The Terrestrial Herpetofauna of the Loyalty Islands¹

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ABSTRACT: The terrestrial herpetofauna of the Loyalty Islands, New Caledonia, is reviewed. This is the first comprehensive account of the reptile fauna of these islands since Roux's monograph on the region in 1913 and is based on recent collections made in August 1987 and a review of the collections made by Roux and Sarasin and housed in the Naturhistorisches Museum, Basel. Seventeen species of lizards and two species of snakes (one boid and one typhlopid) occur in the Loyalty Islands. Approximately half the lizard species are endemic to the New Caledonia/Loyalty Islands region, but only one, *Emoia loyaltiensis* (Roux), is endemic to the Loyalties alone. The remaining lizard species have widespread distributions throughout the Pacific. Most widespread species also occur on mainland New Caledonia, but several (*Gehyra vorax* Girard, *Emoia cyanura* [Lesson], and *Candoia bibroni* [Duméril & Bibron]) do not.

THE LOYALTY ISLANDS lie in a line parallel to and ca. 110 km northeast of New Caledonia and 260 km southwest of the southern islands of Vanuatu (Figure 1). The Loyalties are separated from New Caledonia by the Loyalty Basin (<2000 m depth) and from Vanuatu by the Vanuatu Trench (>7000 m depth). From northwest to southeast the major islands of the Loyalties are Ouvéa (160 km²), Lifou (1150 km²), and Maré (650 km²). Also included are a series of smaller islands, mostly lying between Lifou and Maré; the largest of these is Tiga. Walpole Island (Île Walpole), located some 160 km southeast of Maré, is also an emergent island on the same extension of the Norfolk Rise but is often not included in discussions of the main Loyalty Group.

All the islands are low-lying, with the highest elevation of 138 m near the southern point of the island of Maré. The islands are coralline in structure and are the remains of a Miocene reef situated atop a volcanic chain (Paris 1981, Sautter 1981). The raised rims of the islands represent uplifted coral reefs, and the interior regions of the islands are the uplifted lagoons or reef flats. On Lifou and Maré, parts of the interior

are covered by shallow bauxitic soils (Sautter 1981), and on Maré, small basaltic outcrops, representing emergent elements of the volcanic base of the Miocene reef, are also present (Paris 1981). The most substantial uplift of the islands was very recent, probably dating from the late Pleistocene (Paris 1981), and it seems likely that the Loyalties have been continuously emergent only since that period. Rainfall in the Loyalties is similar to that of the drier western part of the New Caledonian mainland. On Lifou, rainfall decreases from ca. 1700 mm per year in the north to under 1300 mm per year in the southwest (Sautter 1981). A similar trend affects Maré, whereas all of Ouvéa experiences low precipitation (1200-1300 mm per year). There is no notable standing or flowing fresh water on any of the Loyalties, and most precipitation enters freshwater lenses within the permeable coralline substrate.

In comparison with the more geologically complex New Caledonian mainland, the Loyalty Islands support a restricted range of vegetation types. Extensive stands of *Araucaria columnaris* (Forster) occur on the southern coasts of both Lifou and Maré (Schmid 1981), and mangroves (*Rhizophora* spp.) are present in some areas. Coastal regions support typical littoral vegetation including coconuts and *Casuarina*, whereas inland areas are covered by humid forest. On Lifou, *Schefflera* spp. are among the dominant

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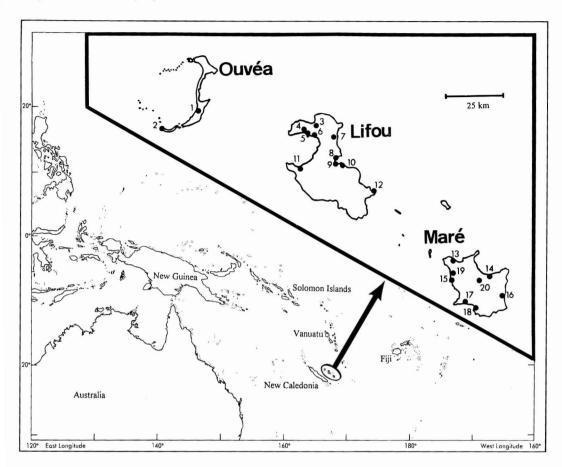


