Finalbin, 14, 17.

AITAPE: Adults monomorphic. Dorsum and sides uniform brown, occasionally with dark scale-edge flecking; flecking sometimes arranged in longitudinal lines. Occasional female with faint dorsolateral white stripe on neck to axilla. Venter cream. Occurrence #11, 14, Kranket Isl., Yabob, Tomab, 15, 16, 23C, 30.

WEWAK: Adults monomorphic. Dorsum and sides uniform brown, occasionally with dark scale-edge flecking. Venter grayish cream. Occurrence #12, 15, 20, 21,

MANUS: Adults monomorphic with juvenile pattern. Dorsum and sides brown, nearly uniform. Venter cream to ivory, rarely dusky throat. Occurrence — #18, 99.

MUSSAU: Adults monomorphic. Dorsum and sides brown, nearly uniform. Venter cream to ivory, rarely dusky throat. Occurrence — #19, 23A, 27.

NEW BRITAIN: Adults slightly dimorphic. Dorsum uniform tan from head to tail base. Laterally, faint white dorsolateral stripe from neck to anterior trunk in females, uniform in males. Venter cream to ivory. Occurrence — #22.

KOKODA: Adults monomorphic with juvenile pattern. Bright pulla pattern producing a six-lined pattern, usually strongly faded in largest individuals. Venter cream to ivory. Occurrence — #24, 25,

COLLINGWOOD: Adults monomorphic. Dorsum uniform brown. Laterally uniform brown or faint tan dorsolateral and midlateral stripes on neck to axilla. Venter cream . Occurrence — #26

MILNE BAY: Adults monomorphic or dimorphic depending upon location. At monomorphic sites and males everywhere, dorsum and sides uniform brown; head, anterior neck, chin and throat dusky to black; chest and belly grayish cream to cream. For females, dorsum and sides uniform brown, except dorsolateral white stripe and dark brown band on neck to axilla. Occurrence — #28, 29.

MUYUA: Adults dimorphic. Females with faded juvenile pattern; dorsum uniform brown; laterally faded dorsolateral white stripe and lateral dark band on neck to anterior trunk, no midlateral light stripe. Male dorsum and sides light to orangish tan except for black lateral band from cheek to mid-neck, lips and lower neck mottled with vivid black edged, white centered scales. Venter of all ivory. Occurrence — #31

LOUISIADE: Adults monomorphic. Dorsum and sides uniform brown, occasionally with faint dorsolateral white stripe on neck to axilla. Venter cream. Occurrence — #29, 30, 32.

LUCTUOSA: Adults dimorphic. Female, dorsum and sides dark brown with numerous black scale-edge flecking; faint tan dorsolateral and midlateral stripes from eye to ear; venter grayish ivory with black smudges along lower jaw. Male, dorsum and sides darker brown with head and neck (snout tip to axilla or slightly beyond) black; venter black from chin to base of neck, dark mottling on anterior chest and grayish ivory posteriorad. Occurrence — #33, 34, 35, 36.

KUNDIAWA: Adults monomorphic. Dorsum brown with numerous dark scale-edge flecks from shoulders posteriorad. Laterally, dorsolateral tan stripe from above eye to anterior trunk, occasionally broken and faded over ear and anteriorly; dark brown band from eye to inguen, reddish from ear to mid-trunk; midlateral series of widely spaced tan spots and dashes from ear to mid-trunk, commonly absent in males; brown below mid-lateral to ventrolateral edge. Venter usually grayish cream; males commonly with dark longitudinal lines on throat. Occurrence — #37, Mt. Wilhelm, 38, Wonenara, 40, 41, 43B, 46.

BAIYER R: Adults monomorphic. Dorsum and sides brown (darker than wewak pattern) with numerous dark scale-edge flecking, occasionally arranged in longitudinal lines over shoulders and anterior trunk. Dark brown edging of pre- and supraocular border of orbit. Venter grayish ivory; dusky smudges on side of neck in some males. Occurrence — #39.

WARO: Kundiawa pattern, except many males melanistic from snout to mid-trunk; ventrally black on chin and neck, dark gray posteriorad, but light in pelvic area. Occurrence — #42.

BALIMO: Adults di- & monomorphic. Young (small) females 4-striped; dorsum brown with some dark scale-edge flecks and white single-scale spots; dorsolateral white stripe from canthus to inguen, diffuse from mid-trunk posteriorad; lateral dark brown band from eye to inguen; midlateral white stripe from below eye to inguen; venter cream to ivory. Older (larger) females and males unicolor; dorsum and sides brown, dorsally numerous dark scale-edge flecks and some white single-scale spots; venter dark cream, occasionally somewhat dusky. Occurrence — #43A, 44, 45

DARU: Adults monomorphic. Dorsum and sides brown with some dark scale-edge flecks. Occasionally faint dorsolateral and midlateral light stripes encompassing dark lateral band on neck of females. Venter cream. Occurrence — #46, 47, 48, 49.

MAKA: Adults dimorphic. Balimo pattern but less bright lateral stripes and band in females. Occurrence — #50, 51, 52.

MERAUKE: Adults dimorphic. Daru pattern for most females with faded dorsolateral and midlateral white stripes enclosing dark lateral band from neck onto trunk; males uniform brown dorsally and laterally. Venter, immaculate cream to ivory; many males with dusky cheeks and throat. Occurrence — #53.

DIGULIENSIS: Adults with less bright juvenile pattern and possibly seasonally dimorphic. Dorsum brown with some dark scale-edge flecks posteriorly. Incomplete dorsolateral light stripe from canthus to anterior trunk, often absent or indistinct tan on head to ear, distinct and white behind ear to axilla, then fading with occasional diffuse spot to inguen; lateral band reddish brown from behind ear to axilla, lighter but evident on trunk to inguen; midlateral white stripe from below eye to ear (rarely absent), broken and series of white spots to inguen (occasionally solid on posterior trunk); apparently in sexually active males postaxillary trunk uniform orange and anterior trunk and neck more uniformly brown. Venter cream to ivory. Occurrence — #54, 55, 56, 57, 58, 66.

AGATS: Adults dimorphic. Dorsum brown with some dark scale-edge flecks posteriorly. Laterally females with reduced juvenile pattern; dorsolateral white stripe from eye to post axilla, fading and usually indistinct by mid-trunk; lateral reddish brown band from eye to inguen, faded from mid-trunk posteriorad; midlateral white stripe from below eye to mid-trunk, fragmented thereafter; ventrally cream to ivory, occasionally slightly dusky sides of throat. Laterally dorsolateral and midlateral light stripes in males reduced to series of small spots on head and neck, largely absent behind axilla; dark lateral band nearly black, often from loreals to anteriormost trunk, and extending ventrally onto chin and throat; ventrally chest and abdomen cream. Intensity of “black” head and chin-throat varies geographically, greatest in Lorentz R. area. Occurrence — #59, 60, Sabang [male], 61, 62, 63, 64 [females].

AYAMARU: Adults dimorphic, agats-like pattern. Dorsum of both sexes brown, sides somewhat darker and reddish; dorsal and lateral scales regularly dark brown edged and often forming longitudinal lines, with a middorsal dark but diffuse line or stripe regularly present. Females commonly with remnant dorsolateral stripe from temporal to axilla, fade posteriorad and occasionally small spots; dorsolateral stripe uncommon in males; distinct lateral band and midlateral stripe rare in both sexes. Venter cream to ivory; males with dusky chin and throat. Occurrence — #65.

BECCARII/KAI I: Adults monomorphic. Dorsum moderate dark brown, regularly flecked with black scale edges. Laterally, no dorsolateral or midlateral white stripes; lateral brown band from eye to ear mottled with cream, black band from behind ear to mid-trunk or somewhat beyond, brown thereafter and band bordered above and below by some white flecking; labial area and ventrolateral neck area to axilla white spotted by strong black scale edging. Venter immaculate ivory. Occurrence — #67A.

KAI II: Adults monomorphic. Dorsum and sides uniform brown with indistinct dark brown scale edges, occasionally producing longitudinal lines. Venter cream to ivory. Occurrence — #67B.

BABARENSIS: Adults monomorphic, retaining juvenile pattern. Dorsum brown to dark brown, heavily mottled with light scale centers, densest mid-neck to mid-trunk. Laterally, dorsolateral white stripe from above ear to just beyond axilla, variously interrupted; dark brown to black band from behind ear to just beyond axilla, brown before and after, heavily mottled with white ventrolateral from labial area to axilla; no midlateral stripe; posterior half of trunk orange. Venter immaculate cream to ivory. Occurrence — #68, 69.

LEUCOTAENIA: Adults monomorphic. Dorsum brown with dark scale edges commonly forming middorsal and parasagittal lines from midneck to posterior trunk, and few scattered white-centered scales. Indistinct dorsolateral stripe from eye to postaxilla, reappearing as broader but faded stripe of tail; remainder of side brown as dorsum, occasional faded lateral band on neck and axilla; midlateral stripe absent; dorsolateral stripe and lateral band brighter in some females. Venter immaculate cream to ivory. Occurrence — #70.

SERAM: Adults monomorphic, typically retaining more of juvenile pattern than Ambon specimens. Dorsum variable from near uniform brown or with longitudinal dark lines. Laterally, dorsolateral white stripe from eye to axilla or mid-trunk; lateral dark brown band from behind eye or behind ear to mid-trunk or inguen; midlateral white stripe absent or faded from behind ear to axilla. Venter cream to ivory. Occurrence — #71.

HALMAHERA & MOROTAI: Adults monomorphic. Faded juvenile pattern in some young (smaller) mature females to largely uniform brown dorsally and laterally in males and older females. Venter cream to ivory. Occurrence — #72A, 72B, 73.

PALAU: Adults monomorphic, faded juvenile pattern. Largest males and females with brown dorsum and sides, occasionally dark scale-edge flecks arranged in longitudinal lines on dorsum. Laterally, dorsolateral tan stripe nearly indistinct on neck and absent posteriorad; similarly for lateral band; no midlateral stripe. Ventrolateral edge of throat and neck occasionally with brown lines. Venter immaculate ivory. Occurrence — #96.

GUAM: Adults monomorphic, same pattern as juveniles. Occurrence — #99.

YAP: Adults monomorphic. Roon and toem-like patterns; largest individual uniform brown dorsum and sides. Venter immaculate ivory. Occurrence — #98.

Color pattern resume— The "*fusca*" populations show a complex set of intra- and interpopulational variation in color patterns. The preceding color descriptions are of small juveniles (generally <35 mm SVL) and adults; ontogenetic changes create, at least to my eyes, even greater variation at both levels and do not improve the ability to recognize similarities and differences among adjacent and distant populations. Because of the generally high level of uniformity among the quantitative characters, I am convinced of the importance of color patterns in identifying the patterns of regional differentiation, and I am equally frustrated and dissatisfied with my inability to quantify or even to categorize coloration consistently. Part of this inability lies with my reliance on preserved specimens, variously prepared and maintained. Another part is the potential composite nature of some samples and the extended period over which the data were compiled. This latter aspect yields a changing perspective and possibly differences in data recording; I attempted to minimize this by re-examining critical specimens and samples. Nevertheless, I declare my dissatisfaction with the subjective manner in which I interpret this character complex, even though I emphasize its importance below in the examination of geographic variation and the recognition of regional differentiation.

Geographic Patterns of Variation

The "*fusca*" skinks are geographically variable, yet geographically uniform. The contradiction in that statement is real. Color pattern and adult body sizes display a smorgasbord of varieties; yet, scalation shows low variation within and among samples (Table 3) and similar color patterns appear in geographically distant populations. These aspects of variation and uniformity were summarized in the preceding section; here, I attempt to integrate these aspects into the geography of the New Guinea region and to differentiate among clusters of populations that represent different species. I suggest that the uniformity of New Guinean "*fusca*" denotes their origin from one, perhaps two, vicariance or colonization events from Australia.

If this origin hypothesis is correct, "*fusca*" skinks entered New Guinea across the Sahul/Carpenteria plains, but because the name-bearer derives from Waigeo Island off the Vogelkop Peninsula, the analyses and discussion begin there and continue clockwise around the island as with the preceding color pattern descriptions. Further, because color pattern offers the best evidence of regional affinities and differentiation, I propose a geographic grouping based on adult coloration as a working hypothesis of differentiation. The homogeneity of these population groups is tested by concordance with juvenile coloration and the groups' composition adjusted, then statistically examined with the meristic and mensural characters.

Adult color patterns suggest at least 12 population group (Table 7). This grouping does not include all samples, for example, the numerous north coast Papua New Guinea (PNG) and Bismarck ones. The fusca pattern is a mainly uniform brown with a variously faded dorsolateral stripe and lateral band on neck to postaxilla. This pattern occurs from Waigeo to Toem; it or a very similar pattern reappears on the PNG north coast (localities: #11, 14–16), New Britain, Shortland/Bougainville, and Trobriands. A similarly erratic occurrence is found for the 2 other north coast patterns: pulla and unicolor. The pulla pattern is a striped one. Dorsolateral and midlateral light stripes and a lateral dark band are evident on neck and anterior trunk; faded stripes also occur on dorsum and the parasagittal and dorsolateral ones merge over the hips to produce a distinctly striped tail. The pulla pattern occurs from Sermowai to Vanimo, Karkar I., Finschhafen, Popondetta,

Table 7. **Potentially unique populations of New Guinean "*fusca*" skinks based on adult coloration**. These groups do not include all samples examined.

Name	Distribution
fusca	1–6. Waigeo and north coast of Irian Jaya from Sorong to Toem.
pulla	9–10. Seromawi drainage to Vanimo.
unicolor	12–15, 18–21, 39. North coast Papua New Guinea.
luctuosa	33–36. Central Province.
kikori	37–38, 40–43. Kikori-Okapa-Waro-Emeti polygon.
fly	43–45, 50–52. Ariama and Fly drainage.
daru	46–49, 53. Coastal plains from Fly delta to Merauke.
diguliensis	54–58, 66. Digul drainage and Aru.
lorentz	59–65. South coast of Irian Jaya from Agats to Ayamura.
beccarii	67. Kai island group.
babarensis	68–69. Tanimbar and Babar island groups.
schlegelii	70–71. Ambon, Seram, and adjacent islets.

Kokoda, and Milne Bay. The unicolor pattern occurs in the Admiralty Ids. and the north coast (#12, 15), as well as at a scattering of localities from Wakde I. (#7), Bismarcks (#19–21), Sohano/Bougainville, Menapi, and Baiyer R.

Juvenile patterns offer a better resolution of the disjunct adult pattern distributions. The fusca juvenile pattern has the same dorsolateral stripe and lateral band as the adult pattern, but its occurrence is only Waigeo to Manokwari. Juveniles are lacking from the intermediate area, and Toem juveniles are strongly striped laterally. A new juvenile pattern (pulla) appears in the Humboldt Bay area, and variants of this pattern occur along the entire PNG north coast to Milne Bay, in the Bismarcks, Bougainville, the southeastern PNG islands. The only exception is the Admiralty Ids. with a unicolor juvenile pattern.

Combined, juvenile and adult patterns indicate a different clustering of populations: fusca, Waigeo to Manokwari; Toem; pulla, widespread or numerous unique populations; and Manus, Admiralty Ids. The pulla variants are difficult to categorize, even if juvenile patterns are included, because of variable completeness of dorsal and lateral striping and the discordant distribution of pattern types. Thus, there is no unambiguous grouping of populations, and this condition recommends a combination of all pulla variants for the initial multivariate analysis. In contrast, the unicolor juvenile and adult pattern suggests a unique population in the Admiralty Ids.

The occurrence of 2 juvenile and 2 adult patterns in the mainland Milne Bay (mainland & adjacent islets) sample indicates a mixed sample. The outer island group populations differ somewhat from the mainland and from one another. Additionally, the dark heads of some adult specimens suggest a luctuosa pattern and the eastward extension of this group. The patterns of Central Province adults and juveniles are unique and concordant, although some of the male dark-headedness appears to be reduced in the Kapakapa area.

Coastal Gulf and Western Province samples possess a variety of patterns, although they seem to segregate into 2 pattern groups. A large sampling gap exists between Inawi and Kikori, and the luctuosa pattern does not reappear on the Kikori side. The kikori juvenile and adult patterns are shared "up-river" with the highlands samples (#37, 38, 40, 42) and westward with one (#43B) of 2 pattern groups at Emeti; a few Orimo adults display this pattern also. The dichotomy of 2 adult patterns in Emeti is supported by 2 juvenile patterns. As in adults, one juvenile pattern is shared mainly with populations to the east and north, and the other with populations to the west. The kikori juvenile pattern, including that of the highlands and Emeti II (#43B), is somewhat similar to the juvenile luctuosa pattern. The other juvenile pattern of Emeti I (#43A) and more westward populations (#44–49) is a lighter ground color with 2 lateral light stripes; however, not all westward PNG pop-

Table 8. **Potentially unique populations of New Guinean "*fusca*" skinks based on juvenile and adult coloration**. These groups do not include all samples examined.

Name	Distribution
fusca	1–3, 65. Waikeo to Manokwari, possibly Ayamura area.
toem	6. Toem.
pulla	9–17, 19–32, 39. North coast from Seromawi to Milne Bay, Bismarcks, Bougainville, and southeast PNG island groups.
manus	18. Admiralties.
luctuosa	33–36. Central Province and likely south-coastal Milne Bay Province.
kikori	37–38, 40–43B. Kikori-Bamu drainages to highlands
balimo	43A, 44–52. Ariama-Fly drainages to Morehead plains.
diguliensis	54–58, 66. Digul drainage and Aru.
lorentz	59–65. South coast of Irian Jaya from Agats to Ayamura.
beccarii	67. Kai island group.
kai	67. Kai island group.
babarensis	68–69. Tanimbar and Babar island groups.
schlegelii	70–71. Ambon and Seram.
halmahera	72–73. Halmahera and Morotai island groups.
halmahera	72. Halmahera [unicolor].

ulations fit neatly into this pattern because of presumed local variation**.** For example, Daru juveniles tend toward a kikori-like pattern and Maka juveniles have the double lateral stripes but a dark venter; a few Orimo adults have the kikori pattern, hinting at a mixed sample. The discordance among juveniles and adults among the population west of Emeti hints at regional sympatry of 2 species. The up-river Fly samples (#50–52) match the Emeti I and westward lowland group. The Merauke sample possesses this pattern in general although some males have dusky throats and chins, which are not seen in the eastern populations. A single highlands sample, Baiyer R., remains unassigned, and no juvenile specimens have been seen. Because the adult pattern is a dark match with Wewak adults, I tentatively assigned it to the pulla pattern group.

Adults, particularly females, of the Digul drainage (#54–58) retain much of the juvenile pattern, and even though this diguliensis pattern shares elements with the kikori one, it is different and unique. The Aru population has the diguliensis pattern.

Although it is a relatively short distance to the next sample site (Agats, #59), a different set of adult and juvenile patterns occur. Adults are strongly dimorphic with dark headed males and the female retaining some of the juvenile lateral striping. This general pattern type occurs along the entire south IJ coast to Ayamura although with local variants. The juvenile sample from Ayamura contains 2 distinct color patterns, indicating the sympatry of 2 "species" in that area; however, the collecting data for the specimens are insufficient to discern the level of sympatry, microhabitat or regional.

The Kai Ids. clearly has 2 pattern types; one is unicolor as juvenile and adult, the other with a dark lateral band on juveniles and adults. Both pattern types occur on the 2 major islands, Kai Besar and Kai Kecil.

Babar and Tanimbar share a brightly colored juvenile pattern that adults retain. The samples for both islands are largely immature specimens; potentially, adults are sexually dimorphic although available specimens do not show dimorphism.

The patterns of Ambon and Seram adults fall within the range of variation of the adult fusca pattern, but the brightly laterally striped juvenile pattern suggest a different genetic/phylogenetic unit. A similar situation applies to adults of the Halmahera and Morotai samples. Again, the presence of lateral double light-striped juveniles break the fusca link. The Halmahera juveniles display 2 patterns, unicolor and double lateral stripes, and suggest the presence of 2 distinct populations on

Halmahera. All unicolor adults in the sample, however, appear to be faded striped derivatives.

The combination of juvenile and adult patterns yields a greater number of unique populations (Table 8) in the New Guinea area, even though some juvenile-pattern groups converge, e.g., the unicolor juveniles sporadic occurrence along north coast, Admiralty Ids., Kai, and Halmahera. In addition, "*fusca*" skinks occur elsewhere (Guam, Yap, Palau) outside the New Guinea region. The Guam population is definitely an introduction; this taxon was unknown there until after WWII (Rodda et al., 1991). The Yap sample was collected recently and appears to be derived from Guam; it matches the Guam-unicolor juveniles and adults. The Palau population also appears to be a recent introduction but likely not from Guam (Crombie & Pregill, 1999). Palau juveniles have a light dorsolateral stripe on head and neck and a dark lateral band from head to inguen; the stripe and band fade variously in adults, and the larger adults are nearly unicolor.

Multivariate statistical analyses of the quantitative characters offer a means to test these pattern groups. Comparisons use only the major characters identified by PC in the character evaluation section and again proceed in a clockwise manner from Waigeo. Generally, the total sample (adult females, adult males and juveniles) is used for the scalation set and adult females for the mensural (natural logarithms) and proportional character sets. Ideally, intersample (interpopulational) comparisons should be pairwise; however, the 70+ samples of 3 character sets each would require thousands of individual discriminant analyses (DA). Instead, DAs are performed sequentially to examine the amount of differentiation among adjacent samples and sets of samples. This procedure tests the putative geographic groups recognized by shared color patterns. I accept a ≥90% classification as an indicator of genetic differentiation and likely speciation. This level of classification in both meristic and mensural sets provides an arbitrary, yet objective, benchmark for a hypothesis of speciation in *Carlia* "*fusca.*" The initial data analyses of the north coast samples (localities #1–15) revealed that body proportion characters are the poorest discriminators of the 3 character sets; they regularly yield classification scores about 10% lower than body measurements. Because they derive from body measurements, they are excluded in the following comparisons. The DA classification data are summarized in Tables 9–11 and the comparison sets in Appendix Table C.

The fusca pattern group (#1–3) shows unity in scalation (Eyeld, AuricN, Dorsal, Midbody, 3FingL, 4ToeL). DA results provide low accuracy (59%) in classification based on scalation. Various combinations of the Waigeo sample with northwest coast samples (#2–7) yield slightly better classifications, but scalation DA (Table 9) does not support differentiation among these local populations. Mensural DA (SVL, HeadL, PalpbD, EarD, TrunkL, HndlL) also does not support local differentiation in the northwest coast populations. The marginal 90% classification for localities 1 and 3 derives from females of the former averaging slightly larger than those of the latter locality (see Table 3 for summary of major mensural and meristic characters). These northwest populations vary in adult coloration from unicolor to faded lateral stripes on neck and shoulder, with the Toem juveniles possessing the brightest juvenile pattern.

A distinct break occurs between the northwest populations (#1–8) and the pulla populations of the west-central coast (#9–10). Classification accuracy is high (98% scalation and 100% mensural) in the locality #6 to 9 comparison (Table 9), thus matching the break in coloration. Scalation similarities link the west-central populations (#9–11) to one another and possibly to Wewak (#12). Notably the west-central (also Toem) populations are sufficiently different in mensural traits to yield 100% classification in the interpopulational comparisons. This phenomenon of low classification accuracy in scalation with high accuracy for measurements occurs regularly in subsequent interpopulational comparison, seemingly indicating a greater flexibility in adjusting body size to local environments. A higher accuracy for scalation occurs much less frequently and seldom with 100% accuracy. A possible explanation for this latter phenomenon is less evident.

The relationships among the north-PNG coast populations are perplexing. The differentiation of Wewak (#12) from pulla (#9–11) populations appears real, but the former's differentiation from the more eastward populations appears weaker. DA shows strong differentiation between Wewak and Manam I. (#13), and Wewak and Karkar I. (#14); yet differentiation is marginal (89% classifi-

Table 9. **Discriminant analysis comparison of scalation characters among north coast New Guinea populations of *Carlia “fusca”*.**

	fusca & luctuosa	Waigeo to Toem						Humboldt Bay to Wewak			
Localities	1,36	1,3	3,6	4,5	1,2,3,4,5	6,7	6,9	9, 10	9,10,11	9,10,11,12	9–11,12
Classification Accuracy	**100**	76	84	86	61	88	**98**	84	85	82	**93**

	north-central PNG coast - Wewak westward								Bismarcks
Locality	12,13	12,14	12,13,14,	12–14,18	12,15	14,15	15,16	15,16,17	19,20,21,22
Classification Accuracy	**100**	**93**	**93**	83	87	81	70	67	69

	Admiralty & Bismarcks		Bougainville		northeast PNG coast – to Milne Bay			
Locality	18,19,20,21,22	18,19–22	23A,B,C	19–22,23	24,25	15–17,24–25	24–25,26–27	26–27,28
Classification Accuracy	54	73	84	71	84	72	70	**92**

	Milne Bay and islands					MB & luctuosa
Locality	26–27,29	28,29	28,32	29,30,31	30,29&31	29,33
Classification Accuracy	**92**	85	69	88	86	**97**

The comparison proceeds from east (type locality of *Carlia fusca*) to west and includes two comparison to *luctuosa* samples (#33, 36) as standards of differentiation. Sample numbers separate by a comma denote the localities compared; a hyphen or ampersand denotes the combination of samples into a larger unit sample. Classification scores (%) are for DA of the standard set of scalation characters; bold scores highlight strong differentiation between samples. The locality numbers are explained in the text; additional information on the localities is available in Table B of the Appendix.

cation) between Wewak and Madang (#15), and even less (81%) between Karkar and Madang. Body size differences support pairwise differentiation among all these north-PNG populations except Karkar-Madang. I interpret the seemingly low affinities of Wewak to the coastal islands but its marginal differentiation to the more distant coastal Madang as a weak indicator of genetic continuity among all the populations from Wewak to Madang. This interpretation of continuity is re-enforced by low classification accuracy between Karkar and Madang, 2 populations geographically nearby yet separated by a water gap for the last 10 to 15 thousand years. Continuing eastward along the PNG coast, the Huon Peninsula populations (#16, 17) have low differentiation from the Madang population and in turn low differentiation from the Popondetta-Kokoda ones (#24, 25). The latter are in turn similar to Cape Vogel populations (#26, 27). Low classification scores occur for DA scalation comparisons and for most mensural ones along this 600+ km length of coastline from Madang to Menapi. In spite of a variety of coloration morphs, I interpret the similarities in quantitative traits to indicate genetic continuity; more hesitantly, I extend this continuity to include the Wewak population.

These PNG-north coast populations also are poorly differentiated from those of the Bismarcks (#19–22), Bougainville (#23A–C), and the Admiralties (#18). All scalation and body measurement DA comparisons yield poor classification scores (<90%). The juvenile pattern of the Admiralty populations is unique from the north coast and the Bismarck Islands populations. How real is this uniqueness, and if unique, does this indicate speciation? I lack personal field observations of Admiralty *C.* "*fusca*," but photographs and fresh specimens (unpublished data, C.C. Austin, Dec. 2001) confirm the unicolor of adults and juveniles. Unicolor adults occur regularly in many north coast populations with brightly patterned juveniles. Unicolor juveniles and adults are much less common but do occur elsewhere, e.g., Kai and Halmahera. This unicolor juvenile-adult trait may be more widespread because "*fusca*" samples are still unavailable from many areas; however, present evidence suggests it is an uncommon trait and possibly independently derived in its distant occurrences. The similarity of the quantitative characters and the uncertainty about coloration argue for an interpretation of the Admiralty populations as outlier of a widespread PNG-north coast *C.* "*fusca,*" but I interpret the different juvenile-adult coloration among the Bismarck and north coast PNG populations to indicate speciation of these Admiralty populations.

Unlike the Admiralty sample, the northeast islands (#29–32, D'Entrecasteaux, etc.) and Milne Bay (#28) populations share color patterns with the PNG-north coast populations, yet they differ among one another and from the north coast populations in scalation (Table 9) although not in body measurements (or at least not strongly so). The possibly mixed Milne Bay sample adds unreliability to my interpretation of interpopulational relationships; nevertheless, interisland comparisons (both excluding and including Milne Bay/28) suggest genetic affinities of some populations throughout the Milne Bay area and the northeast island groups.

A 300 km long specimen-free gap separates Milne Bay (#28) and the Central Province (#33–36) populations. Though a few Milne Bay *C.* "*fusca*" possess a slight *luctuosa*-like darkened head, the quantitative data support a differentiation of these 2 groups with high classification scores (Table 9). The Central Province samples have low interpopulational differentiation and represent a unique genetic unit. Another 300 km specimen-free gap exists between the Central Province populations and the first Gulf coast one (Kikori/#41). The Kikori sample is small and contains only 2 adults making the Central-Gulf comparison weak, nonetheless 100% classification for both scalation and body measurements indicates a genetic discontinuity. The interpretation of genetic discontinuity is supported by the 100% scores of the luctuosa and Emeti I (#43A) comparison. In contrast, the Kikori drainage samples (#41, 42) are similar to one another, and these samples represent a coastal (#41) and a highland (#42) population. When these 2 populations are compared to Emeti I (#43A) in a single DA, the classification score (74%) suggests weak differentiation; pairwise comparison (#41&43A, 41&43B, 42&43A; Table 10) yields high discrimination, suggesting discontinuity between the Kikori and Bamu drainages. However, the few individuals of the Kikori sample enable the DA model to obtain their accurate classification even though character ranges overlap among the samples.

Fascinatingly, the Kikori drainage populations seemingly are related to the "*fusca*" of the upper

Table 10. Pairwise discriminant analysis comparison of Papua New Guinea highlands’ *Carlia “fusca”*.

Localities	12 Wewak	15 Madang	37 Okassa	38 Kundiaw	39 Baiyer	41 Kikori	42 Waro	43A Emeti I	43B Emeti II
12	•	89	100	89	94	100	81	96	96
15	100	•	88	76	75	90	77	98	87
37	100	78	•	100	89	100	91	85	100
38	100	80	100	•	84	100	83	98	90
39	100	69	78	100	•	84	86	81	88
41	100	93	100	100	100	•	72	96	90
42	100	95	100	100	79	100	•	90	85
43A	100	100	100	100	100	100	100	•	100
43B	100	100	100	100	85	100	92	100	•

The upper right half of the matrix presents the classification scores (%) for the standard set of scalation characters, the lower left half for the body measurement set. The locality numbers are explained in the text; additional information on the localities and DA comparisons are available in Table B and D of the Appendix.

Fly (#50–52) and the Digul (#55) drainages. Various pairwise comparisons (#42&51, 42&50–52, 50&55) show low differentiation (75%, 64%, 76%, respectively). The affinities of these regions and the highlands are examined after the discussion of the Gulf coast populations.

The pattern of differentiation along the Gulf coast is variable. Two distinct populations occur in the Emeti area; DA of #43A and 43B produce 100% classification for scalation and measurements. Scalation DA suggests Emeti II (#43B) links (84%) with the Balimo (#44) and shows Emeti II and Uraru (#40) strongly differentiated (94%). This erratic pattern of strong and weak differentiation continues across the Fly R. lowlands to the Digul R. Pairwise comparisons reveal both moderate to weak (#45&46, 47&48, 49&53) and strong (#46&47, 48&49) differentiation for scalation; strong differentiation for body measurements occurs for all pairs. These Fly lowland populations appear closely related to the upper Fly populations (#50–52) and to the Digul R. populations (#54–58), and there is no evidence of differentiation along the Digul R. This assorted and generally moderate differentiation suggests genetic continuity among these populations with local adaptation of body size and coloration to local environments. Two contrasting interpretations arise from the DA comparisons: 1) a single species from the Kikori R. to the Digul R., and another species (Emeti I/#43A) of limited distribution embedded in the former’s range; or 2) 2 or more species with overlapping or mosaic distributions. The issue of relatedness of the Australian *C. longipes* to the Gulf species is addressed in the final section of this geographic review.

Four samples represent the PNG highlands and 3 different drainages: Purari River (#37, Okassa, Eastern Highland Prov.; 38, Kundiawa, Chimbu Prov.), Sepik R. (#39, Baiyer R., Western Highland Prov.); and Kikori R. (#42, Waro, Southern Highland Prov.). Coloration suggests potential relationships of the Baiyer population to the north-PNG coast populations, Okassa and Kundiawa to Kikori and Emeti II, and Waro to the same south coast populations although Waro males have black throats and chins that reappear in the Agats (#59) and westward populations. Pairwise DA comparisons among the highlands populations (Table 10) yield conflicting results. In scalation, the Okassa population differs strongly from nearby Kundiawa and is marginally differentiated from Baiyer and Waro populations. Kundiawa, Baiyer and Waro populations appear to represent a single genetic unit yet their differentiation from Madang differs. Okassa, Kundiawa, and Baiyer, share low ($\leq$78% classification) differentiation from the Madang and Waro high (95%). Okassa is least differentiated (85%) from Emeti I and highly (100%) from Emeti II. Waro show conflicting affinities with its least DA score (72%) to Kikori and an 85% score to Emeti II. Differentiation is high in most pairwise comparisons using body measurements (Table 10). This lack of differentiation supports a hypothesis of affinities of these highlands populations to north coast populations in contrast to the south coast affinities suggested by coloration. The mensural data for

Baiyer yields low differentiation also with Waro and Emeti II, but these classification scores exceed the 69% score in the Madang comparison.

The DA results for the highlands populations become increasingly contradictory when compared westward to the upper reaches of the Fly and Digul Rivers because Waro shows slight differentiation from Maka and Kiunga populations of the upper Fly R. (64%) and as noted previously, these upper Fly populations are poorly differentiated from those of the Fly plains and the upper Digul R. Overall, these DAs indicate genetic continuity across a wide geographic area.

Coloration shows a distinct break between the Digul populations (#54–58) and those of Agats (#59) and Lorentz River (#60), yet scalation and body measurement have low differentiation (<88%, 54–55&59–60). DA comparison of Agats and Lorentz yields 100% classification, contrasting to the 85% score of Asike (#55, *diguliensis* syntypes) and Agats. Similar contrasting differentiation exists between adjacent pairs along the southern Irian Jaya coast although the populations throughout share the adult dimorphic pattern with dark chin and throat males. Strong differentiation (≥90%) occurs between Agats and Gariau (#62), Uta (#61) and Gariau, but not between Gariau and Mandiwa (#63), Mandiwa and Fakfak (#64), and Mandiwa and Ayamura (#65). Coloration suggests genetic continuity across this long stretch of southern coast and lowlands, but scalation DA indicates discontinuities between Agats and Gariau, and continuity thereafter into the Vogelkop. The Ayamura sample (#65) is potentially mixed; 2 color morphs occur among the small juveniles. One matches the fusca pattern and the other the south-coast pattern. Thus, it is not unexpected that the Ayamura sample has low differentiation (70%) from the northwest coast fusca populations (#1–3), but low differentiation (73%) also occurs between the Mandiwa-Fakfak populations to these fusca populations. Again coloration and scalation yield contradictory evidence for relationships among populations.

Aru is isolated now from the south Irian Jaya lowlands by a shallow sea, although it was continuous during the lower sea levels of the Pleistocene glacial periods. Additionally, bathymetric features indicate that the Digul River emptied into the Banda Sea south of the Aru area. The Digul population (#54–55) is weakly differentiated (81% scalation) from Aru (#66); similarly weak differentiation exists for Aru from Agats (88%) and even poorer classification score for Gariau-Uta to Aru (75% scalation, 83% body measurements). Indeed, the combined Gariau-Uta samples show the greatest similarity to Aru with scores of 75% (scalation) and 83% (body measurements) The more westerly south coast populations (#63–64) have greater differences (91%) from Aru. Coloration for juveniles and adults matches the digul pattern, not the south-central coast populations.

Two morphotypes occur on Kai. Kai I (#67A) is one of the largest "*fusca*" morphs and strongly sexually dimorphic in size but not in coloration. Adults and juveniles are boldly marked laterally. Kai II (#67B) is a moderately small "*fusca;*" it is not sexually dimorphic in size or color, and is uniform brown. DA yields strong differentiation (100%) of the 2 Kai populations. Kai I also differs strongly from Aru and south coast populations. Kai II is weakly differentiated in scalation from Aru (80%), Gariau-Uta (73%), and Mandiwa-Uta (76%), and in its body measurements from them (≤89%).

Tanimbar (#68) and Babar (#69) populations are poorly differentiated (68%) from one another in scalation and, as a combined sample, weakly from Kai II (82%) and strongly from Kai I (100%). Tanimbar-Babar coloration is, however, most similar to the bold Kai I pattern although still clearly different. Tanimbar-Babar populations are similar in scalation (81%) and measurements (82%) to Ambon (#70) although Ambon adults are indistinctly striped.

Ambon adults possess a faded dorsolateral stripe and lateral band. This stripe and band is less faded in Seram (#71) adults and a white midlateral stripe also is evident. Ambon and Seram populations are also similar in scalation (73%) and measurements (88%). Presumably they represent a single genetic unit although there is some evidence of regional differentiation in Seram (Zug, unpublished data). Ambon-Seram has low differentiation from the Irian Jaya south coastal populations (#63–65, 81%), north coastal ones (#1–3, 80%), and Halmahera (#72A, 84%). Halmahera and Ternate (#72B) differentiate from the Morotai (#73) population in scalation (91%) and measure-

Table 11. **Pairwise discriminant analysis comparison of exotic populations of *Carlia "fusca"*.**

Localities	98 Yap	96 Palau	73 Morotai	72 Halmah.	1-3 *fusca*	4 Roon	6 Toem	11 Aitape	12 Wewak	18 Admir.
Guam	90	80	81	78	67	74	86	76	85	74
Palau	100	•	86	59	83	84	93	87	92	87

The classification scores (%) are for the standard set of scalation characters. The New Guinea localities extend from west to east. The locality numbers are explained in the text and Table B and D of the Appendix.

ments (100%). Adults of both populations (72A&B, 73) retain a faded double lateral-striped pattern. Two patterns occur in the Halmahera juveniles examined, a strongly striped pattern and a unicolor one. All adults in the statistical sample (#72A) are thought to derive from striped juveniles, although owing to pattern fading with maturity and variable specimen preservation, the Halmahera sample may be mixed. Both Halmahera and Morotai are poorly differentiated (scalation, 81% and 69%, respectively) from north coast "*fusca*" (#1–3) but moderately to strongly differentiated by measurements (91% and 98%, respectively).

The 2 major outlier populations of "*fusca*," Palau and Guam, possess different color patterns but share similarities in scalation (80%, Table 11). The differences in coloration and different pattern of discriminant scores from New Guinea "*fusca*" populations suggest that each population derives from different source areas. Because these populations did not become evident until after WWII, they are hypothesized to have been transported to Palau and Guam with the transfer of military materials from the north coast of New Guinea and adjacent islands. I hypothesized Admiralty Islands as the source-island for the Guam population owing to the shared unicolor juveniles and adults. A number of north coast populations are poorly differentiated from Guam by scalation, and the lowest classification score (67%, Table 11) is with the *fusca* populations of Waigeo and north-coast Vogelkop; however, the Admiralty sample also has a low score, denoting little differentiation. Palau is least differentiated (59%) from Halmahera; they share a similar, but by no means identical, juvenile and adult color pattern. I tentatively propose Admiralty Islands and Halmahera as the source populations for the Guam and Palau populations, respectively. The Yap population likely derives from Guam, even though it shows moderate differentiation (90%); I suggest that the small size of the Yap sample and possibly even limited variation resulting from the founder effect produced the moderate discriminant score. Similarly, the single specimen (USNM 284572) from Kosrae, Caroline Islands is most likely from Guam; it possesses the Guam-Admiralty unicolor pattern.

The borderline discrimination of Yap from Guam highlights some limitations of DA evidence. In most comparisons, whether of scalation or mensural character sets, the differences between the means of each character are miniscule and the ranges are nearly concordant. Because the DA model functions to find differences, slight shifts of means yield significant segregation. Further unequal sample sizes, especially when one sample consists of one or a few specimens, regularly yield strong discrimination (= high classification accuracy). Thus, as noted earlier, DA classification serves as an indicator of relative degree of genetic relatedness not as an absolute measure.

DECISIONS ON SPECIATION OF *CARLIA"FUSCA"*

The preceding examination of geographic patterns yields a few strong indications of population differentiation, which I equate with speciation, and many more instances of weak and conflicting evidence for differentiation. While I wish it were otherwise, the interpretation of the weak, conflicting, and insufficient evidence relies on my subjective judgment of which populations and sets of populations represent unique genetic units, i.e., ones that have begun independent evolutionary histories. Because of the high levels of speciation among other New Guinea herps (Allison, 1993, 1996) and the great genetic differences among other morphologically uniform skinks (e.g., Donnellan & Aplin, 1989), it seems likely that many of the color morphs represent distinct species. I have, however, reined in this enthusiasm for high speciation, even though some readers will doubt the strength of my tug on the reins. Morphometry, other than large versus small or strong sexual dimorphism, has little influence in my interpretation of speciation.

The populations from Waigeo Island and the northwestern New Guinea coast to the Toem area (#1–8) share a similar scalation and morphometry (Tables 3, 9), although some populations display sexual dimorphism (Table 5) and others do not. Adult coloration ranges from near uniform brown to a faded lateral striping; the juvenile pattern typically shows a complete dorsolateral stripe and a midlateral stripe on the neck with the strongest striping in Toem and the greatest reduction in the western populations (#1–3). I am convinced of the uniqueness of this set of populations by the sharpness of the separation in scalation and coloration with populations from Sermowai to Aitape (#9–11); this distinctiveness is reinforced by the strong discrimination (Table 9) of the Toem (#6) and Humboldt Bay (#9) samples. The former populations (#1–8) encompass the nominal population of *Carlia fusca* and, thus, are members of that taxon.

Although the scalation differences are not great between the northwest and southwest coast, the coloration difference is striking. Scalation DA suggests the Ayamura population (#65) is as similar to *C. fusca* populations as to the southwest coast ones (#62–64). This aspect and the presence of 2 juvenile-color morphotypes in the Ayamura area leaves uncertain the specific assignment of Ayamura *Carlia* and suggests the sympatry of *C. fusca* and another *Carlia* "*fusca*" species in this area.

As noted, the Sermowai-Aitape populations (#9–11) share scalation and coloration similarities. Significant size differences exist among these populations, and there is strong SVL dimorphism in the Humboldt and Vanimo males and females. Aitape *Carlia* is smaller and not sexually dimorphic; nonetheless, their coloration and scalation are more similar to the populations of the west than to the east. The Humboldt Bay population provided the holotype of *Carlia pulla* and, hence, that name applies to these populations.

The north coast PNG populations from the east side of the Sepik delta to Cape Vogel, the coastal islands, and the Bismarck Archipelago (#13–27) possess a variety of color patterns that usually includes elements of the pulla pattern. Similarly, these populations show differences in mean adult size (48 to 58 mm, adult females SVL), and although uncommonly SVL sexually dimorphic, they regularly show sexual dimorphism in head and hindlimb length. Scalation is similar and almost always nondiscriminatory among adjacent and distant populations. Even though I suspect multiple discrete genetic units within this broad geographic assemblage of populations, I recommend, for the present, recognition of a single species. I highlight my uncertainty of the status of the Sepik delta (#12) and drainage populations by not assigning them to either *C. pulla* or the north PNG taxon. The distinctiveness of coloration of the Admiralty sample (#18) to the north PNG samples suggests its recognition as separate species.

The Milne Bay and northeast islands (#28–32) show a variety of color patterns, one of which possesses elements of the pulla type. As a group, they average larger than the north PNG coast populations and show a unity in scalation and differ from both north and south PNG coast populations. Again, it seems likely that multiple species occur in this discontinuous set of populations and further that 2 or more species occur in sympatry or parapatry in the lowlands of Milne Bay. A conservative interpretation recommends recognition of a single species until a combined molecular-morphological study reveals the levels of genetic divergence among the different color pattern groups and their relatedness to north and south coast populations.

The populations of the Capital and Central Province area (#33–36) are striking skinks. They are large and strongly dimorphic with males dark-headed above and below. Their uniqueness has been recognized previously and 3 specific names are available. *Carlia luctuosa* is the oldest.

The populations of the PNG Gulf coast (#41, 43–44), the upper Fly R. (#50–52), and Oriomo Plateau and coast (#45–49) display a discordant pattern of inter-relationships. Dissimilarities exist among and within these 3 sets of populations and often between adjacent pairs, yet more distant ones can be quite similar. Interpopulational affinities suggested by scalation DAs are not as revealing or concordant with those of coloration. Because of the relatively slight differences in scalation (Table 3), color pattern similarities bias my interpretation of differentiation in this region and the highlands populations (#37–39, 42). Overall scalation suggests genetic uniformity for the highlands and Gulf lowlands to the Digul R. Where adjacent populations produce high DA scores, the classification accuracy reflects a slight but consistent difference in 1 or 2 traits, but not uniqueness within the region. Adult and juvenile coloration hints at multiple species, perhaps 5, in this region with either parapatry or mosaic occurrences of different species in the east. Conservatively, I suggest a minimum of 3 species occur in this area: 1) Digul R. populations (#54–58), *Carlia diguliensis*; 2) Aramia-Fly populations (#43A, 44–52); and 3) Kikori-Purari populations (#40–41, 43B). The presence of 2 distinct populations in the Emeti area (#43), recognized by a slight size difference and white vs. dusky venters, supports the distinctiveness of the latter 2 sets of populations. The latter 2 population groups are unnamed. *C. diguliensis* has a striking juvenile pattern that is largely retained in adult females and replaced by brightly colored sides in sexually active males; this latter coloration is shared with some *C. longipes* populations and to a lesser degree with some Milne Bay males. The Aramia-Fly populations have a paired lateral stripe pattern in juveniles, retained dimorphically in some populations (#43A, 44–45 and less boldly 50–52) and greatly reduced and monomorphic in other populations (#46–49). The Kikori-Emeti II-Uraru populations have darker adults a complete or nearly complete dorsolateral stripe and a midlateral series of spots on the trunk. Presently I am unwilling to assign the highlands populations to specific taxa because of my uncertainty of their genetic affinities. Even though convinced that highlands' populations (excepting Baiyer R.) have their affinities to the south coast populations, the absence of samples from the lower reaches of the Purari R. prevents accurate assessment of these assumed affinities. Similarly, I am reluctant to assign the Merauke population to the Aramia-Fly taxon; it definitely shares similarities to eastern rather than to western populations, i.e., *C. diguliensis*.

The preceding interpretation of speciation in south-central New Guinea leaves unresolved the relationships of the Gulf taxa and *Carlia diguliensis* with the Australian *C. longipes*. While I have not directly addressed the comparison of Australian and Torres Strait *C. longipes* populations to New Guinean populations, the earlier phylogenetic analysis did not uniquely pair *longipes* and *diguliensis*. More importantly, Ingram & Covacevich (1989) report considerable variation among the Torres St. island populations and suggest several discrete morphotypes. Also, Cape York and south-central PNG lizards can show speciation breaks occurring somewhere within the Torres St. islands (e.g., Zug, 1998). With 7 species names available for Australian *C. longipes* and 4 of them associated with Cape York and the Torres Strait islands, the *longipes* issue cannot be addressed with my data set.

Westward along the Irian Jaya coast, the Agats population (#59) differs (scalation DA) from the nearby Lorentz R. population (#60) and less so from the more distant *C. diguliensis* populations. In spite of the DA differentiation, Agats and Lorentz populations are quite similar in scalation and share a similar dimorphic adult coloration with one another and to the westward populations of the south IJ coast (#61–65). This striking adult pattern suggests that these populations represent an undescribed *Carlia* (Zug & Allison, unpublished data).

The Maluku islands possess a number of distinct *Carlia* populations. The Aru population (#66) is equally similar in scalation and morphometry to *C. diguliensis* and several southwestern IJ populations; however, it shares juvenile and adult coloration with the former and is identified as *C. diguliensis*.

The situation in the Kai Islands is much different. Two *Carlia* morphotypes occur. One (#67A) is large, boldly colored, and strongly sexually dimorphic. This morphotype matches the syntypes of *Carlia beccarii*. The other *Carlia* (#67B, Kai II) is smaller, unicolor, and weakly dimorphic. This Kai *Carlia* is similar to the southwestern IJ coast populations in scalation and morphometry but does not share their juvenile or adult coloration. Although this unicolor Kai *Carlia* might represent a unique population, the recent human-mediated colonization of Guam and Palau urges caution. Lacking recently collected specimens and the inadequate locality data of my Kai sample, I am unwilling to describe the Aru unicolor populations as a new species or even assign them to one of the known or currently proposed species.

The Tanimbar (#68) and Babar (69) populations share scalation, morphometry, and coloration.

These 2 populations differ from all other *Carlia* species and match the syntypes of *C. babarensis*. Because the 2 island groups lack a geologic connection, I suggest that the Babar population derives from a human-mediated colonization from Tanimbar.

The Mollucas populations from Ambon-Seram (#70–71) to Halamahera-Morotai (#72–73) can be considered 1) a single species owing to their shared similarity in scalation and morphometry, 2) part of the *C. fusca* complex of populations, or 3) a series of separate species. I prefer the last interpretation, because juvenile and adult coloration is distinct from the *C. fusca* populations and each of the Mollucan units display a different level of similarity to nonMollucan populations and species. Ambon and Seram samples are sufficiently similar to one another to propose both as *Carlia leucotaenia* (type locality, Seram), although examination of other Seram samples (Zug, unpublished data) suggests the possibility of either regional differentiation or sympatry of 2 Seram species.

Although Halmahera and Morotai are similar (scalation and morphometry) to *C. fusca*, they display moderate (scalation DA) to high (morphometry) differentiation to one another. Further, the Palau population has an extremely low differentiation from Halmahera (Table 11), thus a likely source population for the Palauan colonization. These differences hint at speciation, but for the present, I recognize them as a single evolutionary unit.

Resolution of the origin of the Guam *Carlia* is less certain, although the Guam sample's scalation seems most similar to the core *C. fusca* populations (#1–3). The coloration of Guam *Carlia* does not match the modest striping of *C. fusca* populations. The similarity of the Guam population in scalation and coloration to the Admiralty populations (#18) suggests the latter as the best contender as the source populations, hence I propose the Admiralty Islands as the source for the Guam *Carlia.*

In conclusion, I propose that multiple species (Fig. 11) are encompassed in *Carlia* "*fusca*". I have identified some sets of populations that can be adequately delimited and I formally recognize them below. I have also identified populations and clusters of populations that are potentially unique but presently cannot be satisfactorily delimited.