FIGURE 1. Loyalty Islands, showing the localities represented by specimens examined or reviewed in this paper. Numbered localities are identified in the Materials and Methods section. Southwestern Pacific map courtesy of George R. Zug (U.S. National Museum of Natural History).

forest trees (Schmid 1981). Inland forests are reasonably diverse, Acacia spirorbis Labillardière, Pandanus spp., Ficus spp., and Elaeocarpus spp. are among the important components of these areas (Däniker 1931). South-central Maré alone supports grassy savanna vegetation. Human impact on the native vegetation is most pronounced on Ouvéa, which has the highest human density, but much of the central plateaus of the larger islands is also covered in secondary growth. The original vegetation of Ouvéa may have differed somewhat from that of the larger, higher islands, owing to somewhat drier conditions and less diverse microhabitats (Däniker 1931). Both floristically (Däniker 1931, Thorne 1969) and faunistically (Sarasin 1925, Bauer 1988), the Loyalties are clearly part of the New

Caledonian region, characterized by extremely high levels of endemism for most groups. Although there are some taxa endemic to the Loyalties alone (Däniker 1931), most plants and animals are shared with the New Caledonian mainland. Nonetheless, the Loyalties do show greater affinities to islands to the north and east than does the mainland. This is a result of both a greater absolute number of shared taxa and a lower number of endemic forms than on New Caledonia proper.

Knowledge of the reptile fauna of the group is largely limited to the three largest islands of Maré, Lifou, and Ouvéa. Lizards seem to have played an important role in local folklore and belief (Hadfield 1920, Anonymous 1985). European herpetological investigations in the Loyal-

ties began with Bavay (1869), but the only substantial contributions stem from the collections Fritz Sarasin and Jean Roux made on the three main islands in 1911 and 1912. Although the remains of fossil meiolaniid turtles have been recovered from Tiga Island and from Walpole Island (Gaffney et al. 1984, Balouet 1991), it is unlikely that any but the more widespread and less habitat-specific lizards now occur on Walpole or other small islets in the group. Two unidentified species of lizards, probably both skinks, have been reported from Walpole (A. Renevier and J.-F. Cherrier, unpubl. data), but there are no voucher specimens.

The marine reptiles of the Loyalty Islands are probably similar to those found in the waters of the New Caledonian mainland (Bauer and Vindum 1990). Pritchard (1982) reported hawksbill and green sea turtles on Ouvéa. Sea snakes from the Loyalty Islands include Aipysurus duboisii Bavay, Emydocephalus annulatus Krefft, and Hydrophis caerulescens (Shaw), reported by Bavay (1869) and Boulenger (1898), but several additional species, including the semiterrestrial laticaudines, are probably present. A review of important new sea snake material from the region will soon be published (I. Ineich and A. Rasmussen, pers. comm.). In 1993, a young Crocodylus porosus Schneider was found alive on the coast of Lifou (Vignoles 1993); that record appears to be an accidental stranding. The crocodile was probably originally from northern Vanuatu or the Solomons.

MATERIALS AND METHODS

R.A.S. and H. Cogger made a herpetofaunal survey in August 1987. Sampling was opportunistic and usually centered around the residences at each island as follows: Fayaoué, Ouvéa Island, 10–12 August 1987; Luécilla, Lifou Island, 13–17 August 1987; Cengeïté, Maré Island, 19–21 August 1987. Collection techniques included day searching for surface-active species, raking beneath debris piles for crepuscular species, searching beneath the exfoliating bark of trees for nocturnal or inactive diurnal species, and night spotting with torches for nocturnal species. Weather conditions were overcast for most of the survey because of the influence of

cyclonic activity in the vicinity of Vanuatu. Although this limited the number of diurnal species active at some sites, it was optimal for litter searching when there was sufficient debris.

Most specimens collected by Roux and Sarasin in 1911 and reported by Roux in 1913 were examined. During our studies of the New Caledonian herpetofauna, we have located few records of specimens from the Loyalty Islands; consequently the collections in the Australian Museum, Sydney (AMS), and the Naturhistorisches Museum, Basel (NHMB), provide the majority of locality records. Data derived from the NHMB specimen registers and not confirmed by examination of the specimens are marked by an asterisk (*). Additional material cited is housed in the American Museum of Natural History (AMNH), Natural History Museum, London (BMNH), Brigham Young University (BYU), California Academy of Sciences (CAS), Field Museum of Natural History (FMNH), and Museum of Comparative Zoology (MCZ). The localities represented by voucher specimens are number coded and identified in Figure 1. These number codes also appear in parentheses in the lists of material examined in each species account. The coordinates of these sites are given below. Additional habitat data are provided for those localities visited in 1987 by R.A.S.

Ouvéa Island

Locality 1: Fayaoué, 20° 39′ S, 166° 33′ E. This site was visited by both Roux and Sarasin in 1911–1912 and Cogger and R.A.S. in 1987. The 1987 collections were derived from a 1- to 2-km radius of Fayaoué and included strand-line vegetation facing the lagoon, coconut plantations, and near-coastal closed forest habitat.

Locality 2: Pointe de Mouly, 20° 43′ S, 166° 23′ E. Raised limestone foreshore covered with low scrub.

Lifou Island

Locality 3: Mutchaweng village, 20° 44′ S, 167° 10′ E. Roadside forest.

Locality 4: 1.3 km east of Huneté village, 20° 46′ S, 167° 10′ E. Moderately tall closed forest, inland from coast, edge cleared for native gardens.

Locality 5: 2.5 km west of Huneté village, 20° 46′ S, 167° 05′ E. Low to medium closed forest close to coast.

Locality 6: Képénéé (= Chépénéhé), 20° 47′ S, 167° 09′ E.

Locality 7: Natholo, 20° 47′ S, 167° 09′ E. Locality 8: Luécilla, 20° 54′ S, 167° 16′ E. Collections were made within a 1-km radius along the coast and included the following habitats: coastal scrub in the foredune area, plantations and gardens behind the foredune area, and forest-edge habitat adjacent to the coast.

Locality 9: Wé, 20° 55′ S, 167° 16′ E. Gardens and roadside vegetation in township.

Locality 10: 8.5 km south of Wé, 20° 56′ S, 167° 16′ E.

Locality 11: Douéoulou, 20° 56′ S, 167° 05′ E. Raised limestone foreshore covered with low scrub.

Locality 12: Cap des Pins lighthouse, 21° 04′ S, 167° 28′ E. Tall, closed forest on coastal headland.

Maré Island

Locality 13: Rô, 21° 23′ S, 167° 52′ E. Locality 14: La Roche, 21° 28′ S, 168° 01′ E. Locality 15: Netché (= Nécé), 21° 29′ S, 167° 51′ E.

Locality 16: Pénélo, 21° 34′ S, 168° 06′ E. Locality 17: Cengeïté, 21° 36′ S, 167° 54′ E. The 1987 collections were derived from a 1- to 2-km radius around Cengeïté. Habitats sampled include strand-line vegetation, plantations associated with the local village, and near-coastal closed forest habitat.

Locality 18: Médou (= Médu), 21° 37′ S, 167° 57′ E.

Locality 19: Padaoua (= Padawa), 21° 28′ S, 167° 51′ E.

Locality 20: Raoua (= Rawa), 21° 29′ S, 167° 59′ E.

SPECIES ACCOUNTS
Family GEKKONIDAE

Subfamily DIPLODACTYLINAE

Bavayia crassicollis Roux, 1913

MATERIAL EXAMINED: Lifou Island: AMS

R125691 (8); NHMB 6940 (7); NHMB 6938–39 (6). Maré Island: NHMB 6935 (13); NHMB 6931 (15); NHMB 6936–37 (16); NHMB 6933 (19).

REMARKS: Bavayia crassicollis is superficially very similar to the widespread species B. cyclura (Günther) and differs mainly in being larger and more robust and in having a pattern of muted to barely distinguishable dark crossbars on the dorsal surface. However, not all B. cyclura have distinctive dark markings on the back, and poorly patterned individuals smaller than 70 mm snout-vent length (SVL) cannot be assigned to either species confidently, particularly at coastal localities where both are likely to occur (see Bauer and Sadlier 1994).

Roux (1913) collected specimens that could be unequivocally assigned to *B. crassicollis* from Lifou and Maré Islands. Those from Maré were noted as generally occurring among palm fronds. A single individual collected from Lifou in 1987 was found by day beneath the exfoliating bark of a small tree located behind the foredune. This area was close to habitation and adjacent to a mixed-crop plantation. The general locality was thoroughly searched by day and at night but no further individuals were located.