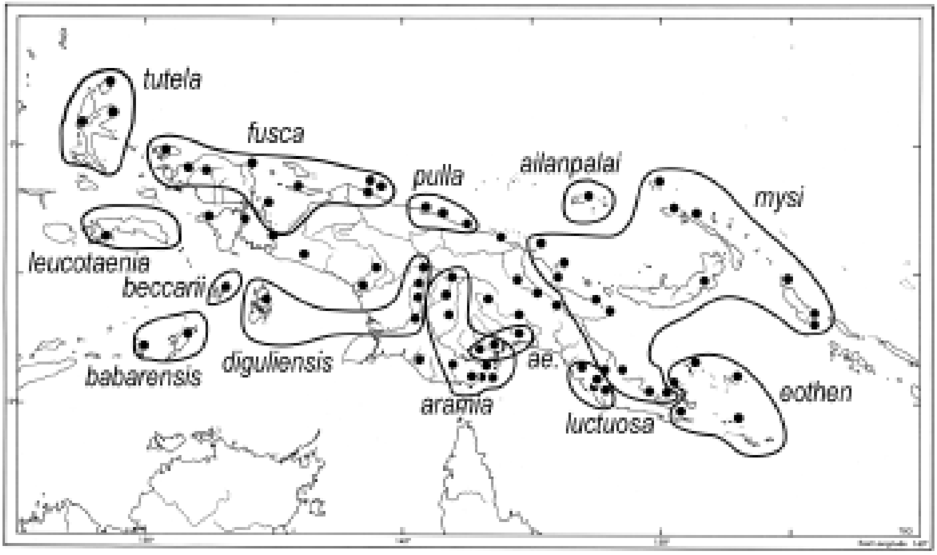

Figure 11. Distribution of the members of the *Carlia fusca* complex on New Guinea and nearby islands. Abbreviation: ae, *aenigma*.

Taxonomy

HISTORY AND DECISIONS

Heteropus fusca Duméril & Bibron, 1839
Brygoo (1986:45) reviewed the status of the Paris types and noted that the Dumerils had reported that only a single specimen existed in 1851, even though the original description listed two distinct localities. Brygoo further noted that Guibé made an error in designating the single specimen MNHN 3036 as the holotype. At best, Brygoo concluded that this specimen is the lectotype. Peters and Doria (1878) also noted that only a single type specimen was extant during their study of the *fusca* group. This specimen, MNHN 3036, is an unsexed adult, somewhat contorted during original preservation, and currently partially macerated and mutilated. All its measurements and counts match those of contemporary specimens from Waigeo. With no evidence for more than a single specimen, MNHN 3060 unquestionably represents the lectotype of *Heteropus fusca*.

The original description listed specimens from "les îles de Waigiou et de Rawack." Waigiou (= Waigeo) is a large island adjacent to northwestern New Guinea. Rawack or Rawak is a small island off the north coast of Waigeo (*in litt*. to A. Allison, July 2000, from D.G. Frodin; presently called Kawe, *in litt*. E. Colijn, Jan. 2002). Loveridge (1948) also listed it as north of Waigeo. Because the MNHN lectotype is labeled Ile Waïgou (*fide* Guibé, 1954), the type locality is restricted to this island.

Heteropus leucotaenia Bleeker, 1860
Bleeker introduced the name *Heteropus leucotaenia* in a short review of specimens from western Seram, specifically in the vicinity of Paulohi and Wahai. Of the 38 species recognized from this area, only the *Heteropus* skink was considered an undescribed species. Bleeker apparently had only one specimen, and it derived from Paulohi, hence the type locality of *H. leucotaenia*.

Boulenger (1887) listed this specimen in his catalog and placed the name *leucotaenia* as a synonym of *fusca*. Unfortunately, the specimen is missing and presumably lost. Its absence from The Natural History Museum collection was noted in 1964 by A. Stimson, and a search in 2002 confirmed its absence *(in litt.* C.J. McCarthy, 8 April 2002). I propose USNM 204786 (adult male; 49.1 mm SVL) as a **neotype**. This individual and 4 other specimens (USNM 204787-790) derive from a site (3° 18'S 128° 02'E) on Piru Bay that is near Bleeker's type locality Paulohi (3° 17'S 128° 46'E) in southwestern Seram.

Heteropus schlegelii Peters, 1864
Peters explicitly stated that he had 2 specimens from Timor and 2 specimens from Amboina (= Ambon) in hand. When I visited the Berlin collection in 1991, 2 series of specimens were labeled as syntypes: ZMB 4951, 6 specimens from Ambon; ZMB 4981, 2 specimens from Timor. Subsequently, Bauer *et al*. (1995) listed ZMB 4951 as containing only 2 specimens; they did not comment on the reduction of this series. This series is critical because the selection of lectotype ensures nomenclatural stability. Even though my observation indicates 6 specimens existed rather than 2 as stated by W. Peters, the 4951 specimens were collected by Dr. von Martens and most likely were the ones seen by W. Peters. The specimens are not individually labeled; therefore I designate the largest specimen of ZMB 4951 as the **lectotype** (an adult male, 53.3 mm SVL, 58 mm tail length). A second adult male (51.4 mm SVL, 74 mm tail length) becomes the paralectotype, and the type locality is restricted to Ambon by lectotype designation. The present analysis does not differentiate the Ambon "*fusca"* specimens from those of western Seram, hence *H. schlegelii* Peters is a junior synonym of *H. leucotaenia* Bleeker.

Heteropus tricarinatus Meyer, 1874
The original description of *Heteropus tricarinatus* suggests that this species was described from a single specimen. However, 3 supposed syntypes (SMTD 170, 176, 262) were present in the Dresden collection and were destroyed during WWII (Obst, 1977). A specimen collected and identified as *Heteropus tricarinatus* by A.B. Meyer is present in the Berlin collection and also labeled as the type of *Heteropus tricarinatus* Meyer. This specimen (ZMB 8784) is from "Ansur, Jobi." The published

type locality of *tricarinatus* is Doré (1° 40'S 136° 12'E), which is on Yapen [formerly Japen or Jappen Island]. Although I am unable to locate Ansur, I designate ZMB 8784 as the **neotype** of *Heteropus tricarinatus*. Ansur is probably an incorrect transcription of Ansoes (now Ansus, 1° 44'S 135° 49'E); Jobi (1° 42'S 136° 27'E) is a town, although this name apparently was used formerly for Yapen Island.

***Heteropus tricarinatus* var. *striata* Meyer, 1874**

The status of *Heteropus tricarinatus* var. *striata* Meyer (1874) is best resolved by considering the name a *nomen dubium*. The original description was based on a single specimen (SMTD 172) and held in the Dresden museum. It was also destroyed during WWII (Obst, 1977). The specimen derived from "Passim". Passim is an uncertain locality. Loveridge (1948) assigned it questionably to Pasi Island [1°15'S 136°30'E] in Geelvink Bay. Wichmann (1910) provided a map plotting Meyer's itinerary, and it shows Meyer visited Bai von Passim (approx. 1°55'S 134°05'E; probably now Mawi Bay). This latter location is a possible source for the lost specimen; nonetheless, the uncertainty of the type locality, the single-line type description, and the destruction of the type specimen offer no clue to this taxon's identity, thus my recommendation for *nomen dubium* status of *Heteropus tricarinatus* var. *striata*.

***Heteropus beccarii* Peters & Doria, 1878**

I was unable to examine the holotype (Museo Civico . . . Genova, MSNG 28070, fide Capocaccia [1961]) of this taxon; however, the description of a large, boldly colored *Carlia* leaves no doubt to the proper assignment of the name.

***Heteropus luctuosus* Peters & Doria, 1878**

I also was unable to examine the holotype (Museo Civico . . . Genova, MSNG 28021, *fide* Capocaccia [1961]) of this taxon. The description indicates that the holotype is an adult female, and the description of color, scalation, and size matches these traits in Central Province *Carlia* "*fusca.*"

***Lygosoma atrogulare* Ogilby, 1890**

I was unable to locate the syntypes of this taxon. Presumably, they were deposited in the Australian Museum, but they were not located in the 1970s when Cogger (1979) assembled a type catalogue for the AMS herpetological collection. Glenn Shea (*in litt*., Aug. 2003) reports the likely rediscover of the type series. The *Carlia* specimens (AMS R852-859, R924-944) were assigned catalog numbers just as Ogilby left the museum in 1890, but no data were entered for them. I have not examined these specimens, and I suspect that only the R852-859 series represent the syntypes. Ogilby did not mention how many specimens he had in hand for his description, but he did state: "The number of specimens at my disposal is not sufficient to warrant an anatomical dissection of two examples, with the view of verifying the sex . . ." This statement suggests that Ogilby based his description only on the smaller series of 8 specimens, not on two series totaling 29 specimens.

Ogilby's description matches specimens from the Inawi sample (#36), and Ogilby's specimens derived from the former St. Joseph River District. Inawi is a Mekeo village on the coastal plains near the Angabunga or St. Joseph River. Thus, *L. atrogulare* Ogilby is a junior synonym of *Heteropus luctuosus* Peters and Doria.

***Lygosoma nigrigulare* Boulenger, 1898**

I was able to examine only a single type specimen, BMNH 1946.8.17.67; 2 others are presumably extant in Genova, MSNG 29142 (*fide* Capocaccia [1961]). Boulenger mentioned 3 specimens although he gave measurements for a single specimen (76 mm SVL). The size data indicates that the measured specimen was a male, which could have been confirmed if Boulenger had mentioned chin and throat coloration. Because the BMNH specimen is available for examination, I designate it as the **lectotype** (an adult male, 66.1 mm SVL, 119 mm tail length). It is a presumed male (not dissected) with dark brown head and neck dorsally and laterally, and a dusky brown chin and throat. The name is a junior synonym of *Heteropus luctuosus* Peters and Doria.

***Leiolopisma pulla* Barbour, 1911**
The holotype, MCZ R7486, is a moderately well-preserved juvenile (47 mm SVL), sex undetermined. Barbour reported 42 scale rows at midbody and 32 fourth toe lamellae. The former count is exceptionally high for any New Guinea "*fusca*" and particularly for an individual from a north coast population. I observed 35 Midbody and 29 4ToeL in the holotype.

***Lygosoma fuscum babarense* Kopstein, 1926**
This form was described from 9 specimens from Tepa, Kepulauan Babar and 62 specimens from Saumlaki, Kepulauan Tanimbar. The Tanimbar part of the syntypic series has become dispersed (see Appendix: Table D for the syntypes that I have located and examined). I designate RMNH 5518 as the **lectotype** of *Lygosoma fuscum babarense* Kopstein; the remainder of Babar syntypic series recataloged as RMNH 25774-80). The lectotype is an adult male of 47.8 mm SVL from Tepa, Babar, Kepulauan Babar. The selection of the lectotype restricts the type locality to Tepa.

***Lygosoma fuscum diguliense* Kopstein, 1926**
Kopstein based his description on 19 specimens from "Asike," on the Digul River. I located 18 specimens designated as syntypes in 4 museums: BMNH 1946.8.16.58; MCZ R38977-979, R38981, 1 without tag; NMW 9954, 16632; RMNH 5804, 5509 (9 specimens). The adult male (53.8 mm SVL, 92mm tail length) from the RMNH 5509 series is selected as the **lectotype**; others from that series are recataloged as RMNH 25765-772.

***Lygosoma* (*Leiolopisma*) *fuscum jamnanum* Loveridge, 1948**
Loveridge identified the holotype, MCZ R7677, as a female. It is a male (by dissection) and 45.7 mm SVL.

Taxa Recognized

Carlia Gray

Heteropus Duméril & Bibron, 1839: 757, not *Heteropus* Fitzinger, 1826 (see explanation in introduction to "*Carlia*: An Analysis" section). Type species: *Heteropus fuscus* D&B, 1839 and *Heteropus Peronii* D&B, 1839; restricted to *Heteropus fuscus* by Fitzinger (1843).
Carlia Gray, 1845: 271. Type species: *Mocoa melanopogon* Gray, 1845 by monotypy (see Greer [1975]).
Myophila de Vis, 1884: 77. Type species: *Myophila vivax* de Vis, 1884 by monotypy.

Definition: *Carlia* is a group III lygosomine skink with a beta palate, 11 or 13 premaxillary teeth, and fore and hind digits covered dorsally by a single row of scales (Greer, 1974). It shares a unique hemipenial morphology of an elongate projection from the base of the everted hemipenis with *Lampropholis*, *Lygisaurus*, and *Saproscincus* (Greer, 1989). Within this 4 taxa group, *Carlia* and *Lygisaurus* share a four-digit forefoot (loss of digit I) and a single (fused) frontoparietal scale. *Carlia* differs from *Lygisaurus* by hindlimb length subequal to or greater than trunk length (HndlL/TrunkL > 90%) and longer digits (4ToeL/TrunkL > 28%).

Content: 35+ species.

Distribution: Species diversity is greatest in Australia with 22 species currently recognized. Australian taxa occur in a broad band from the Northwest Cape, Western Australia north and eastward to the mountains of northern Victoria. In the northern half of this distribution, 2 or more species commonly occur locally and often syntopically. More than a dozen species occur in New Guinea and its associated islands; only a few localities have sympatric or parapatric species and in most localities, a single species occurs. The Bougainville populations (Buka, Sohano, Shortland I.) of the Solomons biotic realm are likely human introductions (McCoy, 1986). Several species occur in the Mollucas and Lesser Sunda islands. Extralimital populations occur in Java (unpublished data, Zug), Palau, the Mariana Islands, Yap, and Kosrae.

Etymology: Gray (1845) provided no explanation.

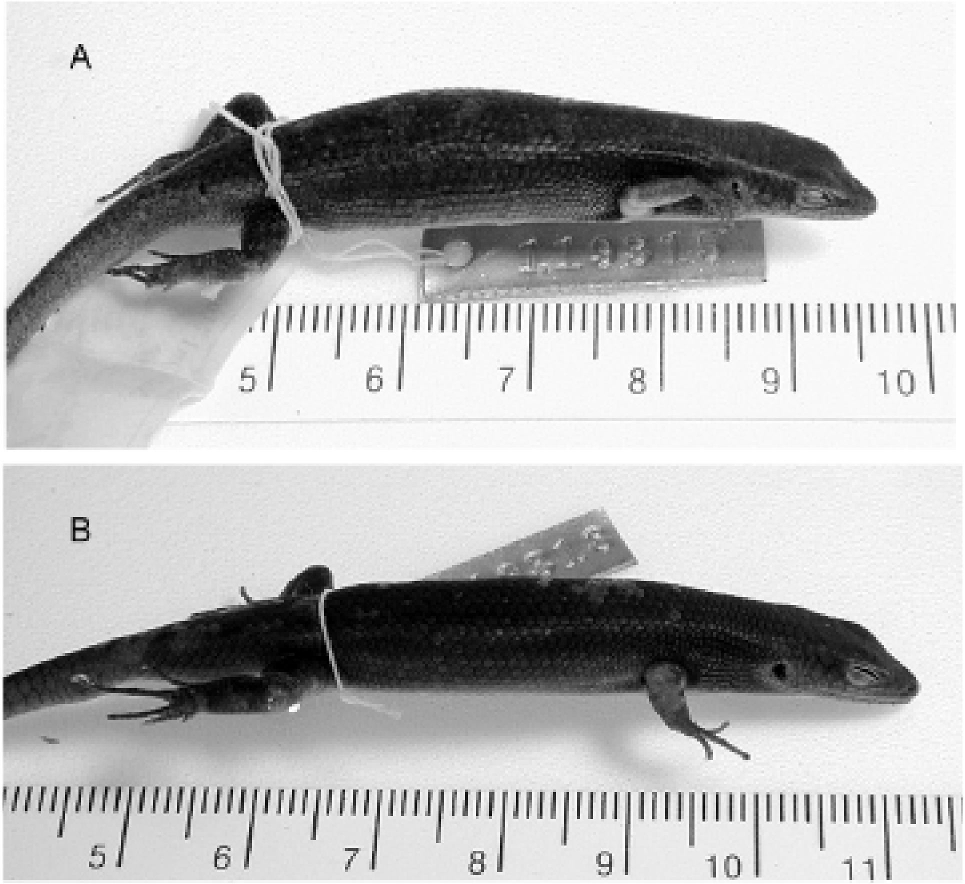

Figure 12. *Carlia fusca* from Toem, Irian Jaya. A, gravid female (USNM 119315; 50.5 mm SVL) and B, adult male (USNM 119313; 54.0 mm SVL).

***Carlia fusca* (Duméril & Bibron)** Fig. 12

Heteropus fusca Duméril & Bibron, 1839: 759. Type locality: "les îles de Waigiou et de Rawack"; restricted to Waigeo by lectotype designation. Lectotype, MNHN 3036.

Heteropus tricarinatus Meyer, 1874: 133. Type locality: "New Guinea (Dore)." Neotype, ZMB 8784 (Ansur, Jobi [Yapen Island]); designation in preceding History & decision section.

Heteropus tricarinatus var. *striata* Meyer, 1874: 134. Type locality: "Neu-Guinea (Passim)." Holotype, SMTD 172 (destroyed). Nomen dubium.

Lygosoma (*Leiolopisma*) *fuscum jamnanum* Loveridge, 1948: 363. Type locality: "Djamna, Papua." Holotype, MCZ R7677.

Description. A moderate-sized *Carlia* ranging in adult size from 49 to 60 mm SVL (females 49.1–56.9; males 48.8–59.5) with HeadL 21–25%, TrunkL 38–53%, and HndlL 40–55% of SVL, and 78–123% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, TrunkL/SVL, HndlL/SVL, and TrunkL/HndlL. Head and nuchal scales smooth; interparietal always present; 4 Supoc, 6–9 Supcil, 7–12 Eyeld, 7 Suplab, 5th (rarely 6th) BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening oblong vertical to oblique with 1–5 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–51 Dorsal, 30–36

Figure 13. *Carlia pulla* from Vanimo, Papua New Guinea. Gravid female (USNM 232092; 56.5 mm SVL).

Midbody. Subdigital lamellae undivided, smooth: 18–23 3FingL, 24–32 4ToeL.

Juvenile dorsum uniform brown to brown with scattered white spots or dark flecks or lines, distinct dorsolateral white stripe from eye to midtrunk, midlateral white stripe variously developed and dark brown lateral band on neck to at least midtrunk; venter cream to ivory. Adults monomorphic (Fig. 12), from uniform brown dorsum and sides to those with remnant of dorsolateral white stripe on side of head and neck, lateral brown band variously faded, midlateral stripe absent; venter cream to ivory.

Distribution. Waigeo, north coast of Irian Jaya from Vogelkop east to Toem and Jamna I. area, including Japen I., and likely southeastern part of Vogelkop to Ayamura area.

Description of lectotype (MNHN 3036). Adult, sex unknown; fragile and bleached. Metrics: 56.9 mm SVL; tail, incomplete; 13.6 mm HeadL; 21.4 mm TrunkL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 6 Supcil, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong vertical with 2 AuricN, bluntly pointed, on anterior margin. Trunk scales weakly tricarinate dorsally and laterally, 45 Dorsal, 32 Midbody; subdigital lamellae undivided and smooth. Specimen too faded for description of color pattern.

Variation. All larger samples (#1, 3, 6) display sexual dimorphism in several morphometric characters, and Waigeo and Toem show significant differences between female and male SVLs (means: 52.7 & 56.3 mm, 50.7 & 53.8 mm, respectively), but there is no dimorphism in coloration. For both mensural and meristic traits, the intrasample variation of larger samples equals or nearly equals the variation among samples. Mean SVL ranges from 49.6 to 52.7 mm, females, and 51.7 to 56.3 mm, males. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6–6.5, 8–9.5, & 3–4, respectively), and Interp is invariably present. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 48–49, 32–35, 20–21.5, & 27–30, respectively).

Etymology. Species name derives from the Latin *fuscus* for tawny or dusky.

Comparison to related species. *Carlia fusca* populations differ from those of the larger bodied *C. pulla*, *C. luctuosa*, and *C. beccarii,* and the smaller bodied *C. aramia*, *C. babarensis*, *C. leucotaenia*, and *C. tutela* by adult females averaging 50 to 53 mm SVL; females and males are on the average equal-sized. *C. fusca* populations share: an average of 32 to 34 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 20 to 22 3FingL with all except *C. beccarii*; and an average of 27 to 30 4ToeL with all except *C. beccarii C. longipes*, and *C. luctuosa*. Unlike juvenile *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. beccarii*, *C. eothen*, *C. leucotaenia*, *C. longipes*, *C. pulla, C. tutela,* juvenile *C. fusca* have a short dorsolateral light stripe from eye to midneck, occasionally to anterior trunk; and unlike *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. beccarii*, *C. diguliensis*, *C. eothen*, *C. leucotaenia*, *C. longipes*, *C. luctuosa*, *C. mysi*, *C. pulla, C. tutela*, the midlateral light stripe of juvenile *C. fusca* is present only occasionally on the neck and rarely from eye to anterior trunk. Adult *C. fusca* females commonly retain the dorsolateral stripe on head and neck but lose the midlateral stripe, sharing this adult female coloration with some populations of *C. eothen*, *C. leucotaenia C. longipes*, and *C. mysi*. Adult *C. fusca* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

***Carlia pulla* (Barbour)** Fig. 13

Leiolopisma pulla Barbour, 1911: 15. type locality: "Humboldt's Bay, Dutch New Guinea." Holotype, MCZ R7486.

Description. A moderate-sized *Carlia* ranging in adult size from 46 to 65 mm SVL (females 46.6–60.5; males 46.0–64.6) with HeadL 21–26%, TrunkL 43–53%, and HndlL 41–55% of SVL, and 68–107% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, PalpbD/EarD, TrunkL/SVL, HndlL/SVL, TrunkL/HndlL, and Dorsal. Head and nuchal scales smooth; interparietal usually (>95%) present; 4 Supoc, 7–9 Supcil, 8–13 Eyeld, 7 (rarely 8) Suplab, 5th (rarely 6th) BlwEye, and 6 or 7 Inflab on each side. Ear opening oblong vertical to oblique with 2–7 AuricN, bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–51 Dorsal, 32–37 Midbody. Subdigital lamellae undivided, smooth: 20–23 3FingL, 25–32 4ToeL.

Juvenile dorsum either nearly uniform brown or distinctly striped in light browns, distinct dorsolateral white stripe widening on tail and above dark brown lateral band on neck and trunk, midlateral stripe interrupted as series of white spots and stripe-fragments; venter cream to ivory. Adults somewhat dimorphic (Fig. 14), females retaining faded lateral pattern and males largely uniform; brown dorsum and sides, although both sexes with distinct broad light dorsolateral stripe on tail; venter cream to ivory.

Distribution. North coast of New Guinea from Sermowai River eastward to Aitape.

Description of holotype (MCZ R7486). Juvenile male; moderately well preserved and darkened. Metrics: 47.0 mm SVL; 83 mm tail, regenerated; 11.0 mm HeadL; 21.3 mm TrunkL; 24.3 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 11 Eyeld, 7 Suplab, 5th BlwEye, and 8 Inflab on right side. Ear opening oblong vertical with 5 AuricN, bluntly pointed, on anterior and dorsal margin. Trunk scales weakly tricarinate dorsally and laterally, 48 Dorsal, 35 Midbody; subdigital lamellae undivided, smooth: 22 3FingL, 28 4ToeL. Faded uniform brown dorsum with dorsolateral light stripe above brown lateral band, midlateral stripe complete at axilla; venter grayish cream.

Variation. All samples display sexual dimorphism in several morphometric characters, and Humboldt and Vanimo show significant differences between female and male SVLs (means: 55.4 & 60.3 mm, 58.2 & 61.6 mm, respectively), and all populations are somewhat dimorphism in coloration. For both mensural and meristic traits, the intrasample variation of individual samples generally equals the variation among samples. Mean SVL ranges from 49.8 to 58.2 mm, females, and 51.7 to 56.3 mm, males; Aitape adults average smaller than the 2 westward samples, but the former sample is small. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6–6.5, 9–11, & 3–5, respectively), and Interp is rarely absent. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 47.5–49, 34–35, 21–22, & 28.5–30, respectively).

Etymology. Barbour provided no explanation. Presumably, he selected the Latin *pullus* for dark-colored or blackish, because he noted the color of the type as "dark mahogany brown above."

Comparison to related species. *Carlia pulla* populations differ from those of the larger bodied *C. beccarii* and *C. luctuosa*, and the smaller bodied *C. aramia*, *C. babarensis*, *C. leucotaenia*, and *C. tutela* by adult females averaging 50 to 58 mm SVL; females and males are on the average equal-sized. *C. pulla* populations share: an average of 34 to 35 Midbody with *C. aenigma* and *C. eothen*; an average of 21 to 22 3FingL with all except *C. beccarii*; and an average of 29 to 30 4ToeL with all except *C. beccarii C. longipes*, and *C. luctuosa*. Unlike juvenile *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. beccarii*, *C. eothen*, *C. leucotaenia*, *C. longipes*, *C. tutela*, juvenile *C. pulla* have a dorsolateral and a midlateral light stripe from eye to axilla, and continuing along anterior trunk as a series of dashes and spots. Adult *C. pulla* females retain the dorsolateral stripe on head and neck and the midlateral stripe as a series of spots on the neck, sharing this adult female coloration with some populations of *C. mysi*. Adults commonly retain broad dorsolateral stripes on the tail; this pattern occurs in some *C. eothen* and *C. mysi*. Adult *C. pulla* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

SEPIK POPULATIONS [unassigned]

Description. A moderate-sized *Carlia* ranging in adult size from 52 to 58 mm SVL (females 55.7–57.8; males 51.6–57.2) with HeadL 21–25%, TrunkL 43–53%, and HndlL 44–52% of SVL, and 40–94% PalpbD/EarD; sexually dimorphic in HeadL and 3FingL. Head and nuchal scales smooth; interparietal always present; 4 Supoc, 8–9 Supcil, 8–13 Eyeld, 6 (rarely 7) Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 5) Inflab on each side. Ear opening oblong vertical to oblique with 0–3 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–48 Dorsal, 32–34 Midbody. Subdigital lamellae undivided, smooth: 20–23 3FingL, 24–31 4ToeL.