Roux also reported this species from Fayaoué, Ouvéa Island. However, one of his two specimens, NHMB 6941, has been examined and when compared with a large (n = 25) series of B. cyclura collected at Fayaoué in 1987 was within the range of size and variation in expression of dark dorsal patterning for that species. This specimen is therefore tentatively reidentified as B. cyclura. Consequently from the material examined B. crassicollis is known with certainty only from Lifou and Maré.

Bavayia cyclura (Günther, 1872)

MATERIAL EXAMINED: Ouvéa Island: AMS R125501–125523, R125597–125600, NHMB 6941 (1). Lifou Island: AMS R125643–125665, R125688 (4); AMS R125687 (5); AMS R125711 (12); NHMB 6912, 6915, 6917–19, 6920 (7); NHMB 6923, 6925, 6929 (6); AMS R6667, Lifou Island (no precise locality). Maré Island: NHMB 6909–10 (15); NHMB 6911 (16).

REMARKS: Most specimens collected in 1987 represent two samples, each of ca. 20 individuals from single localities on Ouvéa and Lifou Islands. These samples provide a sufficient measure of variation in size and coloration of the Loyalty Islands populations of B. cyclura. The adult size class for the combined populations is 50-69 mm SVL. Moderate to bold dark patterning of the dorsal surface occurs in more than half the specimens from Ouvéa (59%) and Lifou (71%); in the remainder the pattern is faint or there are no obvious dark markings. All juveniles (n = 5) under 40 mm SVL had strong dorsal patterning. The size at which muting or the loss of the dark color pattern occurs varies between populations. Muted dark dorsal markings in the Ouvéa population occur in six of the nine larger (SVL > 60 mm) specimens but in only three of the 10 larger Lifou specimens. The presence of a vellow flush on the ventral surface occurs variably in B. cyclura and most other related species. This feature was faint to absent in more than half of the specimens from Ouvéa (68%) and Lifou (67%).

The majority of specimens were collected by day under the bark of standing or fallen trees in near-coastal forest or at night active on leaves or branches of low shrubs or trees. Roux and Sarasin collected B. cyclura and B. crassicollis at two localities on Lifou (Képénéé and Nathalo) and two on Maré (Netché and Pénélo). No indication of the habitat preferences of either species at these localities was given, other than the comment that on Maré B. crassicollis was located in the fronds of coconut palms. Recent field observations of B. crassicollis on the Loyalties (n = 1), Isle of Pines (Île des Pins) (n = 2), and northeastern coast of New Caledonia (n =1) (Bauer and Vindum 1990, Bauer and Sadlier 1994) have all been from coastal habitats that are either modified (man-made structures) or subject to frequent natural disturbance. By contrast B. cyclura appears to be most abundant in near-coastal or inland closed forest rather than strand-line vegetation; it was not recorded from coastal habitat at Luécilla on Lifou or from Cengeïté on Maré (where most of the collecting effort occurred on Maré).

Bavayia sauvagii (Boulenger, 1883)

MATERIAL EXAMINED: Maré Island: AMS R125763–77, R125786, R125802–03, R125811–14, R125823 (17); NHMB 7007, 7009–10, 7012, 7014–16, 7018–19 (15); NHMB 7022 (16).

REMARKS: *Bavayia sauvagii* as it is currently recognized is probably composite, consisting of a number of superficially similar species on mainland New Caledonia (work in progress). The Maré Island population resembles those from southern New Caledonia in their small size (maximum SVL 45 mm), low preanal pore count (19–24), and grayish ventral surface (rather than a suffusion of brown pigment).

Specimens collected in 1987 were taken from the exfoliating bark of trees at the forest edge by day and by night were observed active on the walls of buildings. This appears to be the first recorded instance of this species commensal with human habitation. Elsewhere the species shelters under rocks or bark by day and is active on tree trunks and branches at night (Bauer 1990, Bauer and Sadlier 1994).

Subfamily GEKKONINAE

Gehyra vorax Girard, 1857

MATERIAL EXAMINED: Maré Island: NHMB 7030 (13); AMS R6668 (ex NHMB 7034), NHMB 7032–33, 7035, 7037–38 (16); NHMB 7031 (18); NHMB 7029* (19).

REMARKS: This species is restricted to the Melanesian islands of New Guinea, the Solomons, Fiji, Vanuatu, and the Loyalty Islands (Beckon 1992, Bauer and Henle 1994) and has not been recorded from mainland New Caledonia. Old records from Norfolk Island are certainly in error (Cogger et al. 1983). *Gehyra vorax* is the only member of the genus to occur on the Loyalty Islands, where it is apparently present only on Maré.