Juvenile pattern similar but less intense than pulla pattern and midlateral row of fewer white spots; venter cream. Adults monomorphic, uniform brown dorsum and sides with some dark brown flecks on dorsum; venter grayish cream.

Comment. Perhaps, I have been too influenced by the classification accuracy of the discriminant analyses, especially relative to the high variation and classification scores that are encompassed by the populations within the proposed "mysi" taxon. Nevertheless, I do not assign a specific identity to this population in order to emphasize its differences and the enormity of the sampling gap for the Sepik drainage system.

Distribution. Data presently available only for the Wewak population (#12).

Comparison to related species. Earlier, I noted a possible relationship of the Baiyer River sample (#39) with the Wewak one. They differ little in scalation and overall size although the Baiyer sample is distinctly sexually dimorphic in SVL. The best match for color pattern is Wewak with the other coastal populations.

Carlia mysi new species Fig. 14

Holotype. USNM 119269, adult male from Papua New Guinea, Morobe Province, Gusika [near Finschhafen], collected by William H. Stickel, 11–18 April 1944. **Paratypes**. IRSNB 2584, locality data same as holotype, collected by William H. Stickel and Lawrence Lit Law, 8–13 May 1944. USNM 119259-261, Papua New Guinea, Morobe Province, Finschhafen [6°34"S 147º51"E], collected by William H. Stickel, 2–3 April 1944. USNM 119262-266, 119268, 119270-295, locality data same as holotype, 4–30 April 1944. USNM 119296-298, locality data same as holotype, collected by William H. Stickel and Lawrence Lit Law, 8–13 May 1944. USNM 119299-302, locality data same as holotype, collected by William H. Stickel, 15 May 1944. Juveniles, USNM 119268, 119278-288, 119294-295; adult females, USNM 119259, 119263-265, 119270-271, 119274-276, 119291-92, 119298, 119300-302; adult males, IRSNB 2584, USNM 119260-62, 119272-273, 119277, 119293, 119296-297, 119299.

Description. A moderate-sized *Carlia* ranging in adult size from 45 to 61 mm SVL (females 45.0–61.3; males 45.2–62.3) with HeadL 20–25%, TrunkL 42–53%, and HndlL 38–52% of SVL, and 74–129% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, PalpbD, EarD, HndlL, HeadL/SVL, TrunkL/SVL, HndlL/SVL, TrunkL/HndlL, AuricN, Dorsal, 3FingL, and 4Toel. Head and nuchal scales smooth; interparietal rarely absent; 4 (rarely 5) Supoc, 7–9 Supcil, 8–14 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th or 6th) BlwEye, and 6 (rarely 5 or 7) Inflab on each side. Ear opening oblong vertical to oblique with 1–6 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 42–52 Dorsal, 28–36 Midbody. Subdigital lamellae undivided, smooth: 16–24 3FingL, 23–34 4ToeL.

Figure 14. Holotype of *Carlia mysi* from Gusika, Papua New Guinea. Adult male (USNM 119269; 59.4 mm SVL).

Juvenile pattern variable, populations from uniform brown dorsum and sides through distinct pulla-like pattern to bold dorso- and midlateral white stripes enclosing darker brown lateral band; venter cream to ivory. Adults predominantly monomorphic, but in some populations females and occasionally males retaining juvenile pattern of lateral striping to near uniform brown dorsum and sides; venter cream to ivory.

Distribution. North coast of New Guinea from Manam Island eastward to Cape Vogel, and the islands of the Bismarck Archipelago; the Bougainville populations potentially introduced (McCoy, 1980).

Description of holotype (USNM 119269). Adult male; well preserved and somewhat darkened (Fig. 14). Metrics: 59.4 mm SVL; 102 mm tail, regenerated; 13.8 mm HeadL; 28.6 mm TrunkL; 28.8 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 11 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong vertical with 4 AuricN, bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally, 49 Dorsal, 34 Midbody; subdigital lamellae undivided, smooth: 23 3FingL, 32 4ToeL. Superficially uniform brown dorsally and laterally; dorsum of trunk with pair of parasagittal light brown stripes from midneck to midtrunk and dorsolateral light brown stripes from above eye to; ventrally chin and throat light dusky, remainder of venter whitish.

Variation. *Carlia mysi* occupies the largest area of any NG "*fusca*;" yet in mensural and meristic traits, it shows no greater variation than species with distributions one half or quarter its size. All larger samples (*n*>12) display sexual dimorphism but to varying degrees from 3 dimorphic traits at Finschhafen to 10 at Madang. Only New Ireland and Menapi show significant differences between females and male SVLs (means: 49.0 & 51.4 mm, 51.6 & 54.5 mm, respectively). For both mensural and meristic traits, the intrasample variation of larger samples encompasses the variation among samples. Mean SVL ranges from 47.4 to 59.3 mm, females, and 49.4 to 63.1 mm, males. The coastal samples (#13–17, 24–27) average 3–4 mm larger than the island ones (#18–23). Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 6–8, 6.5–7, 6, 9–12, & 3–4, respectively); Interp is always or usually present in most populations, although at Karkar it is absent in 35% of sample. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 47–50, 32–34, 19–22, & 27–30, respectively).

Etymology. The specific name honors Benoît Mys (sounds like: maize). Mys had a consuming passion for the biology and evolution of New Guinean skinks, especially those of the north coast of Papua New Guinea (Mys, 1988). He died in a vehicle accident in 1990 while doing fieldwork in northern PNG.

Comparison to related species. *Carlia mysi* populations are variable in average adult size of females, ranging from 48 to 57 mm SVL; only *C. beccarii* and *C. luctuosa* are larger and *C. leucotaenia* and *C. tutela* smaller. Female and male *C. mysi* are on the average equal-sized. *Carlia mysi*

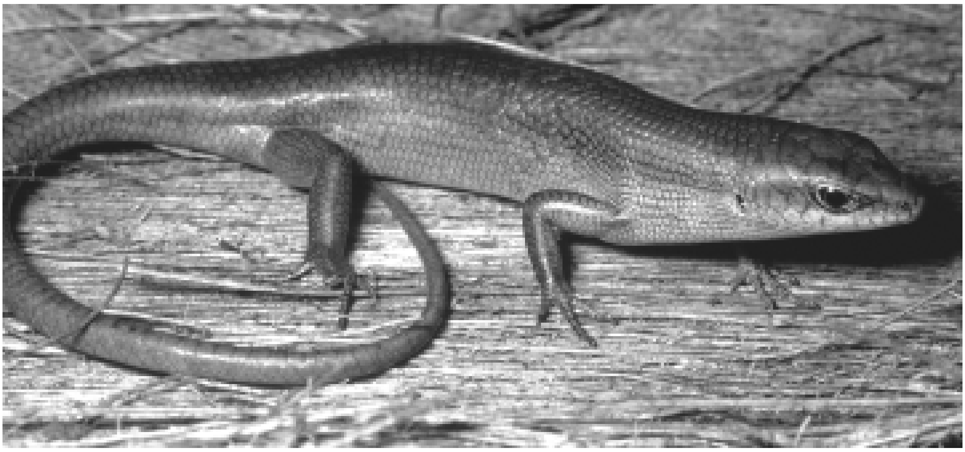

Figure 15. Paratype of *Carlia ailanpalai* from Los Negros Island, Admiralty Islands, Papua New Guinea. Adult male (USNM 560088; 52.6 mm SVL); photographed by C. C. Austin).

populations share: an average of 32 to 35 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 19 to 22 3FingL with all except *C. beccarii*; and an average of 27 to 30 4ToeL with all except *C. beccarii C. longipes*, and *C. luctuosa*. Unlike juvenile *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. beccarii*, *C. eothen*, and *C. tutela*, juvenile *C. mysi* of most populations have a dorsolateral light stripe from eye to axilla, occasionally to anterior trunk; a few populations lack this stripe. Unlike *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. beccarii*, *C. digulensis*, *C. eothen*, *C. leucotaenia*, *C. longipes*, and *C. luctuosa*, most juvenile *C. mysi* lack a midlateral light stripe; occasionally, it occurs on the neck as a series of light spots and dashes. Adult *C. mysi* females commonly retain the dorsolateral stripe on head and neck but lose the midlateral stripe, sharing this adult female coloration with some populations of *C. eothen*, *C. leucotaenia*, *C. longipes*, and *C. fusca*. Adult *C. mysi* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

Carlia ailanpalai **new species** Fig. 15

Holotype. USNM 560085, adult female from Papua New Guinea, Manus Province, Los Negros Island, Salami village [2°01.96'S 147º26.05'E], collected by Christopher C. Austin, 28 Aug. 2001. **Paratypes**. BPBM 1657, Papua New Guinea, Los Negros Island, collected by Warren H. Wagner, Jr., 1945; IRSNB 2581-83, Papua New Guinea, Manus Island, Yiringou [2°05'S 147°7'E], collected by B> Mys, 15–22 April 1985. MCZ R137674, Papua New Guinea, Manus Island, Lorengau [2°01'S 147°16'E], collected by Fred Parker, 6 May 1972; MCZ R141312-313, Papua New Guinea, Manus Island, Lorengau [2°01'S 147°16'E], collected by Fred Parker, 23 June 1972. PNGM 24693, 24696-699, 24701, 24703-706, Papua New Guinea, Rambusto Island, Lengendrowa [2°06'S 147°05'E], collected by Karol Kisokau, 5 January 1972. USNM 120889-891, Papua New Guinea, Manus Province, Ponam Island [1°54'S 146º54'E], collected by D.H. Johnson, 15 August 1944; USNM 122324, Papua New Guinea, Manus Province, Los Negros Island [2°00'S 147º26'E], collected by W. L. Necker, Feb. 1945; USNM 560086, collection data same as holotype; USNM 560087, Papua New Guinea, Manus Province, Los Negros Island, Riu Riu village [2°02.95'S 147º24.12'E], collected by Christopher C. Austin, 28 Aug. 2001; USNM 560088-091, Papua New Guinea, Manus Province, Manus Island, halfway between Yiringau and Tingau villages, [2°05.76'S 147º06.33'E], collected by Christopher C. Austin, 30 Aug. 2001; USNM 560093, Papua New Guinea, Manus Province, Rambutyo Island, Penchal village, [2°19.70'S 147º46.00'E], collected by Christopher C. Austin, 1 Sept. 2001. Juvenile female, BPBM 1657; adult females, IRSNB 2581-82, PNGM 24693, 24698, 24701, 24705-706, USNM 1 20889-890, 560085, 560088, 560090; adult males, IRSNB 2583, PNGM 24696-697, 24699, 24703-704, USNM 120892, 122324, 560086-087, 560089, 560091, 560093.

Description. A moderate-sized *Carlia* ranging in adult size from 46 to 59 mm SVL (females 49.3–57.8; males 45.8–59.3) with HeadL 20–24%, TrunkL 42–52%, and HndlL 40–52% of SVL, and 77–123% PalpbD of EarD. Sexually dimorphic in the following traits: HeadL, PalpbD, HndlL, HeadL/SVL, TrunkL/HndlL, PalpbD/EarD, and Midbody. Head and nuchal scales smooth; interparietal rarely absent; 4 (rarely 5) Supoc, 7–9 Supcil, 7–12 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th or 6th) BlwEye, and 6 (rarely 5 or 7) Inflab on each side. Ear opening oblong vertical to round with 1–8 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–51 Dorsal, 30–36 Midbody. Subdigital lamellae undivided, smooth: 18–24 3FingL, 26–34 4ToeL.

Juveniles with uniform brown dorsum and sides; in some individuals, dark edging of scales produces dark lines; no light dorso- and midlateral stripes; venter cream to ivory. Adults monomorphic, often uniform brown dorsum and sides; venter cream to ivory, rarely dusky throat.

Distribution. Main group of Admiralty Islands, centered on Manus Island. Extralimital in Guam, Mariana Islands, Yap, and Kosrae.

Description of holotype (USNM 560085). Adult female; well preserved. Metrics: 52.6 mm SVL; 72 mm tail, entire; 11.5 mm HeadL; 25.0 mm TrunkL; 24.3 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 7 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening circular with 5 AuricN, bluntly pointed, on anterior and dorsal margin. Trunk scales striated to weakly tricarinate dorsally and laterally, 48 Dorsal, 34 Midbody; subdigital lamellae undivided, smooth: 23 3FingL, 31 4ToeL. Superficially uniform brown dorsally and laterally; scales black edged with light brown centers on neck from ear to axilla; ventrally chin and throat light dusky, remainder of venter whitish.

Variation. The multiple island sample of *Carlia ailanpalai* shows a low intraspecific variation. Four nonratio traits are dimorphic as noted above in the description, males larger in all. Adult females and male SVLs differ slightly (means 52.8 and 54.4 mm; ranges 49.3–57.8, 45.8–59.3 mm, respectively). Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation (medians: 8, 7, 6, 9, & 3; ranges 7–9, 6–8, 5–7, 7–12, &1–8, respectively); Interp is rarely absent. Dorsal, Midbody, 3FingL, and 4ToeL also show little variation (medians: 48, 32, 22, & 29; 45–50, 30–36, 18–24, & 26–34, respectively).

Etymology. The specific name derives from the New Guinean pidgin *ailan* for island and *palai* for lizard. It is proposed as a noun in apposition.

Comparison to related species. *Carlia ailanpalai* populations differ from those of the larger bodied *C. beccarii, C. eothen*, and *C. luctuosa,* and the smaller bodied *C. aramia*, *C. babarensis*, *C. leucotaenia*, and *C. tutela* by adult females averaging 51 to 52 mm SVL; females and males are on the average equal-sized. *Carlia ailanpalai* populations share: an average of 32 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 22 3FingL with all except *C. beccarii*; and an average of 30 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. Unlike juveniles of all other described *fusca* complex members, *C. ailanpalai* are unicolor dorsally and laterally, lacking any indication of light stripes. Adult male and female *C. ailanpalai* retain the uniform coloration although black scale edging may create the appearance of multiple thin stripes; uniform coloration develops in some adults of *C. eothen*, *C. fusca*, *C. leucotaenia, C. longipes*, *C. mysi*, and *C. tutela*. Adult *C. ailanpalai* have light chins, throats (occasionally dusky), and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

***Carlia eothen* new species** Fig. 16

Holotype. AMS R47147, adult male from Papua New Guinea, Milne Bay Province, Trobriand Islands, Kiriwina Island [8°36'S 151º08'E], collected by Harold Heatwole, 15 March 1969. **Paratypes**. AMNH 20920, Papua New Guinea, Milne Bay Province, Trobriand [Kiriwina], collected by S.B. Fellows[?], 1897; AMS R47145-146, R47148-150, R47154-160, collecting data same as holotype; USNM 192883, 525758, Papua New Guinea, Milne Bay Province, Trobriand Islands, Kuia Island [= Kuyau I., 8°35"S 150º52"E], collected by Bruce B. Collette, 13 June 1970; USNM 560092, collecting data same as holotype. Juveniles, AMS R47150, R47156; adult females, AMS R47145-146, R47148, R47154, R47157, R47161; adult males, AMNH 20920, AMS R47147, R47149, R47155-156, R47158-160, USNM 192883, 525758, 560092.

Figure 16. Holotype of *Carlia eothen* from Kiriwina Island, Trobriand Islands. Adult male (AMS R47147; 65.0 mm SVL).

Description. A moderate-sized *Carlia* ranging in adult size from 46 to 69 mm SVL (females 46.4–60.5; males 48.7–68.6) with HeadL 21–25%, TrunkL 39–56%, and HndlL 43–56% of SVL, and 65–142% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, EarD, HndlL, HeadL/SVL, HndlL/SVL, TrunkL/HndlL, and Midbody. Head and nuchal scales smooth; interparietal usually (>98%) present; 4 Supoc, 6–10 Supcil, 8–12 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th or 6th) BlwEye, and 6 (rarely 7 or 8) Inflab on each side. Ear opening oblong vertical to oblique with 2–5 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–53 Dorsal, 31–40 Midbody. Subdigital lamellae undivided, smooth: 18–25 3FingL, 25–34 4ToeL.

Juvenile coloration from boldly six-striped to faded pulla dorsum and variable dorsolateral and midlateral light stripes to series of spots enclosing a dark lateral band. This variation is regional, not local. Similarly, adults display a variety of patterns regionally, and local populations range from mono- to dimorphic. See variation below.

Distribution. Eastern Papua New Guinea from around Milne Bay into the adjacent island groups, d'Entrecasteux Ids., Trobriand Ids., Muyua group, and Louisiade Archipelago.

Description of holotype (AMS R47147). Adult male; well preserved and retaining coloration. Metrics: 65.0 mm SVL; 89 mm tail, regenerated; 14.8 mm HeadL; 28.9 mm TrunkL; 33.5 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 10 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong vertical with 2 AuricN, bluntly pointed on anterior margin. Trunk scales weakly tricarinate dorsally and laterally, 47 Dorsal, 33 Midbody; subdigital lamellae undivided, smooth: 19 3FingL, 25 4ToeL.

Superficially uniform brown dorsally and laterally (Fig. 16); middorsal rows of scales with irregularly dark edges, especially posteriorly yielding a somewhat speckled appearance; faded dorsolateral stripe from behind ear to tail; indistinct midlateral light stripe on neck and indistinct lateral dark band from ear to midtrunk; lower temporal area and lip not dark; venter cream.

Variation. All samples display slight sexual dimorphism in a few morphometric characters; D'Entrecasteaux and Muyua samples have significant differences SVLs between female and male (means: 54.2 & 58.2 mm, 55.8 & 61.6 mm, respectively). Some populations display color dimorphism. For both mensural and meristic traits, the intrasample variation of larger samples equals the variation among samples. Mean SVL ranges from 52.3 to 56.0 mm, females, and 52.2 to 60.3 mm, males. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 9–10, & 3–4, respectively), and Interp is invariably present in all, except for a rare absence in D'Entrecasteaux Ids. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 48–49.5, 33–36, 20–23, & 28.5–31, respectively).

Juveniles throughout the region possess some degree of lateral striping. The strongest striping occurs on the mainland with six-striped juveniles, paired parasagittal, dorsolateral, and midlateral light stripes with distinct dark lateral band from eye to inguen. In D'Entrecasteaux Ids., juveniles have complete or nearly complete dorsolateral and midlateral stripes. On mainland, adjacent islets, Muyua Group, and Louisiade Archipelago, these stripes are variably present, incomplete, or absent. Trobriand juveniles have a faded pulla dorsum and usually complete dorso- and midlateral stripes from eye to inguen, occasionally light stripes broken from anterior trunk to inguen.

Adults show varying degrees of local sexual dimorphism. The basic monomorphic pattern of uniform brown dorsum, slightly darker sides, and remnants of light dorsolateral stripe anteriorly occurs on mainland, D'Entrecasteaux Ids., and Louisiade Archipelago. Mainland dimorphism shows females with the preceding pattern and males with dark heads, chins, and throats. Muyua and Trobriand specimens have nearly uniform brown females (large), males similar except for some with dark patch on cheek, lips, anterior neck, and overlapping onto chin and throat; smaller adults, particularly females, retain a less intense juvenile pattern.

Etymology. From the Greek *eothen* (feminine) for in the morning or eastern, in allusion to these populations being the easternmost naturally occurring *Carlia*.

Comparison to related species. *Carlia eothen* populations differ from those of the larger bodied *C. beccarii* and *C. luctuosa,* and the smaller bodied *C. aramia*, *C. babarensis*, *C. leucotaenia*, and *C. tutela* by adult females averaging 52 to 56 mm SVL; size is variable in adults with equal-sized females and males in some populations and males larger in others. *C. eothen* populations share: an average of 33 to 36 Midbody with other *fusca* complex species except *C. luctuosa*; an average of 20 to 23 3FingL with all except *C. beccarii*; and an average of 27 to 31 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. Unlike juvenile *C. aenigma*, *C. ailanpalai*, *C. babarensis*, *C. beccarii*, *C. fusca*, *C. luctuosa*, *C. longipes* and *C. pulla*, juvenile *C. eothen* usually have a dorsolateral light stripe from eye to inguen; and unlike *C. aenigma*, *C. ailanpalai*, *C. babarensis*, *C. beccarii*, *C. diguliensis*, *C. fusca*, *C. leucotaenia*, *C. longipes*, *C. luctuosa* and *C. tutela*, the midlateral light stripe of juvenile *C. eothen* is variable, either complete from eye to inguen or eye to axilla with series of light spots on trunk. Adult *C. eothen* females commonly retain the dorsolateral stripe on head and neck but lose the midlateral stripe, sharing this adult female coloration with some populations of *C. fusca*, *C. leucotaenia C. longipes*, and *C. mysi*. Adult *C. eothen* commonly have dusky chins and throats, and light venters, differing from the light underside of *C. babarensis*, *C. beccarii*, *C. diguliensis*, *C. fusca*, *C. longipes*, *C. pulla*, *C. tutela*, and some populations of *C. aramia* and *C. mysi*.

Carlia luctuosa (Peters & Doria) Fig. 17

Heteropus luctuosus Peters & Doria, 1878: 364. Type locality: "al Monte Epa nel S. E. Nuova Guinea, poco lonanto dall' Isola Yule." Holotype, MSNG 28021.

Lygosoma atrogulare Ogilby, 1890: 94. Type locality: not specified in description, but elsewhere (p. 89); all specimens are reported to be derived from the " St. Joseph's River District; . . . about eighty miles to the north-west of Port Moresby,". Syntypes, AMS R852-859 (Papua New Guinea).

Lygosoma nigrigulare Boulenger, 1898: 700. Type locality: "Inawi." Lectotype, BMNH 1946.8.17.67.

Description. A large *Carlia* ranging in adult size from 54 to 78 mm SVL (females 53.6–75.4; males 57.1–77.7) with HeadL 21–25%, TrunkL 39–54%, and HndlL 46–60% of SVL, and 62–111% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, HndlL/SVL, TrunkL/HndlL, PalpbD/EarD, Dorsal, Midbody, 3FingL, 4ToeL, and Precl. Head and nuchal scales smooth; interparietal occasionally absent; 4 Supoc, 6–9 Supcil, 9–13 Eyeld, 7 (rarely 6 or 8)

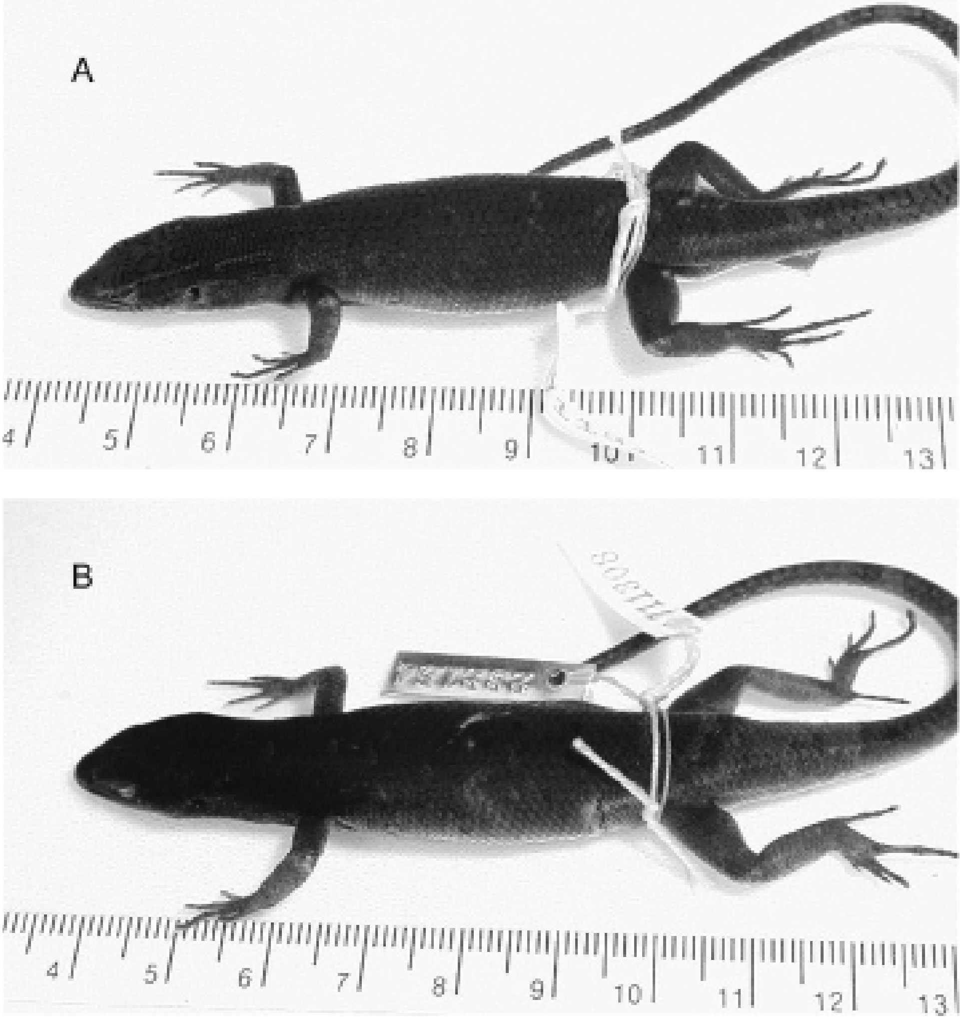

Figure 17. *Carlia luctuosa* from Inawi, Papua New Guinea. A, adult female (USNM 232164; 65.6 mm SVL) and B, male (USNM 232154; 71.5 mm SVL).