Roux (1913) recorded that it lives in coconut trees and that it seemed to be "fairly common." It was not collected during the 1987 survey.

Hemidactylus frenatus Duméril & Bibron, 1836

MATERIAL EXAMINED: Lifou Island: AMS R125689, R125694–96 (8).

REMARKS: This species was not recorded by Roux (1913) in New Caledonia or the Loyalty Islands at the beginning of this century, and its current occurrence in the vicinity of Nouméa, the Île des Pins, and Lifou Island can be considered recent introductions, primarily in association with troop and supply movement during World War II and subsequently (Bauer 1988, Bauer and Vindum 1990).

The specimens obtained in 1987 were collected either from man-made structures in the vicinity of habitation or in cultivated areas, from the axils of coconut palms or banana fronds. Additional individuals were heard calling. Throughout the New Caledonian region *H. frenatus* rarely occurs outside disturbed habitat, whereas *H. garnotii* appears to show a preference for undisturbed lowland habitats.

Hemidactylus frenatus was not recorded from Maré in 1987. In the apparent absence of this species, both Hemiphyllodactylus typus Bleeker and Bavayia sauvagii occurred as commensals on the buildings at Cengeïté.

Hemidactylus garnotii Duméril & Bibron, 1836

MATERIAL EXAMINED: Ouvéa Island: NHMB 7087 (1).

REMARKS: Hemidactylus garnotii is known from the Loyalty Islands only from the single specimen collected by Roux (1913). On the mainland of New Caledonia, this parthenogenetic species has undergone local extripations since the introduction of the sexually reproducing H. frenatus (Bauer and Vindum 1990). Similar local losses of H. garnotii have been documented in Hawai'i (McKeown 1978) and Fiji (Gibbons 1985). Competitive displacement has been proposed as a possible mechanism by which this replacement has occurred (Petren et al. 1993).

Hemiphyllodactylus typus Bleeker, 1860

MATERIAL EXAMINED: Ouvéa Island: NHMB 6980 (1). Lifou Island: AMS R125697, R125699 (8). Maré Island: AMS R125787–88, R125809 (17).

REMARKS: This species is widely distributed throughout the Pacific region, although as currently construed, several biological species may be included under this name (G. R. Zug, pers. comm.). On mainland New Caledonia, *H. typus* occurs on both the northeastern and northwestern coasts, but is nowhere common. In the Loyalty Islands it is known from Ouvéa (Roux 1913), and Lifou and Maré Islands (1987 collections).

Specimens collected at Luécilla on Lifou Island were taken from under the bark of large dead standing trees of coastal scrub forest on dunes backing the beach. In that habitat *H. typus* was locally sympatric with *Lepidodactylus lugubris* (Duméril & Bibron) and *Bavayia crassicollis* (single specimen record). *Hemidactylus frenatus* occurred nearby in marginal disturbed habitat adjacent to the shoreline. At Cengeïté on Maré Island, *H. typus* was collected at night active on coconut palms and the walls of houses in coastal plantation habitat. There it was locally sympatric with *L. lugubris* and *B. sauvagii*, both of which also occurred on house walls, but only *L. lugubris* was found on coconut trees.

Lepidodactylus lugubris (Duméril & Bibron, 1836)

MATERIAL EXAMINED: Ouvéa Island: AMS R125573–82, R125611–17, R125698, NHMB 6941, 6976–77* (1). Lifou Island: AMS R125626, R125692–93, R125704–05 (8); NHMB 6974–75* (6). Maré Island: NHMB 6973* (13); NHMB 6967–68*, 6969–70* (15); NHMB 6971–72* (16); AMS R125762, R125789–91, R125805–07, R125815–17, R125821–22 (17).

REMARKS: Lepidodactylus lugubris was collected around a variety of disturbed or manmade habitats at coastal localities. On Ouvéa and Lifou, most specimens were collected in strand-line vegetation by day sheltering beneath the bark or basal litter of *Casuarina* sp. and in the axils of coconut palms or were captured active at night on the walls of buildings; one was also collected beneath debris in a native garden. Similarly, on Maré this species appeared to be most common in beachfront habitat and was collected active at night on the trunks of coconut trees or walls of bungalows; however, several were found in adjacent forest-edge habitat sheltering beneath the bark of trees by day. The biology of *L. lugubris* in the Loyalty Islands is similar to that of the New Caledonian and Île des Pins populations (Bauer and Vindum 1990, Bauer and Sadlier 1994).

Nactus pelagicus (Girard, 1858)

MATERIAL EXAMINED: Ouvéa Island: AMS R125524, R125554–57, R125601–03, NHMB 6893 (1). Lifou Island: AMS R125641–42 (4); AMS R125676–77 (5); NHMB 6891 (6); NHMB 6893 (7); AMS R125712 (12). Maré Island: NHMB 6879, 6881–83, 6885 (15); NHMB 6890 (16); AMS R125778 (17); NHMB 6886–87, 6889 (18).

REMARKS: The N. pelagicus complex is widespread in the Southwest Pacific region, extending from northeastern Australia and southwestern New Guinea eastward to Niue (ca. 170° W). In New Caledonia, it appears to be widespread on the east coast and occurs on all major islands in the Loyalty Islands group. Its presence on Lifou was first noted by Bavay (1869). Moritz (1987) indicated that the New Caledonian population was unisexual. Bisexual populations from the Solomon Islands and northern Vanuatu have recently been elevated to specific status as N. multicarinatus Gunther by Zug & Moon (1995), with N. pelagicus restricted to parthenogenetic populations from Vanuatu, Fiji, New Caledonia, the Loyalty Islands, and the central Pacific.

Nactus pelagicus was collected by day in ground litter in coastal forest, secondary regrowth, and plantation habitat on Ouvéa Island, from inland forest and at the edge of coastal forest on Lifou, and by night a single specimen was observed active at the base of a

palm tree in plantation habitat on Maré Island. This species did not appear to be abundant at any of the localities where it was collected, which most probably reflects the paucity of suitable terrestrial sheltering sites (rotting logs or rocks) encountered in the forests on the Loyalty Islands.

Family SCINCIDAE

Caledoniscincus atropunctatus (Roux, 1913)

MATERIAL EXAMINED: Ouvéa Island: NHMB 7297–7305* (1). Lifou Island: AMS R125672 (5); NHMB 7285–89*, 7323*, 19006*, 19021* (6); NHMB 7291–93*, 7324*, 19014* (7). Maré Island: NHMB 7282 (14); NHMB 7272–73*, 7276* (15); AMS R125731, R125780 (17); NHMB 7281*, 7322*, 19018* (20).

REMARKS: Too few specimens of *C. atropunctatus* were collected in the 1987 survey to gain a firm impression of habitat preferences for this species on the Loyalty Islands. On New Caledonia, *C. atropunctatus* occurs mainly in closed forest habitat, where it is active in sunlit patches on the forest floor and at its edge (Sadlier 1986, Bauer and Sadlier 1994). In the survey of 1987 there was little opportunity to collect within or at the edge of this habitat under optimal conditions, which may account for the apparent scarcity of this species.

Caledoniscincus austrocaledonicus (Bavay, 1869)

Two species of *Caledoniscincus* allied to *C. austrocaledonicus* occur in sympatry at a number of locations throughout the Loyalty Islands: one is characterized by the presence of a white midlateral stripe in both males and females, the other by the absence of this stripe. A similar situation occurs on the mid- to southwestern coastal regions of New Caledonia. Morphological and genetic (allozyme electrophoresis) comparisons of these populations clearly indicate the presence of sympatric species, but our analysis is not yet sufficient to assign names to the various morphotypes or species. Here we refer to the two Loyalty Island morphotypes as *C. austro-*

caledonicus "striped" and *C. austrocaledonicus* "plain" for those individuals with or without a pale midlateral stripe, respectively.

Caledoniscincus austrocaledonicus "striped"

MATERIAL EXAMINED: Ouvéa Island: AMS R125563, R125565, R125572, R125583–85, R125605–06, NHMB 7296 (1). Lifou Island: AMS R125671 (5); NHMB 7283–84, 7287, 7290 (6); NHMB 7293–95, 19072 (7). Maré Island: NHMB 7274–75, 19070, 19083 (15); NHMB 7280 (16); AMS R125719, R125730, R125795–96 (17); NHMB 7277–79 (18).