Suplab, 5th (rarely 4th or 6th) BlwEye, and 6 (rarely 5, 7, 8, or 9) Inflab on each side. Ear opening oblong vertical to oblique with 2–7 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 47–54 Dorsal, 36–42 Midbody. Subdigital lamellae undivided, smooth: 19–27 3FingL, 27–38 4ToeL.

Juvenile dorsum brown with some white spots and black flecking on trunk, broad dark brown band from head to inguen and containing numerous white spots and bars on trunk, dorso- and midlateral white stripes on head and anterior neck becoming irregular spotting thereafter; venter cream to ivory. Adults dimorphic (Fig. 17), females with dark brown dorsum and sides, somewhat darker anteriorly, and dorso- and midlateral light stripes usually evident on head and anterior neck; males uniformly black on head to shoulders, dark brown thereafter; venter grayish cream or ivory in females, chin and throat black in males.

Distribution. Central Province of Papua New Guinea from Kapakapa westward to Angabunga River area, sea level to 1500 m.

Figure 18. *Carlia fusca* complex member from the Papuan highlands (Chimbu Prov., Kundiawa). Gravid female (USNM 166263; 55.1 mm SVL).

Description of holotype (MSNG 28021). Not seen.

Variation. All samples display sexual dimorphism in several morphometric characters, including significant differences between female and male SVLs (male means 5–8 mm larger than females), and all have color dimorphism. For both mensural and meristic traits, the intrasample variation of Inawi (#36) slightly exceeds the variation among the other samples; it is also the largest sample. Mean SVL ranges from 56.0 to 65.8 mm, females, and 63.7 to 72.4 mm, males. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6–7, 10–11, & 4.5–5, respectively), and Interp is always present in 2 samples but only 50% at Inawi. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 49–50, 37–38, 22–23, & 31–33, respectively).

Etymology. Peters & Doria offered no explanation for choosing the Latin adjective *luctuosus* for sorrowful or mournful. Their choice presumably refers to the black “hood” of adults.

Comparison to related species. *Carlia luctuosa* populations differ from those of the smaller bodied *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. diguliensis*, *C. eothen*, *C. fusca*, *C. leucotaenia*, *C. longipes*, *C. mysi*, *C. pulla*, and *C. tutela* by adult females averaging 56 to 66 mm SVL; males are distinctly larger than females as occurs elsewhere only in *C. beccarii. C. luctuosa* populations have more Midbody (37 to 38) than all other *fusca* complex species except *C. beccarii*, and share an average of 22 to 23 3FingL with all except *C. beccarii*; and an average of 31 to 33 4ToeL with only *C. beccarii* and *C. longipes.* Unlike juveniles in all other *fusca* complex members, juvenile *C. luctuosa* have a dorsolateral and a midlateral light stripe from eye to ear and no light stripes beyond, although the axilla and anterior trunk are mottled with irregular white blotches. Adult *C. luctuosa* females commonly retain the juvenile stripes on head to ear although indistinct owing to darkening of anterior third of body; males become strongly melanistic from shoulders forward, a coloration unknown in any other *fusca* complex species. Adult *C. luctuosa* have dark chins and throats, and dusky to light venters; *C. aenigma* and some populations of *C. aramia* and *C. eothen* have dusky chins and throats but not as intensely black as *C. luctuosa*.

HIGHLANDS POPULATIONS [unassigned] Fig 18

Description. A moderately large *Carlia* ranging in adult size from 48 to 62 mm SVL (females 47.8–59.8; males 50.9–62.3) with HeadL 20–25%, TrunkL 42–60%, and HndlL 42–54% of SVL, and 82–164% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, TrunkL/SVL, HndlL/SVL, Eyeld, Midbody, and 3FingL. Head and nuchal scales

Figure 19. Holotype of *Carlia aenigma* from Emeti, Papua New Guinea. Adult female (MCZ R141880; 53.3 mm SVL).

smooth; interparietal uncommonly absent; 4 Supoc, 6–9 Supcil, 3–13 Eyeld, 7 (rarely 6) Suplab, 5th (rarely 4th) BlwEye, and 6 or 7 (rarely 5 or 8) Inflab on each side. Ear opening oblong vertical to oblique with 2–6 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 44–51 Dorsal, 28–37 Midbody. Subdigital lamellae undivided, smooth: 17–24 3FingL, 23–31 4ToeL.

Juvenile dorsum uniform brown to indistinctly dark flecked or lined, dorsolateral white stripe from head to anterior trunk (occasionally discontinuous) above broad dark brown lateral band marked with white midlateral stripe from eye to anterior neck and scattering of white spots and bars thereafter; venter dusky. Adults monomorphic (Fig. 18) with darker juvenile pattern, often with anterior half of lateral band with reddish hue; venter dusky, edge of chin and throat often black or black-streaked in males.

Comments. The affinities of the individual populations to one another and to the lowland populations remains uncertain.

Distribution. Eastern Highland, Chimbu, and Southern Highland Provinces of Papua New Guinea.

***Carlia aenigma* new species** Fig. 19

Holotype. MCZ R141880, adult female from Papua New Guinea, Western Province, Emeti [7º52'S 143º15'E], Bamu River, collected by Fred Parker, 25 October to 1 November 1971. **Paratypes**. MCZ R141852-53, 141859, 141873, 141882, 141889-891, 141893, 141897, 141901, 141917, collecting data same as holotype. USNM 525769-770, 525772, 525774, 525776, same data as holotype, except 1 November 1971. USNM 232018, Papua New Guinea, Western Province, vicinity of Balimo [8º03'S 142º56'E], collected by George R. Zug and 5 native boys, 4 November 1971. USNM 232061-065, Papua New Guinea, Gulf Province, Kikori [7º25'S 144º15'E], collected by George R. Zug, 22–23 February 1972; USNM 560084 same collecting data same as holotype. Adult females, MCZ R141853, 141859, 141880, 141882, 141891, 141897, 141901, USNM 232061, 232062 (subadult), 525774; adult males, MCZ R141852, 141873, 141889-890, 141893, 141917, USNM 525769-770, 525772, 560084; juveniles, USNM 232018, 232063-065, 525776.

Description. A moderate-sized *Carlia* ranging in adult size from 44 to 58 mm SVL (females 44.2–55.6; males 50.2–57.5) with HeadL 22–30%, TrunkL 40–51%, and HndlL 44–57% of SVL, and 85–200% PalpbD of EarD. Populations sexually dimorphic in HeadL, PalpbD, HndlL, HeadL/SVL, TrunkL/SVL, and Dorsal. Head and nuchal scales smooth; interparietal always present; 4 Supoc, 7–9 Supcil, 7–12 Eyeld, 7 (rarely 6) Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening oblong vertical to oblique with 1–5 AuricN, bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 44–51 Dorsal, 32–36 Midbody. Subdigital lamellae undivided, smooth: 18–26 3FingL, 24–34 4ToeL.

Juvenile dorsum uniform brown to indistinctly dark flecked or lined, dorsolateral white stripe from head to anterior trunk, interrupted midneck above broad dark brown lateral band marked with scattering of white spots and bars on trunk; venter dusky. Adults monomorphic with darker juvenile pattern, often with anterior half of lateral band with reddish hue; venter dusky, edge of chin and throat occasionally black or black-streaked in males.

Distribution. West-central Gulf coast of Papua New Guinea from Kikori R. westward to Aramia R.

Description of holotype (MCZ R141880). Adult female; well preserved and slightly darkened (Fig. 19). Metrics: 53.3 mm SVL; 98 mm tail, regenerated; 12.0 mm HeadL; 26.3 mm TrunkL; 25.7 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 11 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong vertical with 3 AuricN, bluntly pointed, on anterior margin. Trunk scales very weakly tricarinate dorsally and laterally, 49 Dorsal, 35 Midbody; subdigital lamellae undivided, smooth: 24 3FingL, 29 4ToeL. Dorsum brown with double row of light spots edged in black on trunk and laterally dark brown from ear to inguen, darkest on dorsal half and ventral half grading into dusky venter; venter dusky from chin to cream pelvic patch then dusky on underside of tail and limbs.

Variation. Intrapopulational variation is slight. Even the characters displaying sexual dimorphism are not strikingly different although statistically significant, for example, means of HeadL 10.0 and 10.9 (females and males), HndlL/SVL 44.7 and 48.2, and Midbody 31.0 and 32.4. There is coloration dimorphism between adult females and males. For both mensural and meristic traits, the intrasample variation roughly equals intersample variation. Mean SVL ranges from 49.6 to 52.7 mm, females, and 53.4 to 54.6 mm, males. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 9.5–10, & 3–3.5, respectively), and Interp is almost always present. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 45–48, 33.5–34, 20.5–22, & 28–32, respectively).

Etymology. The species name derives from Latin noun *aenigma* (feminine; used in apposition) for riddle or mystery. It refers to the unresolved affinities of this taxon with highlands and eastern Gulf populations and to my continuing perplexity about speciation among the New Guinean populations of *Carlia* "*fusca*."

Comparison to related species. *Carlia aenigma* populations differ from those of the larger bodied *C. beccarii, C. eothen* and C. *luctuosa,* and the smaller bodied *C. leucotaenia* and *C. tutela* by adult females averaging 49 to 51 mm SVL; females and males are on the average equal-sized. *C. aenigma* populations share: an average of 33 to 35 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 20 to 22 3FingL with all except *C. beccarii*; and an average of 28 to 32 4ToeL with all except *C. beccarii, C. longipes*, and *C. luctuosa*. Unlike juveniles of all other *fusca* complex members, juvenile *C. aenigma* have a dorsolateral light stripe from eye to midneck, a break, and then onto anterior trunk; and unlike other *fusca* complex members, the midlateral light "stripe" of juvenile *C. aenigma* consists of a series of light spots and dashes from eye to inguen. Adult *C. aenigma* females commonly retain this juvenile pattern although faded. Adult *C. aenigma* have dusky chins, throats, and venters, differing from the anteriorly darker *C. luctuosa*, and the lighter ventered *C. ailanpalai*, *C. babarensis*, *C. beccarii*, *C. diguliensis*, *C. fusca*, C. *leucotaenia*, *C. longipes*, *C. mysi*, *C. pulla*, *C. tutela*, and some populations of *C. aramia* and *C. eothen*.

Carlia aramia new species Fig. 20

Holotype. USNM 232024, adult male from Papua New Guinea, Western Province, vicinity of Balimo [8º03'S 142º56'E], collected by George R. Zug and 5 native boys, 4 November 1971. Paratypes. All from Papua New Guinea, Western Province, vicinity of Balimo. USNM 167677, by Fred Parker, 7 Nov. 1968; USNM 232013-14, by G. R. Zug, 2 Nov. 1971; 232016, by G. R. Zug, 4 Nov. 1971; USNM 232017, 232019-023, 232025-029, 232032, as for holotype; USMN 232033-036, 232043-048, by native collectors, 4–5 Nov. 1971; USMN 525759, by Fred Parker, 7 Nov. 1968. MCZ R141875, R141900, USNM 525767-768, 525771, 525773, 525775, Papua

Figure 20. Holotype of *Carlia aramia* from Balimo, Papua New Guinea. Adult male (USNM 232024; 49.9 mm SVL).

New Guinea, Western Province, Emeti, Bamu R., collected by Fred Parker, 25 October–1 November 1971 [for MCZ], 1 November 1971 [for USNM]. Adult females, MCZ R141900, USNM 232013, 232016-017, 232020-021, 232023, 232025, 232032-36,525767-768; adult males, MCZ R141875, USNM 167677, 232014, 232019, 232022, 232026-029, 232045-048, 525759, 525771, 525773; juveniles USMN 232043-044, 525775.

Description. A moderate-sized *Carlia* ranging in adult size from 43 to 58 mm SVL (females 43.1–57.1; males 42.7–58.0) with HeadL 20–25%, TrunkL 40–54%, and HndlL 38–54% of SVL, and 75–133% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: HeadL, PalpbD, TrunkL, HndlL, HeadL/SVL, TrunkL/SVL, HndlL/SVL, TrunkL/HndlL, AuricN, Dorsal, Midbody, 3FingL, and 4ToeL. Head and nuchal scales smooth; interparietal rarely absent; 4 (rarely 5) Supoc, 7–10 Supcil, 8–14 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 7 or 8) Inflab on each side. Ear opening oblong vertical to oblique with 0–7 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 43–52 Dorsal, 30–37 Midbody. Subdigital lamellae undivided, smooth: 17–26 3FingL, 23–34 4ToeL.

Juvenile dorsum from brown with flecking to indistinctly pulla-striped or dark lines, dorsolateral white stripe absent or from above eye to midtrunk, midlateral white stripe from eye usually to inguen, and dark brown lateral band; venter cream to ivory. Adults monomorphic to dimorphic; dorsum and sides brown with some dark flecks or females retaining faded lateral light striping to various degrees; venter cream to ivory, occasionally slightly dusky.

Distribution. Western Province, Papua New Guinea, from Bamu R. to Morehead R. and upper reaches of Fly R.

Description of holotype (USNM 232024). Adult male; well preserved and near original coloration (Fig. 20). Metrics: 49.9 mm SVL; 89 mm tail, regenerated; 11.8 mm HeadL; 22.4 mm TrunkL; 26.8 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 9 Eyeld, 7 Suplab, 5th BlwEye, and 7 Inflab on right side. Ear opening oblong vertical with 4 AuricN, usually pointed, on anterior margin. Trunk scales smooth to weakly tricarinate dorsally and laterally, 49 Dorsal, 32 Midbody; subdigital lamellae undivided, smooth: 23 3FingL, 29 4ToeL. Superficially uniform brown dorsally and laterally; dorsum of trunk with numerous black flecks and laterally from ear to midtrunk dark lateral band evident; venter cream, belly light dusky.

Variation. All samples display moderate sexual dimorphism in morphometric characters, but none is dimorphic in SVL. There is dimorphism in coloration in half of the samples (#42A, 44–45, 50–52). For both mensural and meristic traits, the intrasample variation of larger samples is roughly equivalent to intersample variation. Mean SVL ranges from 46.3 to 53.0 mm, females, and 46.4 to 55.1, males; only Daru males and females have mean SVLs greater than 50 mm. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 9–11, & 3–4, respectively), and Interp is almost always present, with only Olsobip lacking (50%) it. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 46–49, 32–36, 19–22, & 26–31, respectively).

Etymology. The specific epithet refers to the origin of the type series from the Aramia River area; *aramia* is used as a noun in apposition.

Comparison to related species. *Carlia aramia* populations differ from those of the larger bodied *C. beccarii, C. eothen* and C. *luctuosa,* and the smaller bodied *C. leucotaenia* by adult females averaging 46 to 53 mm SVL; size is variable in adults with females and males equal-sized in some populations and males larger than females in others. *C. aramia* populations share: an average of 32 to 34 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 19 to 22 3FingL with all except *C. beccarii*; and an average of 26 to 31 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. Unlike juvenile *C. aenigma*, *C. ailanpalai*, *C. babarensis*, *C. beccarii*, *C. fusca*, *C. longipes* and *C. luctuosa*, juvenile *C. aramia* have a dorsolateral light stripe from eye to inguen; and unlike all *fusca* complex members except *C. leucotaenia* and *C. tutela*, the midlateral light stripe of juvenile *C. aramia* extends from eye to inguen, occasionally the stripe on trunk is a series of spots. Adult *C. aramia* females commonly retain the striped pattern, typically faded, and in a few populations, stripes are evident only on neck; some populations of *C. mysi* share a similar adult pattern. Ventral coloration of adult *C. aramia* is variable: some populations are totally white/light ventrally; others are dusky ventrally; and a few populations are mixed.

Carlia longipes (Macleay)

Heteropus longipes Macleay, 1878: 66. Type locality: “Endeavour River.”
Heteropus variegatus Macleay, 1878: 66. Type locality: “Darnley Island.”
Heteropus quinquecarinatus Macleay, 1878: 67. Type locality: “Darnley Island.”
Heteropus sexdentatus Macleay, 1878: 67. Type locality: “Cape Grenville.”
Heteropus Cheverti Macleay, 1878: 67. Type locality: “Barrow Island.”
Heteropus maculatus de Vis, 1885: 169. Type locality: “Cape York.”
Heteropus rubricatus de Vis, 1885: 170. Type locality: “Cape York.”

Description. A moderate-sized *Carlia* ranging to 60 mm SVL. Head and nuchal scales smooth; interparietal always present; 4 Supoc, 6–8 Supcil on each side. Ear opening oblong vertical with 1 to many AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally, 30–41 Midbody; subdigital lamellae undivided, smooth, 25–37 4ToeL. (data from Ingram & Covacevich, 1989). Some populations likely are sexually dimorphic in adult coloration and/or morphometry.

Distribution. Confined to Australia; Cape Arnhem area and Groote Eylandt, NT, and Cape York Peninsula from Cairns area northward into Torres St. islands, QL (Ingram & Covacevich, 1989).

Etymology. Macleay (1878) did not explain his choice of *longipes* (Latin, long foot) for this taxon, although his description notes: “the toes elongate and unequal.” Subsequent description of *Heteropus* species in his 1878 article, either mentioned shorter toes or contained no comment on foot size.

Comparison to related species. Geographic variation of this taxon was not examined in this study. Ingram & Covaceich (1989) observed, but did not detailed, the regional variation within this taxon’s broad distribution, and without a detailed analysis of variation, I cannot provide even a tentative differentiation of *C. longipes* from the New Guinean ”*fusca*.”

MERAUKE population [unassigned]

Description. A moderate-sized *Carlia* ranging in adult size from 45 to 54 mm SVL (females 45.2–50.0; males 46.7–53.9) with HeadL 21–25%, TrunkL 42–55%, and HndlL 41–52% of SVL, and 93–123% PalpbD of EarD. Sexually dimorphic in SVL, HeadL, PalpbD, EarD, HndlL, HeadL/SVL, TrunkL/SVL, HndlL/SVL, and Dorsal.

Figure 21. Lectotype of *Carlia diguliensis* from Asike, Irian Jaya. Adult male (RMNH 5509; 53.8 mm SVL).

Head and nuchal scales smooth; interparietal always present; 4 Supoc, 8–9 Supcil, 8–12 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on each side. Ear opening oblong vertical to oblique with 2–4 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–51 Dorsal, 30–34 Midbody. Subdigital lamellae undivided, smooth: 17–22 3FingL, 24–29 4ToeL.

Juvenile unknown. Adults dimorphic, female with faded dorso- and midlateral light stripes on neck to anterior trunk, male with brown dorsum and sides, occasionally with small dark brown markings; venter cream to ivory, although some males with dusky cheeks and throats.

Distribution. Merauke area of southeastern Irian Jaya.

Comparison to related species. The characteristics of this population do not match well either the *aramia* populations to the east or the *diguliensis* ones to the west.

Carlia diguliensis (Kopstein) Fig. 21

Lygosoma fuscum diguliense Kopstein, 1926: 88. Type locality: "Asike am Oberlauf des Digulflusses, Süd-Neu-Guinea." Lectotype, RMNH 5509 (Fig. 21).

Description. A moderate-sized *Carlia* ranging in adult size from 45 to 54 mm SVL (females 45.2–54.1; males 47.5–54.4) with HeadL 21–25%, TrunkL 38–52%, and HndlL 45–61% of SVL, and 81–131% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: HeadL, PalpbD, EarD, HndlL, HeadL/SVL, HndlL/SVL, TrunkL/HndlL, and 3FingL. Head and nuchal scales smooth; interparietal uncommonly absent; 4 Supoc, 6–9 Supcil, 8–15 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th or6th) BlwEye, and 6 (rarely 5 or 7) Inflab on each side. Ear opening oblong vertical to oblique with 1–5 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 44–51 Dorsal, 30–36 Midbody. Subdigital lamellae undivided, smooth: 18–24 3FingL, 23–34 4ToeL.

Juvenile dorsum brown with light spots on trunk, dorso- and midlateral white stripes from eye to midneck thereafter faded (dorsolateral only) or series of white spots, dark brown lateral band from eye to inguen; venter cream to ivory. Adults with faded juvenile, and potentially with seasonal dimorphism (see Color Pattern. Adult section); venter cream to ivory.

Distribution. Digul River drainage system and Kepulauan Aru, Irian Jaya.

Description of lectotype (RMNH 5509). Adult male; well preserved and retaining coloration (Fig. 21). Metrics: 53.8 mm SVL; 92 mm tail, regenerated; 12.7 mm HeadL; 23.3 mm TrunkL; 26.9 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 9 Eyeld, 7 Suplab, 5th BlwEye, and 7 Inflab on right side. Ear opening oblong oblique with 4 AuricN, bluntly pointed, on anterior and dorsal margin. Trunk scales weakly tricarinate dorsally and laterally, 47 Dorsal, 31 Midbody; subdigital lamellae undivided, smooth: 19 3FingL, 25 4ToeL. Dorsum brown with black flecks on trunk, dorsolateral tan stripe from above eye, interrupted over ear, to midtrunk, midlateral white stripe from eye to beyond ear and series of spots thereafter and reddish brown lateral band from eye to inguen; venter ivory.

Variation. All samples display sexual dimorphism in some morphometric characters, and only Aru has significant differences between females and male SVLs (means: 49.1 & 51.3 mm); however, this minor difference is the same in all samples so sample size produced the statistical significance. For both mensural and meristic traits, the intrasample variation of larger samples equals or nearly the variation among samples. Mean SVL ranges from 47.8 to 52.7 mm, females, and 50.0 to 51.5 mm, males. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 10–11, & 2–4, respectively), and Interp is invariably present in most populations. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 45.5–48, 32–34, 19–22, & 26–30, respectively).

Etymology. The species name refers to the origin of syntypic specimens from Asike beside the Digul River.

Comparison to related species. *Carlia diguliensis* populations differ from those of the larger bodied *C. beccarii, C. eothen* and *C. luctuosa,* and the smaller bodied *C. babarensis*, *C. leucotaenia* and *C. tutela* by adult females averaging 48 to 52 mm SVL; females and males are on the average equal-sized. *C. diguliensis* populations share: an average of 32 to 34 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 20 to 22 3FingL with all except *C. beccarii*; and an average of 26 to 30 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. Unlike the juveniles of all *fusca* complex members except some *C. pulla*, juvenile *C. diguliensis* have a bright dorsolateral light stripe from eye to midneck, faded thereafter or continuing as a series of light spots on anterior trunk; and differing from juveniles of all complex members, *C. diguliensis* has a midlateral light stripe from eye to just beyond the ear, then as longitudinal series of widely spaced spots, occasionally as stripe to midtrunk then spots. Adult *C. diguliensis* females commonly and uniquely retain a faded juvenile pattern or lose the dorsolateral stripe with retention of a midlateral series of light spots on trunk; an adult unicolor coloration is shared with some adults of other complex members. Adult *C. diguliensis* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

Agats to Ayamura [unnamed]

Description. A moderate-sized *Carlia* ranging in adult size from 43 to 58 mm SVL (females 43.9–53.2; males 43.1–58.0) with HeadL 21–26, TrunkL 40–55%, and HndlL 42–58% of SVL, and 77–164% PalpbD of EarD. Some populations sexually dimorphic in one or more of the following traits: SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, PalpbD/EarD, TrunkL/SVL, HndlL/SVL, TrunkL/HndlL, Eyeld, Dorsal, and Midbody. Head and nuchal scales smooth; interparietal rarely absent; 4 (rarely 5 or 6) Supoc, 8–9 Supcil, 612 Eyeld, 7 (rarely 8) Suplab, 5th (rarely 6th) BlwEye, and 6 (rarely 5 or 7) Inflab on each side. Ear opening oblong vertical to oblique with 1–5 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 44–50 Dorsal, 31–36 Midbody. Subdigital lamellae undivided, smooth: 18–24 3FingL, 24–32 4ToeL.

Juvenile dorsum brown with dark flecking on trunk, dorsolateral white stripe from eye to midtrunk faded thereafter, midlateral white stripes from eye to midtrunk or to midneck with series of white spots thereafter, dark brown lateral band from eye to inguen; venter cream to ivory. Adults dimorphic, females retaining faded juvenile pattern, males with a darken of head to anterior trunk, as broad dark lateral band or entire head, neck and anterior trunk darkening; venter cream to ivory with dusky chin and throat in females and dark dusky to black chin and throat in males.

Comment. Data (Zug and Allison, unpubl.) from recent collections from south coastal Irian Jaya should permit a more accurate definition of this taxon, its distribution, and its affinities.
Distribution. Southern Irian Jaya from Agats westward into the Vogelkop.

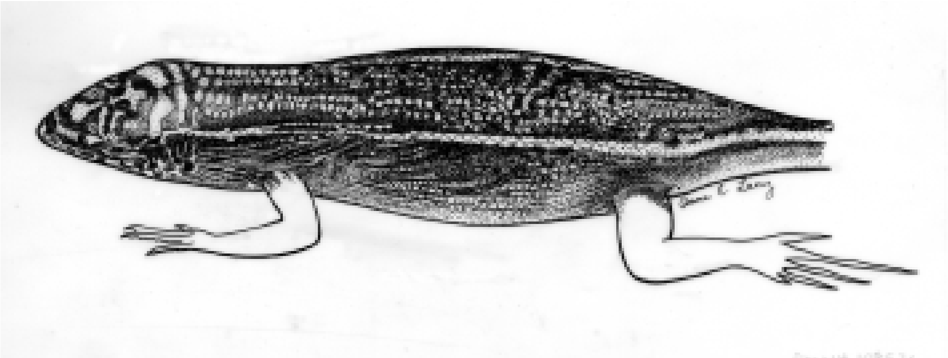

Figure 22. Schematic depiction of *Carlia beccarii*, based on AMNH 108576 (61.4 mm SVL).