REMARKS: This species occurs mainly in open or disturbed habitat. On Ouvéa we recorded it from a coastal habitat and an adjacent copra plantation. At both locations, it was collected sheltering during overcast weather beneath ground litter around Casuarina and shrubs fronting the lagoon and under debris piles in the copra plantation. It was sympatric with C. austrocaledonicus "plain" in the copra plantation. In nearcoastal forest habitat on Ouvéa, the striped species was taken under ground litter in forest or secondary regrowth. On Lifou, it was collected at the edge of inland closed forest habitat and on Maré from ground litter at the edge of coastal dry forest. At all forest localities it was sympatric with, but generally less abundant than, the plain species.

Caledoniscincus austrocaledonicus "plain"

MATERIAL EXAMINED: Ouvéa Island: AMS R125558–62, R125564, R125566–71, R125604, R125624–25, NHMB 7297–305 (1). Lifou Island: AMS R125640 (4); AMS R125669–70 (5); NHMB 7285–86, 7288–89, 19021 (6); NHMB 7291–92, 19079 (7); AMS R125708 (9); AMS R125713–14 (12). Maré Island: NHMB 7272–73, 7276, 19077 (15); AMS R125716–18, R125720–29, R125779, R125792–94, R125797, R125818 (17); NHMB 19018 (20).

REMARKS: Caledoniscincus austrocaledonicus "plain" was generally collected in, or at the edge of, closed forest habitat, where it was noticeably more abundant than the sympatric striped form. It was encountered only rarely at coastal localities. Cryptoblepharus novocaledonicus Mertens, 1928

MATERIAL EXAMINED: Ouvéa Island: AMS R125618–23 (2). Lifou Island: AMS R125678–86 (11). Maré Island: NHMB 7208* (14); NHMB 7207* (15); AMS R125760–61, R125808 (17); NHMB 7209–12* (18).

REMARKS: All specimens were collected from coastal outcropping limestone pavement, usually within the spray zone. The habitat preference is similar to that described and pictured by Sadlier (1986, fig. 74) on New Caledonia and by Bauer and Sadlier (1994, fig. 2b) on the Île des Pins.

Emoia cyanura (Lesson, 1826)

MATERIAL EXAMINED: Ouvéa Island: AMS R125525–53, R125586, R125607–10 (1). Lifou Island: AMS R125706–07 (8); AMS R125638 (4); AMS R125673–75 (5); AMS R125710 (10). Maré Island: AMS R125732–46, R125781–84, R125798–900 (17). Brown (1991) examined AMNH 81767 and MCZ 19603 from Maré, AMNH 61701 from Lifou, AMNH 61704–5 from Ouvéa, and AMNH 105396 from "Nitche Maci" (= Netché, Maré).

REMARKS: On Ouvéa, *E. cyanura* was most frequently observed active around ground litter in coconut plantations or areas of secondary growth during sunny periods and was collected under ground litter in that habitat during overcast periods. On both Maré and Lifou, *E. cyanura* occurred in forest and plantation-edge habitats. These are similar to the habitats utilized in the Solomon Islands (McCoy 1980, Brown 1991).

Emoia loyaltiensis (Roux, 1913)

MATERIAL EXAMINED: Lifou Island: AMS R125629, R125690 (8); AMS R125630–637, R125666–668 (4); NHMB 7133–34 (6); NHMB 7135 (7). Maré Island: AMS R125748–759 (17); NHMB 7123–27, 7130–31 (15); NHMB 7128 (14); NHMB 7132 (18). Additional material from Maré examined by Brown (1991) included AMNH 60460, 60463, 60465, and MCZ 19610.

REMARKS: *Emoia loyaltiensis* is arboreal, and all specimens collected in 1987 were taken while active on trees (up to 3 m from the ground) or from under exfoliating bark of both live and dead trees. This species was recorded from a variety of habitats including secondary scrub on the lee side of coastal dunes (Luécilla, Lifou Island); coastal dry vine forest (Cengeïté, Maré Island); tall inland forest generally at the forest edge or from dead standing timber in adjacent plantations (vic. Huneté, Lifou Island). Brown (1991), who elevated this form from subspecific to specific status, incorrectly regarded *E. loyaltiensis* as restricted to Maré alone.