Carlia beccarii (Peters & Doria) Fig. 22

Heteropus Beccarii Peters & Doria, 1878: 361. Type locality: “Insul. Kei, Tual.” Holotype, MSNG 28070.

Description. A large *Carlia* ranging in adult size from 60 to 80 mm SVL (females 60.4–67.5; males 65.1–79.7) with HeadL 21–24%, TrunkL 39–49%, and HndlL 50–59% of SVL, and 76–133% PalpbD of EarD. Strongly sexually dimorphic in SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, and HndlL/SVL. Head and nuchal scales smooth; interparietal always present; 4 Supoc, 7–9 Supcil, 8–15 Eyeld, 7 Suplab, 5th BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening oblong vertical to oblique with 3–6 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 51–58 Dorsal, 36–41 Midbody. Subdigital lamellae undivided, smooth: 20–28 3FingL, 30–34 4ToeL.

Juvenile dorsum brown uniform or with black flecks on trunk, brown lateral band from eye to behind ear mottled with cream flecks, thereafter band black to inguen and bordered above and below with white flecks; venter ivory. Adults monomorphic (Fig. 22), retaining bold juvenile pattern and accentuating labials and ventrolateral neck with alternating black and white bars; venter ivory.

Distribution. Kepulauan Kai.

Description of holotype (MSNG 28070). Not seen.

Variation. This taxon is represented by a single sample.

Etymology. This species was named for the botanist Odoardo Beccari (1843—1920), a broadly traveled field collector for the Museo Civico di Storia Naturale, Genova. Beccari joined Luigi Maria d’Albertis in several expeditions in Aru, Java, Celebes, Timor, and northern and southern New Guinea (Capocaccia & Poggi, 1982). While in Aru, he collected the type series.

Comparison to related species. *Carlia beccarii* populations differ from those of the smaller bodied *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. diguliensis*, *C. eothen*, *C. fusca*, *C. leucotaenia*, *C. longipes*, *C. mysi*, *C. pulla*, and *C. tutela* by adult females averaging 56 to 66 mm SVL; males are distinctly larger than females as occurs elsewhere only in *C. luctuosa. Carlia beccarii* populations have more Midbody (38) than all other *fusca* complex species except *C. luctuosa*, and average more 3FingL (24) than any other complex member; and an average of 32 4ToeL with only *C. longipes*, and *C. luctuosa*. Unlike juveniles in all other *fusca* complex members except *C. ailanpalai* and some *C. fusca* and *C. mysi*, juvenile *C. beccarii* lack dorsolateral and midlateral light stripes. Adult *C. beccarii* females and males have a unique lateral coloration consisting of a broad dark band from head to inguen, intensely dark from ear through anterior trunk and this is brightly flecked with white above and below. Adult *C. beccarii* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

KAI UNICOLOR [unassigned]

Description. A moderate-sized *Carlia* ranging in adult size from 44 to 55 mm SVL (females 44.0–50.6; males

Figure 23. Lectotype of *Carlia babarensis* from Babar Kepulauan. Adult female (RMNH 5518; 47.8 mm SVL).

41.7–54.6) with HeadL 21–25%, TrunkL 40–50%, and HndlL 41–55 of SVL, and 75–133% PalpbD of EarD. Population sexually dimorphic in HeadL, PalpbD, and HeadL/SVL. Head and nuchal scales smooth; interparietal always present; 4 Supoc, 7–9 Supcil, 8–14 Eyeld, 7 Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening oblong vertical to oblique with 1–4 AuricN, bluntly pointed, on anterior margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–51 Dorsal, 30–34 Midbody. Subdigital lamellae undivided, smooth: 19–24 3FingL, 26–34 4ToeL.

Adults monomorphic; dorsum and sides brown occasionally with dark brown longitudinal lines or dark brown scale-edge flecks; venter cream.

Comment. The sample is too small and too old to determine whether this population represents an endemic taxon or an introduction from elsewhere. No juveniles were available that could be attributed to this Kai taxon. Roux (1910) noted the presence of 2 Kai morphotypes and labeled the unicolor one as "*fuscum*." His description is, however, inconsistent, because he introduces "*fuscum*" as "eine uniformbraune," but in the next paragraph he stated that the dorsolateral stripe is often indistinct, thereby suggesting its occasional occurrence in the unicolored Kai morph. I suspect that he was influenced by the presence of these stripes in his Aru "*fuscum*" specimens, because he does not mentioned stripes in his brief description of the Kai juvenile coloration.

Distribution. Kepulauan Kai.

Carlia babarensis (Kopstein) Fig. 23

Lygosoma fuscum babarense Kopstein, 1926: 88. Type locality: "Tepa, Babar-Inseln," and "Samlakki, Tenimber-Inseln"; restricted to Tepa [7°52'S 129º31'E], Babar Kepulauan. Lectotype, RMNH 5518 (Fig. 23).

Description. A moderately small *Carlia* ranging in adult size from 41 to 52 mm SVL (females 41.1–47.4; males 45.5–51.5) with HeadL 21–25%, TrunkL 41–51%, and HndlL 44–55% of SVL, and 77–144% PalpbD of EarD. Tanimbar population sexually dimorphic in SVL, HeadL, PalpbD, EarD, HndlL, and HeadL/SVL, PalpbD/EarD, and TrunkL/HndlL. Head and nuchal scales smooth; interparietal always present; 4 (rarely 5) Supoc, 6–9 Supcil, 8–11 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th) BlwEye, and 6 (rarely 5 or 7) Inflab on each side. Ear opening oblong vertical to oblique with 2–5 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 46–50 Dorsal, 30–33 Midbody. Subdigital lamellae undivided, smooth: 18–23 3FingL, 29–32 4ToeL.

Juvenile dorsum brown mottled with black flecks on neck and white and black flecks on trunk, dorsolateral white stripe from ear to anteriormost trunk, and brown lateral band from eye to ear, black to anteriormost trunk and brown to inguen; venter ivory. Adults monomorphic, retaining bold juvenile pattern, accentuating labials and ventrolateral neck to axilla with black and white mottling, posterior half of trunk orangish venter cream to ivory.

Distribution. Kepulauan Babar and Kepulauan Tanimbar.

Description of lectotype (RMNH 5518). Adult male; well preserved and retaining coloration (Fig. 24). Metrics: 47.8 mm SVL; tail incomplete; 10.9 mm HeadL; 22.6 mm TrunkL; 23.4 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 11 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong oblique with 5 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally, 48 Dorsal, 31 Midbody; subdigital lamellae undivided, smooth; 20 3FingL, 29 4ToeL. Coloration as in preceding description in Definition.

Variation. The 2 samples are unequal, Tanimbar with 8 adult females and 7 adult males (also 5 unsexed), Babar with 1 adult male (and 6 unsexed). Tanimbar shows strong sexual dimorphism in all, but one, morphometric characters, including significant differences between females and male SVLs (means: 44.6 & 49.1 mm) but no dimorphism in coloration. For both mensural and meristic traits, variation within each sample is nearly identical. Mean SVL is 44.6 for females, and 47.8 to 49.1 mm, males. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 9–10, & 3–4, respectively), and Interp is invariably present. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 48–49, 32, 20–21, & 29–30, respectively).

Etymology. The species name refers to the origin of some specimens of the syntypic series from the island of Babar.

Comparison to related species. *Carlia babarensis* populations differ from all *fusca* complex members except *C. leucotaenia* and *C. tutela,* by small size with adult females averaging 44 to 45 mm SVL; females and males are on the average equal-sized. *C. babarensis* populations share: an average of 32 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 20 to 21 3FingL with all except *C. beccarii*; and an average of 29 to 30 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. Unlike juvenile *C. ailanpalai*, *C. beccarii*, *C. leucotaenia*, *C. mysi*, *C. pulla* and *C. tutela*, juvenile *C. babarensis* have a short dorsolateral light stripe from eye to axilla, occasionally to anterior trunk. Juvenile *C. babarensis* lack a midlateral light stripe or series of light spots, a feature shared with *C. ailanpalai*, *C. beccarii*, and some populations of *C. fusca*, *C. longipes* and *C. mysi*. Adult *C. babarensis* females commonly retain a faded dorsolateral stripe on head and neck and lack a midlateral stripe, sharing this adult female coloration with some populations of *C. eothen*, *C. fusca*, *C. leucotaenia*, *C. longipes*, *C. mysi,* and *C. tutela*. Adult *C. babarensis* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

Carlia leucotaenia (Bleeker) Fig. 24

Heteropus leucotaenia Bleeker, 1860: 38. Type locality: "Paulohi." Neotype, USNM 204786.

Heteropus schlegelii Peters, 1864: 57. Type locality: ". . . aus Timor; . . . auf Amboina . ", restricted to Ambon by lectotype designation. Lectotype, ZMB 4951.

Description. A moderately small *Carlia* ranging in adult size from 39 to 54 mm SVL (females 39.0–51.5; males 43.2–53.3) with HeadL 20–26%, TrunkL 44–54%, and HndlL 42–54% of SVL, and 68–133% PalpbD of EarD. Populations sexually dimorphic in several of the following traits: SVL, HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, PalpbD/EarD, TrunkL/SVL, TrunkL/HndlL, and Dorsal. Head and nuchal scales smooth; interparietal rarely absent; 4 Supoc, 6–9 Supcil, 7–12 Eyeld, 7 (rarely 6 or 8) Suplab, 5th (rarely 4th or 6th) BlwEye, and 6 (rarely 5) Inflab on each side. Ear opening oblong vertical to oblique with 2–5 AuricN, usually bluntly pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 45–50 Dorsal, 28–34 Midbody. Subdigital lamellae undivided, smooth: 18–24 3FingL, 26–32 4ToeL.

Figure 24. Neotype of *Carlia leucotaenia* from Ambon, Molluca Islands. Adult male (USNM 204786; 49.1 mm SVL).

Juvenile dorsum uniform brown occasionally with some black flecks, distinct dorso- and midlateral white stripes enclosing darker brown lateral band; venter cream to ivory. Adults dimorphic with females and smaller mature males retaining lateral striping and banding (Fig. 24), faded in larger (older) males with black flecks forming dark lines on dorsum and dark lateral band only evident on neck, and much reduced lateral striping in some females; venter cream to ivory.

Distribution. Ambon, Seram, and presumably adjacent islets.

Description of neotype (*leucotaenia*; USNM 204786). Adult male; well preserved and retaining coloration (Fig. 24). Metrics: 49.1 mm SVL; tail incomplete; 11.4 mm HeadL; 20.9 mm TrunkL; 22.9 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 9 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong oblique with 3 AuricN, pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally, 48 Dorsal, 31 Midbody; subdigital lamellae undivided, smooth; 21 3FingL, 27 4ToeL. Coloration as in preceding description.

Description of lectotype (*schlegelii*; ZMB 4951). Adult male; moderately well preserved and somewhat bleached. Metrics: 53.3 mm SVL; 58 mm tail, regenerated; 12.2 mm HeadL; 24.5 mm TrunkL; 23.8 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 10 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong vertical with 2 AuricN, bluntly pointed, on anterior margin. Trunk scales very weakly tricarinate dorsally and laterally; 47 Dorsal, 30 Midbody; subdigital lamellae undivided, smooth; 21 3FingL, 29 4ToeL.

Variation. Both samples (#70, 71) display sexual dimorphism in many morphometric traits; however, only the Ambon sample, the larger of the 2 samples, shows significant differences between females and male SVLs (means: 43.7 & 47.5 mm, 48.0 & 48.9 mm, respectively). Neither population displays color dimorphism. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 9–10, & 3–4, respectively), and Interp is rarely absent. Dorsal, Midbody, 3FingL, and 4ToeL also show little intersample variation (medians: 48, 31–32, 21, & 28–29, respectively).

Etymology. Bleeker offered no explanation for choosing *leucotaenia*, from the Greek *leukos* for white and *tainia* for ribbon. His choice presumably refers to the white dorsolateral and midlateral stripes.

Comparison to related species. *Carlia leucotaenia* populations differ from those of the larger bodied *C. beccarii, C. eothen* and *C. luctuosa,* and the moderate sized *C. aenigma*, *C. aramia*, *C.*

fusca, *C. mysi* and *C. pulla*, by adult females averaging 44 to 48 mm SVL; females and males are on the average equal-sized. *C. leucotaenia* populations share: an average of 31 to 32 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 21 3FingL with all except *C. beccarii*; and an average of 28 to 29 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. Unlike *C. aenigma*, *C. ailanpalai*, *C. aramia*, *C. babarensis*, *C. beccarii*, *C. diguliensis*, *C. eothen*, *C. leucotaenia*, *C. longipes*, *C. luctuosa*, *C. mysi* and *C. pulla*, *C. leucotaenia* has well-developed dorsolateral and midlateral light stripes. Adult *C. leucotaenia* females retain a faded dorsolateral stripe on head and anterior neck and lose the midlateral stripe, sharing this adult female coloration with some individuals of *C. fusca*, *C. eothen*, *C. longipes*, and *C. mysi*. Adult *C. leucotaenia* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

***Carlia tutela* new species**

Fig. 25

Holotype. USNM 237403, adult male from Indonesia, Moluccas Islands, Halmahera, Jailolo District, Kampung Pasir Putih [0º53'N 130º53'E], collected by Paul M. Taylor, August 1981. **Paratypes**. RMNH 6965A-B, Halmahera, no additional locality data, collected by H.A. Bernstein, no date; USNM 215857-858, locality as holotype, by Habel Singou, April 1979; USNM 237397, data and collector as holotype, 2 February 1981; USNM 237398-399, data and collector as holotype, 2 June 1981; USNM 237400-402, data and collector as holotype, 4 June 1981; USNM 237404-405, 237408, all data as holotype; USNM 237409-10, data and collector as holotype, 14 August 1981; USNM ;237413-418 data and collector as holotype, 19 August 1981. BYU 7340-41, 7351, 7353, 7400, 7412-14, 7620, 7622-23, 7625-27, 7630, Indonesia, Moluccas Islands, Morotai, vicinity of Pitu Airfield [1º40'N 128º00'E], collected by Ernest Reimschiissel, October 1944–January 1945; RMNH 8659, Morotai, collected by H. Boschma, 3–7 June 1930; USNM 159958, Morotai, Wama airstrip, [2º02'N 128º18'E], collected by Robert M. Roecker, 11 October 1944; USNM 560143, Morotai, vicinity of Pitu Airfield [1º40'N 128º00'E], collected by Ernest Reimschiissel, 1944. Adult females, BYU 7340, 7353, 7400, 7413-14, 7620, 7622, 7626-27, 7630, RMNH 6965B, 8659, USNM 237398, 237410, 237415-417; adult males, BYU 7341, 7351, 7412, 7623, 7625, RMNH 6965A, USNM 215857-858, 237397, 237399-401, 237403-405, 237409, 237413-414, 237418, 560143; juveniles USNM 237402, 237408.

Description. A moderate-sized *Carlia* ranging in adult size from 43 to 54 mm SVL (females 42.9–49.3; males 41.0–53.7) with HeadL 21–26%, TrunkL 39–51%, and HndlL 41–54% of SVL, and 75–220% PalpbD of EarD. Populations sexually dimorphic in HeadL, PalpbD, EarD, TrunkL, HndlL, HeadL/SVL, TrunkL/SVL, TrunkL/HndlL, and AuricN. Head and nuchal scales smooth; interparietal rarely absent; 4 Supoc, 8–9 Supcil, 8–12 Eyeld, 7 (rarely 6) Suplab, 5th BlwEye, and 6 (rarely 7) Inflab on each side. Ear opening oblong vertical to oblique with 2–5 AuricN, usually pointed, on anterior and dorsal margin. Trunk scales smooth to weakly tricarinate dorsally and laterally: 44–51 Dorsal, 30–37 Midbody. Subdigital lamellae undivided, smooth: 18–24 3FingL, 23–32 4ToeL.

Juvenile dorsum uniform brown or with light black flecking, distinct dorso- and midlateral white stripes at least to anterior trunk enclosing darker brown lateral band from eye to inguen; venter cream to ivory. Adults largely monomorphic, smaller (younger) females retaining faded lateral light striping; males and larger females mainly brown dorsally and laterally, uniform or some black flecking; venter cream to ivory.

Distribution. Halmahera, Ternate, Morotai, and their associated islets. Extralimital in Palau.

Description of holotype (USNM 237403). Adult male; moderately well preserved and slightly darkened (Fig. 25). Metrics: 45.9 mm SVL; 70 mm tail, regenerated; 10.7 mm HeadL; 18.9 mm TrunkL; 21.0 mm HndlL. Head and nuchal scales smooth; small interparietal; 4 Supoc, 8 Supcil, 10 Eyeld, 7 Suplab, 5th BlwEye, and 6 Inflab on right side. Ear opening oblong oblique with 3 AuricN, bluntly pointed, on anterior margin. Trunk scales weakly tricarinate dorsally and laterally, 47 Dorsal, 33 Midbody; subdigital lamellae undivided, smooth: 20 3FingL, 27 4ToeL. Uniform brown dorsally and laterally, hint of dark lateral band from ear to inguen; laterally dark brown spot behind eye; venter creamy beige.

Variation. Both samples (#72, 73) display sexual dimorphism in 7 or more morphometric traits, but neither possesses SVL dimorphism (means: 46.0 & 46.5, 45.7 & 46.1, respectively) nor color dimorphism. Supcil, Suplab, Inflab, Eyeld, and AuricN have little variation between and within samples (medians: 8, 7, 6, 9–10, & 3, respectively), and Interp is rarely absent. Dorsal, Midbody,

Figure 25. Holotype of *Carlia tutela* from Halamahera. Adult male (USNM 237403; 45.9 mm SVL).

3FingL, and 4ToeL also show little intersample variation (medians: 48, 32, 20–22, & 27–30, respectively).

Etymology. The specific name derives from the Latin *tutela* (feminine; noun in apposition) for defense or guard and is proposed to honor the men and women who served in the defense of New Guinea and the Mollucas during WW II.

Comparison to related species. *Carlia tutela* populations differ from those of the larger bodied *C. beccarii, C. eothen* and *C. luctuosa,* and the moderate sized *C. aenigma*, *C. aramia*, *C. fusca*, *C. mysi* and *C. pulla*, by adult females averaging 46 to 47 mm SVL; females and males are on the average equal-sized. *C. tutela* populations share: an average of 32 Midbody with all other *fusca* complex species except *C. luctuosa*; an average of 20 to 22 3FingL with all except *C. beccarii*; and an average of 27 to 30 4ToeL with all except *C. beccarii*, *C. longipes*, and *C. luctuosa*. *C. tutela* either has well-developed dorsolateral and midlateral light stripes, shared with *C. leucotaenia*, or dorsolateral stripe from eye to axilla and midlateral stripe from eye to midtrunk, shared with some individuals of *C. fusca*, *C. longipes* and some *C. mysi*. Adult *C. tutela* females retain faded stripes anteriorly or become unicolor, sharing this first coloration with some individuals of *C. fusca*, *C. longipes* and *C. mysi,* and the second coloration with *C. ailanpalai* and some *C. fusca* and *C. mysi*. Adult *C. tutela* have light chins, throats, and venters, differing from the dark underside of *C. aenigma*, *C. luctuosa*, and some populations of *C. aramia* and *C. eothen*.

Biogeography of *Carlia fusca* Complex

Several ingredients are essential for a robust biogeographic analysis and interpretation: 1) hypotheses of the phylogenetic relationships of the organisms; 2) precise delineation of the occurrence of each taxon examined; and 3) hypotheses or well-defined scenarios of the geological history of the region occupied by the taxa to be examined. The first 2 criteria are not met for the *Carlia* "*fusca*" species. Nonetheless, even with the uncertainty of the actual number of New Guinean *Carlia* "*fusca*" species and their interspecific relationships, a tentative biogeographic examination remains appropriate.

My approach to this examination rests on the assumption that the "*fusca*" of mainland New Guinea and the adjacent coastal islands are a clade, recognizing that the neither Stuart-Fox's (2002) nor my cladistic analysis provide evidence for this clade. My assumption of monophyly rests on a broad sharing of scalation and morphometry among the New Guinea "*fusca*" and leads to my proposition that we continue to recognize these taxa as members of a *C. fusca* complex, even though there is presently no support for this clade.

This complex is characterized by: dorsal and lateral trunk scales smooth to weakly tricarinate in adults; prefrontal scales rarely in contact; interparietal uncommonly absent (fused); typically 4 supraoculars, 8 supraciliaries, 7 supralabials with 5th beneath eye, and 6 infralabials; size of palpebral disk usually subequal ear opening; ear opening round to vertical oblong with weakly pointed auricular lobules on anterior and dorsal edge; average dorsal scale rows 46–50; average scales around midbody 30–38; average fourth digit of hindfoot lamellae 26–32; average adult female SVL 46–54 mm, occasionally larger; head 21–23%, trunk 46–50%, and hindlimb 45–55% of SVL. This paradigm also encompasses several Australian species of *Carlia*, but for the present, I recommend its content as only New Guinea and adjacent island species, *C. leucotaenia* and *C. tutela* of the Mollucas, *C. longipes* of Cape York Peninsula and Torres Strait islands, and tentatively *C. babarensis* and *C. beccarii*. I specifically exclude *C. peronii* until I complete my analysis of the *C. peronii* and other *Carlia* populations in the Lesser Sundas.

My second assumption sets the beginning of the *fusca* complex diversification in the mid Miocene (15–10 Ma). This date derives from Stuart-Fox's interpretation (1998) of rapid diversification (starburst radiation) of *Carlia* based on the amount of DNA sequence divergence, yet the absence of structured (hierarchical) differences. I further assume that the *C. fusca* complex ancestor occurred broadly in the northern portion of the Australian craton (i.e., future New Guinea and Cape York) at that time and that NG populations were soon isolated by the submergence of the Sahul shelf (Pigram et al., 1989) between Australia and the accreting and geologically active New Guinea. Further, these NG populations experienced subsequent isolation by vicariance and dispersal events.

Before comparing the distributional patterns of *Carlia fusca* complex members to a geological scenario, it is important to determine whether distributions within the *fusca* complex are shared (i.e., a track analysis) with any other reptiles or other New Guinean vertebrates. For this distributional comparison of herpetofaunal elements, I simply divide the NG lowlands and adjacent islands into a series of geographic segments and note which species occurs in each segment (Table 12). These segments are *fusca* complex biased because they emphasize the allopatry of *fusca* complex species, thereby increasing the visibility of potential concordance to other taxonomic groups that may share allopatric distributional patterns.

The distribution and taxonomy of other skinks (*Emoia* [Brown, 1991], *Lipinia* [Austin, 1995; Zweifel, 1979]) have groups of species with comparable lowland distributions, and these skinks are often syntopic with *Carlia fusca* complex members. None of the 4 *Emoia* groups (Table 12) displays total or even a moderate level of distributional concordance. *Emoia reimschisseli* of the *E. caeruleocauda* complex appears to be a Morotai endemic; elsewhere in the Mollucas and New Guinea, its sister taxon (*E. caeruleocauda*) shows no apparent regional differentiation. Several members of the *E. aenea*, *baudini*, and *pallidiceps* subgroups have north NG coast endemics, but none match the distribution of a *C. fusca* complex taxon. These *Emoia* endemics either occupy only a portion of the *fusca* taxon's range or overlap 2 or more contiguous *fusca* taxa's ranges. *Lipinia* species's distributions similarly fail to show concordance with those of *C. fusca* taxa. Importantly, no *Emoia* or *Lipinia* species displays a speciation break between the Mamberamo R. and the Sentani regions (i.e., btw *C. fusca* and *C. pulla* distributions) or between the north PNG coast and the Milne Bay areas (i.e., btw *C. mysi* and *C. eothen*), although the distribution of *E. cyclops* is totally within that of *C. pulla*.

Mys's study (1988) focuses on scincid lizard distributions of the north coast of New Guinea. His examination of distributional patterns is more fine-scaled than Brown's (1991), but its data do not conflict with the latter. Mys's data confirm the absence of a Mamberamo-Sentani break for *Emoia* and all other skinks; although, one species pair (*Cryptoblepharus novaeguineae*/*pallidus*) shows a Sentani-area break, and a few other taxa (*Emoia popei*, *Prasinohaema virens*) have their western distribution end within the Mamberamo-Sepik expanse. Most north-coast skink species occur along the length of the coast or at least to the Cape d'Urville area. 3 skinks (*Emoia mivarti*,

Table 12. **Lowland distributions of select groups of New Guinea reptiles and frogs**.

Region	Carlia fusca	Emoia aurulenta	Emoia aenea	Emoia baudini	Emoia caeruleocauda	Emoia pallidiceps	Lipinia	Gehyra	Ramphotyphlops flaviventer	Typhlops ater	Stegonotus	Tropidonophis	Hylophorbus rufescens	Callulops	Rana papua
South Mollucas	t	.	.	.	c	.	.	.	.	.	m	e	.	f	.
North Mollucas	s	.	.	.	c, r	.	n	v	f	a	.	e, ha, pu, t	.	k, d	.
Waigeo	f	.	.	o, v	c	.	.	.	.	a	.	pi	.	.	p
North Vogelkop	f	.	.	b, v	c	.	n	.	f, su	a	c, d, p	e, m, pi, t	r	.	p, s, su
NW Irian Jaya	f	.	.	o, v	c	mh	c, l,. n, p		f, si	.	d	d, e, m, pi		l, r	p
IJ & NW PNG	p	.		c, v	c	l, m	c, l, n, p	v	.	.	c, d, m, p	d, m, mc, pi	r	p	p, s, su
Sepik	?	.	p	v	c	mh	n	v	.	d	c, d, m, p	d, m, mc, pi		l, p r	s, su
N Central PNG	m	.	p	o, v	c	p, mh	l, p	v	.	d	c, d, m, p	a, d, m	r	l, r	d, s, su
Bismarck/NB-NI	m	.	bm	.	c	.	n, r	o	d	.	h, p*	d, hy	.	.	d, k
Bismrck/Admrlty	ai	.	,	.	c	.	n	v, o	d	.	m	.	.	.	s
Northeast PNG	m	.	g	o	c	p	n	o	.	in	c, d	a, m, pi	r		d, s, su
Milne Bay	e	.	.	o	c	p	n	.	.	.	c	m	r	l	d, g
Trobriand-Muyua	e	.	.	.	c	.	l, n	o	.	.	c	a	m	.	.
Southeast Savanna	l	.	.	o	c	p	.	m, v		f, in, m	c, d	d, m, mm, n, pi	r	l, r	d, g, su

see footnotes on next page

Table 12 (continued).

Region	Carlia fusca	Emoia aurulenta	Emoia aenea	Emoia baudini	Emoia caeruleocauda	Emoia pallidiceps	Lipinia	Gehyra	Ramphotyphlops flaviventer	Typhlops ater	Stegonotus	Tropidonophis	Hylophorbus rufescens	Callulops	Rana papua
East Papua Gulf	ae, ar	.	.	.	c	p	.	.	.	.	c, d	d, n, pi		s	d, n
West Papua Gulf	ar	a	a	.	c	.	.	v	.	.	c, d, p	d, m, mp, pi	r	l, r	d, n
Southeast IJ	d	?	a	.	.	d	.	.	.	.	d, p	m, pi	r		d, n
S Central IJ	u*	a, p	a, j	.	.	.	l	.	.	.	c, p	d, h, m, mc, pi	r	r	d, n su
South Vogelkop	u*	.	.	.	.	l, m	v	.	.	.	.	e, m, pi	r	e	g, su
Aru	d	.	.	.	.	.	.	.	.	.	.	d	.	.	.

Taxonomic abbreviations. Carlia fusca complex: a, aramia; ae, aenigma; ai, ailanpalai, d, diguliensis; e, eothen; f, fusca; l, luctuosa; m, mysi; p, pulla; s, leocotaenia; t, tutela; u*, undescribed. Emoia aurulenta group: a, aurulenta; p, paniai. Emoia aenea complex: a, aenea; b, bismarckensis; g, guttata; j, jamur; p, popei. Emoia baudini complex: b, baudini; c, cyclops; o, obscura; v, veracunda. Emoia caeruleocauda group: c, caeruleocauda; r, reimschisseli. Emoia pallidiceps complex: d, digul; l, loveridgei; m, maxima; mh, pallidiceps mehelyi; p, p. pallidiceps. Lipinia: c, cheesmanae; l, longiceps; n, noctua; p, pulchra; r, rouxi; v, venemai. Gehyra: m, membranacruralis; o, oceania; v, vorax. Ramphotyphlops flaviventer group: d, depressus; f, flaviventer; s, supranasalis; si, similis. Typhlops ater group: a, ater; d, depressiceps; f, fredparkeri; in, inornatus; m, mcdowellii. Stegonotus: c, cucullatus; d, diehli; g, guentheri; h, heterurus; m, modestus; p, parvus; p*, cf. parvus. Tropidonophis: a, aenigmaticus; d, dahli; e, elongatus; ha, halmahericus; hy, hylomelas; m, multiscutellatus; mc, mcdowelli; mp, mairii plumbea; mm, m. mairii; n, novaeguineae; pi, picturatus; pu, punctiventris; t, truncatus. Hylophorbus rufescens subspecies: m, myopicus; r, rufescens. Callulops: d, dubia; e, eurydactyla; f, fusca; k, kopsteini; l, lateralis; p, personata; r, robusta; s, slateri. Rana papua group: d, daemeli; g, garritor; k, kreffti; n, novaeguineae; p, papua; s, semelvella; su, supragrisea.

Data sources: Carlia fusca complex: data herein; Emoia: Brown (1991); Lipinia: Austin (1995), Zweifel (1979); Gehyra: Beckon (1992), King and Horner (1989); Ramphotyphlops flaviventer: Wallach (1996); Typhlops ater: McDowell (1974), Wallach (1997); Stegonotus: McDowell (1972); Hylophorbus rufescens: Zweifel (1972); Callulops: Zweifel (1972); Rana papua: Menzies (1987).

Geomyersia coggeri, *Tribolonotus brongersmai*) share *Carlia ailanpalai*'s Admiralty endemism.

The gecko *Gehyra* has no north NG coast concordance (Table 12), but the limited distribution of *G. membranacruralis* does suggest a SE savanna speciation center. Some of the snake distributions are slightly more concordant with the *C. fusca* complex. The distributions of *Ramphotyphlops flaviventer* and *Typhlops ater* match that of *C. fusca*, although both blindsnakes also occur in the north Mollucas. The *T. ater* group has 2 SE savanna endemics. The watersnake *Tropidonophis* has 3 north Mollucas endemics (Table 12), and the distribution of *T. elongatus* is nearly conconcordant with *C. fusca*, but 3 *Tropidonophis* species cross the *fusca-pulla* break. In contrast to north coast distributional concordance, no *Tropidonophis* displays distributional similarities to the *Carlia fusca* complex on the south coast. The terrestrial *Stegonotus* shows endemicity in south Mollucas, otherwise no distributional similarities to the *C. fusca* complex.

A recent review of scrub pythons (*Morelia "amethistina"* Harvey et al., 2000) recognized several new taxa, whose distributions match those of some *fusca* complex members. *Morelia tracyea* is endemic to the Halmahera area as is *C. tutela*; *M. nauta* shares the Tanimbar endemism with *C. babarensis*; and *M. clastolepis* is an Ambon-Seram endemic like *C. leucotaenia*. Harvey and colleagues also note a strong genetic divergence of north and south coast populations of the scrub pythons. Even though I trust their recognition of new taxa, their biogeographic and phylogenetic interpretations seem overly detailed for the weight of their evidence; that is, their interpretations rest on too few New Guinean and Australian samples. For example, their consensus phylogram (Harvey et al., 2000: fig. 4) based on mtDNA sequence data closely links Biak and Merauke samples, contrary to their interpretation of north and south coast genomic differentiation.

Frog distributions (Table 12) also have poor concordance with the *C. fusca* complex. *Callulops* has north and south Mollucas endemics, and possibly *C. pulla* and *C. aenigma* distributional matches. The *Rana papua* group displays no concordance.

Among the other terrestrial vertebrates, shared distributions with the *fusca* complex are also uncommon. I have not make a detailed comparison of mammals and birds to the *fusca* complex, rather I wish only to note a few similarities and differences; these observations are based on the distribution maps in Coates (1985, 1990), Coates et al. (1997), and Flannery (1995a, b). A major difference results from mammal and bird speciation being largely montane and that of the *fusca* complex being mainly lowland. From an insular perspective, birds and mammals show a modest amount of speciation or geographic differentiation in the Admiralty Islands, similarly for Seram, and Halmahera in the mammals and birds (Coates et al., 1997). An interesting feature of mammalian speciation in Seram is the absence of these endemics in Ambon; I assume that this feature results from a predominantly montane isolation and/or the early destruction of forest habitats in lowland Seram and Ambon, eliminating lowland populations. I could find no match of north coast New Guinea distributions by birds and mammals. Indeed, their differentiation patterns suggest that my geographic delineation of *fusca* complex species is incorrect. Both mammals and birds show a number of taxa with Bismarck-north coast pairs. Neither of these vertebrates shows a species confined to coastal Milne Bay and the adjacent island groups. The speciation pattern tends to be single-island or island-group endemics but seldom, if ever, encompassing the broader distribution proposed for *Carlia eothen*. Savanna mammals, in particular, regularly show a SE savanna and Morehead plains pattern; a pattern present but less common for birds. This paired savanna pattern was formerly observed for reptiles, but detailed studies reveal that reptilian populations in the 2 savanna areas are different species, e.g., *Carlia bicarinata* and *C. storri*. Finally, I found no mammal distribution matching the *C. diguliensis* pattern linking the Digul drainage area with Aru but excluding the south-central IJ coast.

What does this general lack concordance indicate? Foremost, it re-enforces my uncertainty on the accuracy of species boundaries within the *C. fusca* complex; however, with possible exception of some bird groups, the absence of concordance likely highlights weak geographic sampling (e.g., Wallach's blindsnakes) and/or absence of in-depth geographic analyses (Malnate & Underwood, excepted) of New Guinean amphibians, reptiles, and mammals. Although *C. fusca* complex speciation is only weakly or not supported by the preceding distributional comparisons, the SE savanna,

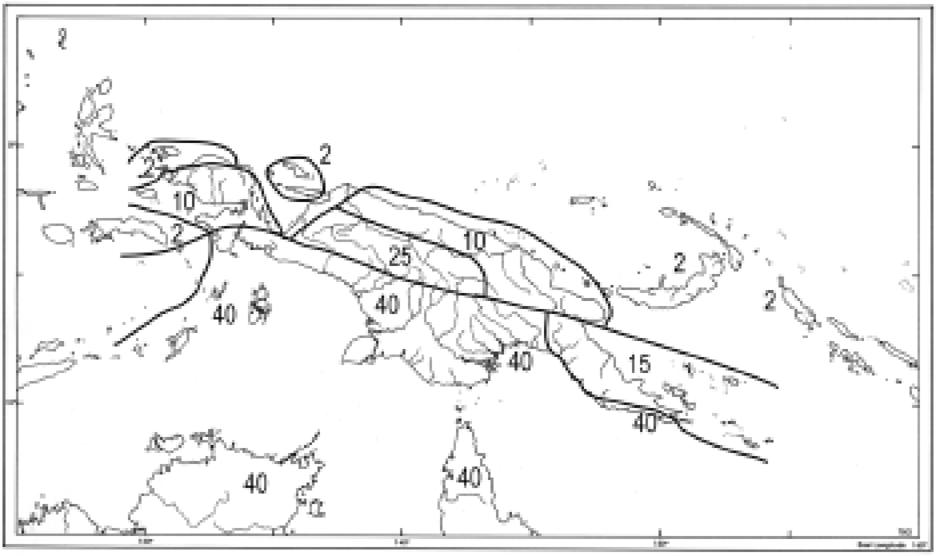

Figure 26. Schematic depiction of the geologic ages of the craton (40 Ma) and terranes (25, 15, 10, & 2 Ma) creating present day New Guinea. Reconstruction derives from Pigram and Davies (1989) as redrawn by van Welzen (1997) and others.

Milne Bay environs and islands, Papuan Gulf, and central IJ lowland populations are morphologically well-supported speciation foci for the *C. fusca* complex. I also am confident of the speciation of the north coast *C. fusca* and *C. pulla*, and the Admiralty *C. ailanpalai*.

If *C. fusca* complex species are not matching other vertebrate, do they match other animal or plant groups and equally critically do they show any concordance with post-mid-Miocene geological events? Several botanical studies offer excellent comparative bases and geological scenarios for examining the potential speciation foci of the *fusca* complex. Again, I offer only a superficial comparison to highlight a few fits for this complex.

Van Welzen (1997) examined the distribution of Malesian plant endemics relative to the Pigram & Davies (1989) accretion model of New Guinea evolution. In van Welzen's distributional model (1997:fig. 19), he recognized 10 areas (Fig. 26) for examining endemicity: 1) Craton, 40 Ma: 2) Central mountains, 25 Ma; 3) North-central lowland, 25 Ma; 4) Peninsula mountains, 15 Ma; 5) Peninsula lowland, 15 Ma; 6) Vogelkop, 10 Ma; 7) North lowland, 10 Ma; 8–10) Waigeo, Bismarck, Bougainville, 2 Ma. He also recognized that the accretionary and tectonic history was much more complex than portrayed by his model but noted that the simplifications facilitated analysis. I will ignore the mountain areas, other than recognizing the role of mountains in the isolation of populations. The 40-Ma craton area currently harbors 6 species of the *Carlia fusca* complex but offers no explanation for the evolution of the mainland species (*aenigma*, *aramia*, *diguliensis*, and the unnamed south-central IJ population). I am disinclined to suggest that the recent Pleistocene sea level fluctuation isolated the insular taxa. The origin of *C. beccarii* on Kai and *C. babarensis* on the Tanimbars likely results from a more ancient isolation event and similarly for *C. luctuosa* on a 40 Ma land wedge in south-central PNG. Presently no *fusca* complex member is endemic to the 25-Ma areas. The peninsula lowland 15-Ma unit provides for the possible differentiation of *C. eothen*, and the lowland 10-Ma for the evolution of *C. pulla* and *C. mysi* but not for their differentiation in this area. Waigeo 2 Ma allows for the differentiation *C. fusca*, and subsequent appearance of this species in the northern Vogelkop.

Entomologists (e.g., de Boer & Duffels, 1996; Polhemus & Polhemus, 1998) have contributed greatly to interpretation of Malesian-Melanesian biogeography and have outlined a number of scenarios for the geological history of New Guinea and more broadly for the landmasses from Sundaland into the Southwest Pacific. Because all these scenarios derive from the same group of geological studies, they all portray a similar history to that presented above. In all cases, the major aspects are ancient ones beginning at Eocene-Oligocene boundary with the first major events of the collision of the Australian plate with the Asian one. As the entomologists have noted, these ancient events are more appropriate for the examination of cladogenesis in families and genera, rather than providing a ready interpret of the current distribution of species. Tentatively molecular data (Stuart-Fox et al., 2002) suggest a rapid diversification of *Carlia* during the mid to Late Miocene; details of the geologic and environmental events of this time are too sketchy to map the isolation of populations and their subsequent speciation for any New Guinea *fusca* complex member.

Further biogeographic analysis will require a phylogenetic hypothesis of the *fusca* complex member's relationships. As noted in the preceding morphological analysis and discussion, a substantial hypothesis will not derive from morphological data. A reliable hypothesis of relationships will require molecular data and a dense geographic sampling of populations. *Carlia* is only one component of the New Guinean herpetofauna that has widespread geographic differentiation that is masked by morphological uniformity. To uncover these patterns of evolution, a molecular approach is necessary but must have as many or more regional samples than examined here.

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APPENDIX

Table A. **Specimens examined**, ***Carlia* phylogenetic analysis**.

C. amax. WAM R45018, R46828, R46946, R60792, R74055, R77147, R83599-600, R96839, R101390, R101420.

C. babarensis. See Table D, locality 69.

C. beccarii. See Table D, locality 67A.

C. bicarinata. MCZ R102566, R102572, R102574, R115544, R1155446-549, R115552-554; R135531; USNM 213076, 213083-084, 213090, 213095, 213112, 2131135, 2131137, 213153, 213155, 213924, 213927, 213932, 213935, 213938, 213942, 213944, 231947-948, 231951, 231954-155, 231967-168.

C. coensis. AMS R16294, R16332; MCZ R37170-171 (paratype & holotype).

C. diguliensis. See Table D, locality 55.

C. dogare. AMS R6951, R36515, R37197, R37211, R133216-217.

C. fusca. See Table D, locality 1.

C. gracilis. WAM R13610, R13615, R40477, R43133, R44471, R56375-377, R56381, R77053, R99493.

C. jarnoldae. AMS R142656-657, R143179, R21319, R28463, R3702, R63793, R63856, R87148, R87155, R87161.

C. johnstonei. WAM R97999, R98007, R99422-423, R99438, R99497, R100026-029, R100031-033.

C. leucotaenia. See Table D, locality 70.

C. longipes. AMS R86698-699, R86701, R86711-712, R86715, R86979, R115290, R115293-294; WAM R13501, R13931.

C. luctuosa. See Table D, locality 36.

C. munda. WAM R90791, R99815, R100732, R102180-181, R126003, R126030, R126042, R126050, R135264, R135423.

C. mundivensis. AMS R62482, R113417-420, R113423-425, R142658, R143186, R143197.

C. parrhasius. QM J58678-682, J58999.

C. pectoralis. AMS R81092-093, R81147-148, R81893, R81969, R89657; WAM R45005-007, R45607.

C. peronii. BMNH 1946.8.10.81, 1946.8.16.32, 1946.8.17.58 (syntypes, *spinauris*); MNHN 3037 (holotype, *peronii*); WAM R107305, R107312, R107312, R107319-320, R107322, R107328-340, R107343, R107345, R107355; ZMB 47918-920.

C. pulla. See Table D, locality 9.

C. rhomboidalis. AMS R87116, R87118, R87125, R87127, R87136, R114029, R126075; WAM R9902-903, R64489.

C. rimula. AMS R94198, R94200.

C. rostralis. WAM R45601-602, R45609,R55831, R64490.

C. rufilatus. WAM R23117, R23312, R23512-513, R23515, R32234-235, R58507, R79029, R116449.

C. schmeltzi. AMS R65921, R89626, R89635, R97794, R111823, R120427; WAM R21487, R55549-550, R55833, R58269.

C. scirtetis. AMS R26719, R64158, R64160-161.

C. storri. PNGM R1178-79, R1431-33, R1435-41; USNM 525748-752.

C. tetradactyla. AMS R75074, R76691-693, R76696, R81691, R87560, R88489-490, R96640.

C. triacantha. WAM R61702-703, R79066, R83612-613, R83626, R83966, R84460, R94829, R95323, R96829, 99649.

C. vivax . AMS R93976, R112029, R113323, R120392, R139143, R141619, R146111; WAM R45000-001, R45003, R45603-604.

OUTGROUP

Lampropholis delicata. USNM 518627-628, 518630-632, 518634-637, 518644-645, 518737.
Lygisaurus “*curtus*”. BNMH 1946.8.17.85-88 (syntypes).
Lygisaurus “*novaeguineae*”. USNM 232257-263, 232265-266, 232270.
Saproscincus mustelinus. USNM 120897-899, 120901, 120903-907, 120912-913, 120915, 120920.

Table B. **Gazetteer of sample localities**, ***Carlia* “*fusca*” analysis**.

These samples contain the entire character data set and are the ones subjected to statistical analyses; sample size is total and adult females, adult males, juveniles & unknowns are in brackets. Each sample is assigned a unique integer to identify its position on the sample distribution map (Fig. 6) and a name to facilitate discussion within the text. The localities are arranged roughly in a clockwise manner from Waigeo Island, the type locality of *Carlia fusca*. Topotypic samples are in bold. Spelling of geographic names follows Mottler (1986), The Times Atlas of the World (10th ed.; 1999), National Geographic Atlas of the World (5th ed.; Hall 1981), and miscellaneous other sources with priority of use given to Mottler, et seq. Latitude and longitude for each sample derive from Loveridge (1948)$^{\mathrm{LV}}$, NIS Gazetteers$^{\mathrm{NS}}$, and The Times Atlas$^{\mathrm{TA}}$.

Locality (**No**. / **Name**)	**Latitude & Longitude**	**Sample Size**
MAJOR SAMPLES		
1 **Waigeo** (Is.)	0° 10'S 130° 35'E $^{\mathrm{LV}}$	21 [12, 7, 2]
3 Manokwari	0° 52'S 134° 05'E $^{\mathrm{NS}}$	19 [10, 6, 3]
6 Toem	2° 00'S 139° 01'E $^{\mathrm{NS}}$	20 [8, 12 ,0]
9 **Humboldt Bay** [Jayapura]	2° 35'S 140° 45'E $^{\mathrm{LV}}$	22 [11, 9, 2]
10 Vanimo	2° 40'S 141° 18'E $^{\mathrm{NS}}$	24 [12, 12, 0]
11 Aitape	3° 08'S 142° 21'E $^{\mathrm{NS}}$	08 [5, 3, 0]
12 Wewak	3° 34'S 143° 38'E $^{\mathrm{NS}}$	09 [4, 3, 2]
14 Karkar (Is.)	4° 40'S 146° 00'E $^{\mathrm{NS}}$	20 [10, 10, 0]
15 Madang	5° 13'S 145° 48'E $^{\mathrm{NS}}$	23 [18, 3, 2]
17 **Finschhafen**	6° 34'S 147° 51'E $^{\mathrm{NS}}$	20 [11, 9, 0]
18 **Admiralty** (Ids.)	2° 05'S 147° 00'E $^{\mathrm{NS}}$	35 [15, 17, 3]
20 Lavongai [New Hanover]	2° 30'S 150° 15'E $^{\mathrm{NS}}$	09 [3, 6, 0]
21 New Ireland	3° 20'S 152° 00'E $^{\mathrm{NS}}$	41 [20, 17, 4]
22 New Britain	4° 12'S 152° 12'E $^{\mathrm{NS}}$	29 [14, 12, 3]
23 Bougainville	6° 00'S 155° 00'E $^{\mathrm{NS}}$	19
A. Sohano (Is.)	5° 15'S 154° 35'E $^{\mathrm{NS}}$	05 [1, 4, 0]
B. Buin	6° 50'S 153° 42'E $^{\mathrm{TA}}$	05 [3, 1, 1]
C. Shortland Is.	10° 32'S 151° 05'E $^{\mathrm{NS}}$	09 [5, 4, 0]
24 Popondetta	8° 46'S 148° 14'E $^{\mathrm{NS}}$	13 [6, 3, 4]
25 Kokoda	8° 52'S 147° 45'E $^{\mathrm{NS}}$	08 [5, 1, 2]
27 Menapi [Cape Vogel]	9° 46'S 149° 56'E $^{\mathrm{NS}}$	20 [12, 8, 0]
28 Milne Bay	10° 22'S 150° 30'E $^{\mathrm{NS}}$	21 [11, 10, 0]
29 D’Entrecasteaux Ids.	9° 40'S 150° 50'E $^{\mathrm{NS}}$	20 [12, 6, 2]
30 **Trobriand Ids**.	8° 40'S 151° 07'E $^{\mathrm{NS}}$	18 [6, 10, 2]
31 Muyua (Is.) [Murua or Woodlark]	8° 44'S 151° 00'E $^{\mathrm{NS}}$	12 [4, 6, 2]
32 Louisiade Archipelago	11° 12'S 153° 00'E $^{\mathrm{NS}}$	11 [4, 3, 4]
33 Kapakapa	9° 48'S 147° 30'E $^{\mathrm{NS}}$	12 [8, 4, 0]
34 Boroko	9° 33'S 147° 10E $^{\mathrm{NS}}$	11 [8, 3, 0]
35 Sogeri	9° 31'S 147° 25'E $^{\mathrm{NS}}$	30 [11, 13, 6]
36 **Inawi**	8° 37'S 146° 33'E $^{\mathrm{NS}}$	40 [19, 21, 0]

Table B (**continued**).

Locality (**No. / Name**)		**Latitude & Longitude**	**Sample Size**
37	Okassa [nr. Okapa]	6° 31'S 145° 39'E $^{\mathrm{TA}}$	10 [5, 2, 3]
38	Kundiawa	6° 01'S 144° 55'E $^{\mathrm{TA}}$	36 [16, 18, 2]
39	Baiyer River	5° 33'S 144° 55'E $^{\mathrm{NS}}$	25 [14, 8, 3]
40	Uraru	6° 53'S 144° 52'E	21 [15, 6, 0]
42	Waro	6° 32'S 143° 11'E $^{\mathrm{TA}}$	12 [6, 6, 0]
43	Emeti	7° 52'S 143° 15'E $^{\mathrm{TA}}$	32
	A. Emeti I	7° 52'S 143° 15'E $^{\mathrm{TA}}$	17 [10, 7, 0]
	B. **Emeti II**	7° 52'S 143° 15'E $^{\mathrm{TA}}$	15 [7, 8, 0]
44	**Balimo**	8° 03'S 142° 56'E $^{\mathrm{NS}}$	26 [12, 14, 0]
45	Oriomo	9° 02'S 143° 11'E $^{\mathrm{NS}}$	21 [11, 10, 0]
46	Daru (Is.)	9° 05'S 143° 12'E $^{\mathrm{NS}}$	20 [10, 7, 3]
47	Boze	9° 03'S 143° 03'E $^{\mathrm{NS}}$	09 [7, 1, 1]
48	Mabaduan	9° 16'S 142° 44'E $^{\mathrm{NS}}$	12 [6, 6, 0]
49	Morehead	9° 09'S 141° 19'E $^{\mathrm{TA}}$	11 [6, 5, 0]
50	Maka, Lake Murray	7° 00'S 141° 30'E $^{\mathrm{NS}}$	20 [11, 9, 0]
51	Kiunga	6° 07'S 141° 18'E $^{\mathrm{NS}}$	10 [4, 1, 5]
53	Merauke [Katow]	8° 28'S 140° 20'E $^{\mathrm{NS}}$	17 [8, 9, 0]
54	Digul (River)	7° 07'S 138° 42'E $^{\mathrm{NS}}$	17 [10, 5, 2]
55	**Asike**	6° 39'S 140° 24'E $^{\mathrm{NS}}$	14 [3, 2, 9]
56	Tanahmerah	6° 05'S 140° 17'E $^{\mathrm{NS}}$	18 [15, 3, 0]
57	Tanahtinggi	5° 57'S 140° 15'E $^{\mathrm{NS}}$	12 [2, 7, 3]
58	Sibil	4° 54'S 140° 40'E $^{\mathrm{NS}}$	20 [10, 10, 0]
59	Agats	5° 33'S 138° 08'E $^{\mathrm{NS}}$	19 [8, 8, 3]
62	Gariau [Yamur (Jamaur) Lake]	3° 42'S 134° 56'E $^{\mathrm{NS}}$	20 [10, 10, 0]
63	Mandiwa [Kaimama]	3° 07'S 133° 39'E $^{\mathrm{NS}}$	18 [9, 9, 0]
65	Ayamaru [Ajamaru]	1° 16'S 132° 12'E $^{\mathrm{NS}}$	30 [13, 17, 0]
66	Aru (Kepulauan)	6° 00'S 134° 30'E $^{\mathrm{NS}}$	43 [23, 20, 0]
67	Kai (Kepulauan)	5° 45'S 132° 50'E $^{\mathrm{NS}}$	63
	A. **Kai I**	5° 45'S 132° 50'E $^{\mathrm{NS}}$	28 [10, 11, 7]
	B. Kai II	5° 45'S 132° 50'E $^{\mathrm{NS}}$	35 [15, 14, 6]
68	Tanimbar (Kepulauan)	7° 30'S 131° 30'E $^{\mathrm{NS}}$	20 (8, 7, 5)
70	**Ambon** (Is.)	3° 40'S 128° 10'E $^{\mathrm{NS}}$	41 [14, 16, 11]
71	Seram (Is.)	3° 00'S 129° 00'E $^{\mathrm{NS}}$	21 [11, 5, 5]
72	Halmahera (Is.)	1° 00’N 128° 00'E $^{\mathrm{NS}}$	25
	A. **Halmahera** (Is.)	1° 00’N 128° 00'E $^{\mathrm{NS}}$	20 [6, 14, 0]
	B. Ternate (Is.)	0° 48'S 127° 20'E $^{\mathrm{NS}}$	05 [2, 2, 1]
73	Morotai (Is.)	2° 20'S 128° 25'E $^{\mathrm{NS}}$	29 [16, 13, 0]
96	Palau (Ids.)	7° 21’N 134° 28'E $^{\mathrm{TA}}$	39 [18, 18, 3]
99	Guam [Mariana Ids.]	13° 29’N 144° 45'E $^{\mathrm{TA}}$	37 [15, 16, 6]
MINOR SAMPLES			
2	Sorong	0° 49'S 131° 13'E $^{\mathrm{NS}}$	07 [5, 2, 0]
4	Roon (Is.) [Yende]	2° 22'S 134° 07'E $^{\mathrm{NS}}$	05 [3, 2, 0]
5	**Yapen** (Is.) [Japen]	1° 41'S 135° 49'E $^{\mathrm{NS}}$	01 [unsexed adult]
7	Wakde Is.	1° 56'S 139° 01'E $^{\mathrm{NS}}$	04 [1, 3, 0]
8	**Jamna** (Is.)	2° 01'S 139° 15'E $^{\mathrm{NS}}$	01 [0, 0, 1]
13	Manam (Is.)	4° 05'S 145° 03'E $^{\mathrm{NS}}$	03 [1, 0, 2][
16	Wasu	5° 59'S 147° 12'E $^{\mathrm{NS}}$	04 [1, 0, 3]
19	Mussau [St. Matthias Gp.]	1° 25'S 149° 38'E $^{\mathrm{NS}}$	05 [3, 1, 1]
26	Collingwood Bay	9° 36'S 149° 28'E $^{\mathrm{NS}}$	08 [2, 1, 5]

Table B (**continued**).

Locality (**No. / Name**)		**Latitude & Longitude**	**Sample Size**
MINOR SAMPLES			
41	Kikori	7° 25'S 144° 15'E ^{NS}	06 [2, 0, 4]
52	Olsobip	5° 23'S 141° 30'E	03 [1, 2, 0]
60	Lorentz (River)	5° 23'S 138° 04'E ^{TA}	05 [3, 2, 0]
61	Uta [Oeta]	4° 33'S 136° 00'E ^{NS}	07 [3, 2, 2]
64	Fak-Fak	2° 55'S 132° 18'E ^{NS}	05 [4, 1, 0]
69	**Babar** (Kepulauan)	7° 50'S 129° 45'E ^{NS}	07 [0, 1, 6]
98	Yap (Is.)	9° 30’N 138° 08'E ^{TA}	04 [2, 2, 0]

Table C. **Discriminant function analysis samples sets**.

Comparisons were usually made among geographically adjacent sample localities. Comparisons begin clockwise with the *Carlia fusca* type locality: Waigeo. Numbers refer to the sample localities in Table B. An asterisk indicates a set’s proportional data was also examined by DA . Each number denotes a discrete locality-sample used in the DA; numbers in parentheses denote the combination of a set of adjacent samples into a regional sample.

MENSURAL			SCALATION		
Adult females	Adult males	All	Adult females	Adult males	All
01,03*			01,03	01,03	01,03
01,02,03*		01,02,03*	01,02,03		01,02,03
01,36*	01,36*		01,36	01,36	
03,06*					03,06
					01,02,03,04
					04,05
	06,07*				06,07
06,09*		06,09*			06,09
09,10*					09,10
09,10,11*					09,10,11
09,10,11,12*					09,10,11,12
99,18	99,18*	99,18*			99,18

All subsequent DAs examined mensural characters in the adult female portion of each locality sample and scalation in the total locality sample. These comparisons are: 12,13; 12,39; 12,13,39; 12,14; 12,13,14; (12–14),18; 12,15; 12,37; 12,38; 12,39; 12,41; 12,42; 12,43A; 12,43B; 14,15; 15,16; 15,16,17; 15,38; 15,39; 18,19,20,21,22; 18,(19–22); 19,20,21,22; 23A,B,C; 23,(19–22); 24,25; (24–25),(15–17); (24–25),(26–27); 26,27; (26–27),28; (26–27),29; 28–3 subsets; 28,29; 28,32; 29,30,31; (29,31),30; 29,33; 33,34,35,36; 36,41; 36,43A; 36–37; 37,38; 37,39; 37,42; 37,41; 37,43A; 37,43B; 38,39; 38,41; 38,42; 38,43A; 38,43B; 39,41; 39,42; 39,43A; 39,43B; 40,41; 40,43A; 40,43B; 40,43A,44; 40,43B,44; 40,44; 41,42; 41,42,43A; 41,43A; 41,43B; (41–42,43B),(45–46); 42,43A; 42,43B; 42,51; 42,(50–52); 42,52; 43A,43B; 43B,44; 45,46; (45–49),(54–55); 46,47; 47,48; 48,49; 45,46,47,48,49; 45,50; 45,55; (45–49),53; 49,50; 49,53; 49,55; 50,51,52; 50,55; 53,55; 54,55; (54–55),59; (54–55),(56–58); (54–55),66; (54–55),59; (54–55),(59–60); 55–59; 56,57,58; 59,60; 59,62; 59,66; (59–60),(61–62); 61,62; 62,63; (61–62),(63–64); 63,64; (63–64),(1–3); (63–64),66; 65,(1–3); 66,(61–62); 66,(63–64); 66,67A; 66,67B; 67A,B; 67A,(61–62); 67A,(63–64); 67A,(68–69); 67A,70; 67B,(61–62); 67B,(63–64); 67B,(68–69); 67B,70; 68,69 (adult males, not females); (68–69),70; 70,71; (70–71),(1–3); (70–71),63–65; (70–71),72A; 72A,B; 72A,73; (72A–B),(1–3); (72A–B),73; 73,(1–3); 98,99.

The following DA examined only scalation: 1,2,3,4,5; 9,(10–12); (9–11),12; (72A–B),73; 73,(1–3); 96,(1–3); 96,4; 96,6; 96,11; 96,12; 96,18; 96,72A; 96,73; 96,98; 96,99; 98,99; 99,(1–3); 99,4; 99,6; 99,11; 99,12; 99,18; 99,72; 99,73.

Table D. **Specimens Examined**, ***Carlia* “*fusca*” analysis**.

The arrangement follows the sequential numbering of Table B for the locality samples. Museum name abbreviations follow the recommended standards of Leviton *et al*. (1985). Type specimens are in bold. Locality data beyond the sample place name is in parentheses following the museum number(s).

Carlia fusca

1 Waigeo. MCZ R7873, R42718–723; MNHN **3036** (lectotype: *fuscum*); USNM 40029–031; ZMA 15311[10].
2 Sorong. MCZ R7675[3]; RMNH 8853[4].
3 Manokwari. MCZ R7679[9]; MNHN 5095[2] (Mansinam I.), 5129[3] (Andai); RMNH 30307-310, not cataloged[1]; ZMB 8784.
4 Roon Island. MCZ R7684; RMNH 5276, 8849[2]; ZMA not cataloged.
5 Yapen Island. ZMB **8784** (neotype: *tricarinatus*).
6 Toem. USNM 119306, 119308-311, 119313-320, 119322, 119325-327, 119329, 119331, 119333.
7 Wakde Island. RMNH 30303-306.
8 Jamna Island. MCZ R**7677** (holotype: *jamnanum*).

Carlia pulla

9 Humboldt Bay. MCZ R**7486** (holotype); RMNH 4964, 5814[9] (Sentani Lake); ZMA 15312[10] (Hollandia & Sentani Lake); USNM 119303 (Hollandia).
10 Vanimo. USNM 232066-075, 232078-083, 232085, 232090, 232092-093, 232095, 232097-098, 232100.
11 Aitape. MCZ R581-582, R583[3]; RMNH 851[3].

No species assignment

12 Wewak. AMS R30791-792, R31511, R31513, R31516, R31518; USNM 213192-194.

Carlia mysi

13 Manam Island. IRSNB 25848[3].
14 Karkar Island. AMS R25115-118, R25120-133, R25136, R25138.
15 Madang. AMS R127477-478, R127482-483, R127491, R127494-495, R127502, R127508, R127614 (Finalbin village); MCZ R125398, R125401-402, R25404, R125406-408, R125410-415, R132784, R150826; PNGM R2001-04; RMNH 4441[4] (Astrolabe-baai).
16 Wasu. MCZ R145962-965.
17 Finschhafen. USNM **119259-265**, **119269** (holotype), **11270-277**, **119291-293**, **119296**.

Carlia ailanpilai

18 Admiralty Ids. BPBM **1657** (Los Negros I.); MCZ R**137644**, R137645, R**137674**, 137675, R**141312-313**, R153027, R154603-604, R154606 (Manus); PNGM **24693**, **24696-699**, **24701**, **24703-706** (Rambusto I.); USNM **120889-891** (Ponam I.), **122324** (Los Negros).

Carlia mysi

19 Mussau. MCZ R150282; USNM 120892; ZMB R47659 (Talumalaus), R47670 (Talsital), R47853 (Talumalaus).
20 Lavongai. AMS R69440 (Lukus I.); MCZ R152792-794, R152796-799 (Lukus I.); ZMB R47660.
21 New Ireland. AMS R64927-930, 69441-442 (Kavieng); MCZ R145356 (Kalili Bay), R152780-784 (Kavieng), R152786 (Kavieng), R152791 (Namatanai); IRSNB Mys colln. [19], unable to match originally untagged specimens with newly assigned catalog numbers (Letet); ZMB R47661-668 (Kalili Bay).

Table D (**continued**).

Carlia mysi (continued)

22 New Britain (Rabaul). AMS R64939-40; MCZ R64275-277, R64279-81, R64283-84, R64287-290, R64292-293, R72532-533, R78379-380, R88378; NMW 9946[2], 9947[2], 9949[2]; USNM 61837; ZMB 9447[2]; ZMB R47669.

23 Bougainville.
  23A Sohano Island. MCZ R67685-688, R73792.
  23B Buin. MCZ R65865-867, R96182, R97314.
  23C Shortland Island. MCZ R89699-702, R89704-708.

24 Popondetta. AMNH 95231-235; AMS R12798, R12800 (Dobodura); MCZ R141072, R152775, R152800-801, R154598-599.

25 Kokoda. AMNH 95223-25, 95228; USNM 232108-111.

26 Collingwood Bay. AMNH 74002-05, 74087, 74275-276, 74370.

27 Menapi. AMNH 74151, 74213-215, 74220-22, 74228, 74230, 74232, 74237-338, 74240-742, 74245, 74247, 74249, 74256, 74306.

Carlia eothen

28 Milne Bay. AMS R129500-501, R132240, R132245, R132249-250, R132257 (all preceding: Sideia I.), R132267, R132273, R132277, R132281, R132285 (preceding: Sariba I.); BPBM 4130 (Alotau); MCZ R146101 (Alotau); USNM 119186-188 (M.B. Mission, possibly Keia 10°31'S 150°34'E), 201631-632, 201634 (Allatai, coast opposite Samari).

29 d’Entrecasteaux Islands. AMNH 74288, 74298, 74300 (all Goodenough I.), 76783-784 (Fergusson I.); AMS R129797, R129799, R129801, R129820, R129864, R129870 (all Normanby I.); MCZ R146084-092 (Goodenough I.).

30 Trobriand Islands. AMNH **20920** (Trobriand); AMS **R47145-146**, **R47147** (holotype), **R47148-150**, **R47154-160**, R47161 (preceding: Kiriwina I.); USNM **192883**, **525758** (Kuyau I.), **560092** (Kiriwina).

31 Muyua Island. AMNH 76799, 76808; AMS R124831, R124865, R124871-873, R124876, R125193, R125196; MCZ R142478, R142489.

32 Louisiade Archipelago. AMNH 76739 (Rossel I.), 76757-760 (Sudest I.), 76847 (Misima I.), 76850 (Misima I.); AMS R48333 (Louisiade A.), R124949 (Misima I.); USNM 201635 (Wari I.), 201648 (Panaeta I.).

Carlia luctuosa

33 Kapakapa. USNM 232204, 232206-016.

34 Boroko. MCZ R145961, 152006; PNGM R109-10; UMMZ 181191A; USNM 232198-201, 23224-225.

35 Sogeri. AMNH 102229 (Rouna Falls); MCZ R102893 (McDonald’s Corner), R102909 (Rouna Falls), R102936, R102938-941, R146083, R152008, R152010 (Rouna Falls), MCZ/fs 40744[3] (Sogeri); PNGM R85 (Subitana), R331, R355 (Rouna Falls), R356-58 (Sogeri), R472-76 (Itikinumu Plateau), R519-22 (Sogeri); UMMZ 181191B (Rouna Falls).

36 Inawi. BMNH **1946.8.17.67** (holotype: *nigrigulare*), USNM 232113-143, 232146, 232149, 232151-154, 232156-157.

No species assignment

37 Okassa. MCZ R102913-916, R102918-921, R102923, R102929.

38 Kundiawa. AMNH 75383-391 (Kondiu), 98515-516, 98519-520, 98522, 98541-543, 98545-546; MCZ R84448 (Wahgi R.), R88621-623 (Bomai), R88627 (Wahgi R.), R88629 (Wahgi R.); PNGM R965-66, R871-873 (Kundiawa); USNM 166263-264, 166269-271 (Kundiawa).

Table D (**continued**).

No species assignment (continued)

39 Baiyer River. AMNH 101113, 103282-286; MCZ R99202, R99204-205, R99209, R99213, R99215, R99217, R99219-21, R99223-225, R99227-228, R102899-900; PNGM R585; USNM 166224.
42 Waro. AMS R122697 (Namosado), R122700-702, R122705, R122710-711, R122718, R122720, R122732, R122740-741.

Carlia aenigma

40 Uraru. AMNH 102227-228; FMNH 169910-913; MCZ R102960-962, R102964-965, R102968, R102970-972, R102974-977; PNGM R832-33.
41 Kikori. MCZ R150827; USNM **232061-065**.
43B Emeti II. MCZ R**141852-853**, R**141859**, R**141873**, R141876, R**141880** (holotype), R**141882**, R**141889-891**, R**141893**, R**141897**, R**141901**, R**141917**, USNM **560084**.

Carlia aramia

43A Emeti I. MCZ R141856, R141860, R141862, R141865-867, R141869, R**141875** (paratype), R141877, R141896, R**141900** (paratype), R141905, R141908-909, R1419670, R141985.
44 Balimo. USNM **167677**, **232013-014**, **232016-017**, **232019-023**, **232024** (holotype), **232025-029**, **232032-036**, **232043-048**, **525759**.
45 Oriomo. AMS R23698, R23700, R23709, R23718, R23728, R23745, R23749; MCZ R135652, R135674, R135676, R135688, R135705, R135724, R135749, R135755, R135766, R135793, R135803-805, R135869.
46 Daru Island. MCZ R123607, R123612-613, R123619, R123621, R125267-271, R125274, R141297-98; USNM 167686[2], 167688[5].
47 Boze. PNGM R1102, R1175-76, R1655-57; USNM 167700[3].
48 Mabaduan. MCZ R134794-795, R134798, R134813, R134817-819, R134839; USNM 195875[4].
49 Morehead. MCZ R135510, R135512, R135516-517, R135577, R135579, R135582, R135584, R134487, R137601-602.
50 Maka. MCZ R123540-541, R123543, R123546-553, R125306-307, R125309, R125311-313; PNGM R1131-33.
51 Kiunga. MCZ R123600-604, R125298-300, R137662; PNGM R1174.
52 Olsobip. CAS 127257; MCZ R125399-400.

No species assignment

53 Merauke. ZMA 15327[17].

Carlia diguliensis

54 Digul River. RMNH 25729-737, 25750-756, not cataloged [1].
55 Asike (*diguliensis*). BMNH **1946.8.16.58**; NMW **9954**, **16632**; RMNH **5084**, **5509** (lectotype), **25765-768**; MCZ R**38977-979**, R**38981**, not cataloged [1].
56 Tanahmerah. RMNH 25739, 30251-260, 30282-288
57 Tanahtinggi. RMNH 19465-468, 19470-471, 19473-475, 19482, 19484, not cataloged [1].
58 Sibil. RMNH 30162-164 (Mibibabul= ?Mabilabol), 30165-181.

No species assignment

59 Agats. IRSNB 24.868[19].
60 Lorentz River. ZMA 15315[2], not cataloged [3].
61 Uta. RMNH 30392-398.

Table D (continued).

No species assignment (continued)

62 Gariau. RMNH 30380-388, not cataloged [11].

63 Mandiwa. RMNH 30340-357.

64 Fak-Fak. MCZ R7309; RMNH 6745 (Babo), 7295, 303378-379.

65 Ayamaru. RMNH 30358-377 (Ayamaru), not cataloged (Semu [2], Djitmau [5], Takum [2]).

Carlia diguliensis

66 Aru. NMW 9945[8]; SMF 14717-720 (Wamar), 14723-724 (Wamar), 14726-727 (Wokam), 14729-731 (Terangan); WAM 109598-601, 109603, 109606-607, 109611, 109790, 109792, 109794, 109799, 109809-810, 109812, 109817, 109832 (all Wokam); ZMB R7965[4].

Carlia beccarii

67A Kai I. AMNH 108574-576 (Taam I.); AMS R141811, R141817-818, R141822 (all Kai Besar); MCZ R33537; WAM 109643; ZMA 15330 [2] (Gn. Daab), 14550[14] (Kai Besar); ZMB R47931, R47941-943 (Kai Besar).

No species assignment

67B Kai II. SMF 14734-738 (Kei Dulah), 14752-755 (Elat), 14763 (Langgur); WAM 109676-677, 109692, 109707, 109726, 109831; ZMA 15324 (Kei Doelah); ZMA 14550[5] (Kai Besar), 14552 (Toeal), not cataloged [6] (Elat); ZMB R47932-935 (Elat), R47937 (Elat), R47943.

Carlia babarensis

68 Tanimbar. BMNH **1946.8.10.89**, MCZ R**38982-990**; RMNH **5092**, **5511**, **25781-784**; WAM 112254, 112330, 112361-62 (Yamadena).

69 Babar. RMNH **5083**, **5518** (lectotype), **5815**, **25774-775**, **25777-778**.

Carlia leucotaenia

70 Ambon. BMNH 57.10.28.74, 82.8.29.156-163; 1913.10.31.45-54; RMNH 30311-325; ZMB **4951**[6] (syntypes: *schlegelii*) .

71 Seram. BMNH field series S168-169 (Wahai), S176-77 (Wahai), S190, 193-94, 196, 200, 208, 215 (Sanulu); MCZ R7681[3] (Wahai); SMF 14709-710 (Saparua I.); USNM **204786** (neotype), 204787-790 (Piru Bay); WAM 109401-402, 109413-414, 109416-417, 109419, 109421-422, 109424-427, 109437, 109442-443, 109458, 109460, 109462, 109470-471, 109485 (Bandi).

Carlia tutela

72 Halmahera

    72A Halmahera: RMNH **6965**[2]; USNM **215857-858**, **237397-401**, **217403** (holotype), **217404-405**, **217409-10**, **217413-418** (all from Pasir Putih).

    72B Ternate. MCZ R7676[5].

73 Morotai. BYU 7339, **7340-41**, 7342, 7349-50, **7351**, **7353**, 7392-93, **7400**, 7402, 7405-06, **7412-14**, 7443, 7589, **7620**, **7622-23**, **7625-27**, **7630**, 7787; RMNH **8659**; USNM **560143**.

96 Palau. USNM 284564-566, 495072, 495074-076, 495078-082, 495087, 560120, 560124, 560130-133, 560824, 560827-829, 560833, 560836-37, 560845, 560849-850, 560854, 560857, 560867, 560873, 560879, 560915-16, 560918-819, 560921.

Table D (**continued**).

Carlia ailanpalai

98 Yap. USNM 560094-097.

99 Guam. FMNH 176941-943 (Saipan); MSB 46097-101, 46103-112 (Guam); USNM 192894-895, 506400-406, 506409-410, 506412-414, 506418, 506420, 506423, 506427-428 (Guam).

Table E. **Specimens Examined**, **but not part of the 76 sample localities**.

The arrangement is alphabetical by species name. Museum name abbreviations follow the recommended standards of Leviton *et al*. (1985). IJ, Irian Jaya; PNG, Papua New Guinea.

aenigma
PNG: Balimo. USNM **232018** (paratype); Emeti. MCZ R141856, -860, -862, -864, -865, -867, -875, -877, -896, R141900, -908.

ailanpalai
PNG: Los Negros I. USNM **560085** (holotype), **560086-091** (paratypes); Manus I. IRSNB **2581-2583** (paratypes); Rambutyo I. USNM **560093** (paratype). Mariana Islands: Guam USNM 323715-16 (hatchlings); 506258-506439. Micronesia: Kosrae USNM 284572.

aramia
PNG: Balimo ZFMK 38326-28; Emeti MCZ R**141900** (paratypes), USNM **525767-768**, **525771**, **525773**, **525775** (paratypes); Maka PNGM R1131-33.

babarensis
Babar ZMB 14204[3].

diguliensis
IJ: Digul R. NMW 995, 16632; Kauh Digul RMNH not cataloged [16]; Mabilabol RMNH not cataloged [1]; North River ZMA 15315; Ok Sibil Basik RMNH not cataloged [20]; Takum RMNH not cataloged[[2]. Aru: WAM R109491, R109494-495, R109487, R109501-502, R109504-505, R109507, R109513, R109596-597, R109600, R109602-604, R109611, R1096617-618, R109786-787, R109789, R109798, R109803, R109807, R109816 [color ontogeny series]; ZMB 47916-17.

eothen
PNG: Bubaleta village USNM 560098; Netuli I. USNM 560099; Lelgalu village USNM 560100; Cloudy Mtns. USNM 560101-103.

fusca
IJ: Babo RMNH 6745 (from stomach of an *Aspidomorphus*); Padaido Ids. USNM 120353; Sabang ZMA 15322.

leucotaenia
Ambon: NMW 9953, ZMA 15320, 15328.

luctuosa
PNG: Brown River MCZ R145961, R152006; Mt. Diamond MCZ R152760.

Table E (**continued**).

mysi

PNG: Awaiama . USNM 560105-106; Bunibuni; USNM 560113-114; Cloudy Mtn. USNM 560118; Finschhafen BPBM-AA 12887-900; Gusika IRSNB **2584** (paratype), USNM **119266**, **119268**, **119278-290**, **119294-295**, **119299-302** (paratypes); Iapoa . USNM 560107-111; btw Kokoda and Popondetta. USNM 23107 (hatchling, pulla pattern); Lelegalu . USNM 560117; Little Ndrova Valley MCZ R141351-353; Madang ZMB R47659, 47670, 47853; Mioko MNW 9949[2]; Mt Wilhelm. MCZ R47097 [pulla pattern]. Netuli I. USNM 560115-116; Bismarck Archip,. NMW 9948[2]; Duke of York I. AMS R142990; New Britain ZMB 14608[2]; Tyaul I. ZMB R47675; Wanigela USNM 560104.

pulla

IJ: Sentani Lake ZMA 15312[22]; Sermonwai ZMA 15317; Teluk Yos Sudarso USNM 119303, ZMA 15314[13]. PNG: Finalbin village AMS R127477-478, -482-83, -491, -494-95, R127502, -508, R127614.

tutela

Halamahera: USNM **237402**, **237408**; Morotai: USNM **159958**. Palau: USNM 207007-015, 207034, USNM 560119-125.

No species assignment

IJ: Astrolabe-gebirge NMW 9938[3]-39[3]; Bivak I. ZMA 15321; Freeport area BPBM-AA 14821-822, -14825-826, 14875-880, 14931-934, 15004, 15009, 15012-015, 15167-172, 15717, 15720-725, 16059,16062-063; Lavongai ZMB R47660; Sabang ZMA 15322.
PNG: Chimbu AMS R115643; Musha I. IRSNB 15719 [16]; Ninbo I. IRSNB 15874 [11]; Wewak BPBM-AA 11548-553; Wonenara MCZ R152239-240.