At the three localities collected, *E. loyaltiensis* was regionally sympatric with *Lioscincus nigrofasciolatum*, and on one occasion specimens of both species were taken from the same tree trunk (at the forest edge of tall inland forest). The most obvious difference in habitat preference between the two species is reflected in their relative abundance in coastal scrub/plantation habitat and forested habitats. In the former habitat *L. nigrofasciolatum* was common, whereas *E. loyaltiensis* was only occasionally observed

in coastal scrub (Luécilla) and was absent from plantation habitat (Cengeïté). Although both species were encountered in forest-edge habitat, *E. loyaltiensis* was far more common than *L. nigrofasciolatum* in the interior of the forest.

A series of 26 specimens collected in 1987 included what appear to be adults (64–81 mm SVL, n = 13), large juveniles (52–61 mm SVL, n = 12), and a single small juvenile (38 mm SVL).

There is a noticeable difference (with some overlap) in dorsal color and pattern between the Lifou (Figure 2) and Maré Island (Figure 3) populations, with the great majority of Lifou specimens being more boldly marked. The dorsal surface of *E. loyaltiensis* is gray-olive to light or medium brown, either uniform or with variably distributed darker flecking. These dark markings either form irregular transverse bars or are restricted to the dorsolateral margin where they edge the adjacent broad band of lighter color (most obvious in the majority of well-marked Lifou specimens). The lateral surface is of similar color to the dorsal but generally darker in tone, particularly in boldly marked individuals

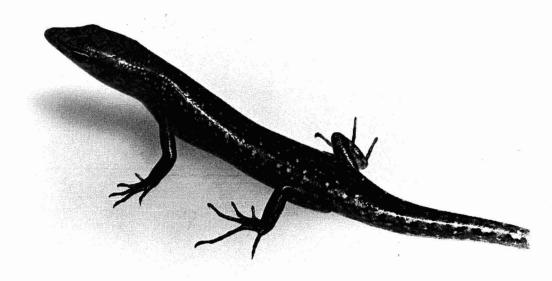


FIGURE 2. Emoia loyaltiensis from Lifou, showing the bold markings typical of this population.

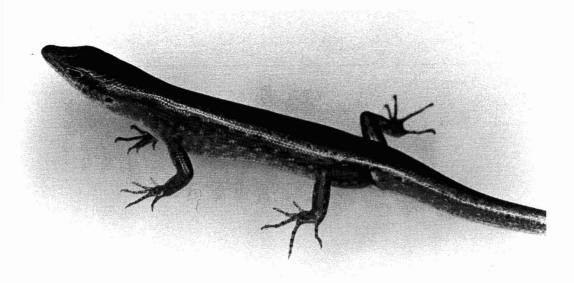


FIGURE 3. Emoia loyaltiensis from Maré, showing the relatively uniform dorsal coloration of individuals from this population.

(the condition in the majority of Lifou specimens). In life there is a bronze tinge to the dorsal surface of the more boldly marked individuals. The ventral surface usually had a yellow flush to the abdomen, underside of limbs, and base of tail or was white.

Lioscincus nigrofasciolatum (Peters, 1869)

MATERIAL EXAMINED: Ouvéa Island: AMS R125587–96, NHMB 7140, 7147–50 (1). Lifou Island: AMS R125700–03 (8); AMS R125639 (4); AMS R125709 (10); AMS R125627–28 (9); AMS R125715 (3); NHMB 7142–43, 7145–46 (6); NHMB 7151–52 (7). Maré Island: NHMB 7160* (13); NHMB 7155*, 7157* (14); NHMB 7156*, 7158* (15); NHMB 7154* (16); AMS R125747, R125785, R125804, R125819–20 (17); NHMB 7159* (18); CAS 38825 (no precise locality).

REMARKS: Lioscincus nigrofasciolatum is mainly an arboreal species; most specimens collected were active on trees in open or forestedge habitat, particularly on the trunks of coconut palms in plantation (Fayaoué, Ouvéa; and Cengeïté, Maré) or beach-front situations (Luécilla, Lifou). Some were also collected

from under exfoliating bark of both live and dead trees at the edge of closed forest habitat, but the species was rarely encountered within the forest. Several individuals were also observed active on the raised, weathered limestone platform at the high-tide zone on the northern tip of Ouvéa. Bauer and Vindum (1990) made similar observations in coastal outcrops at Goro on the southeastern coast of New Caledonia.

Roux (1913) identified differences in scalation between specimens from New Caledonia and the Loyalty Islands. The specimens collected in 1987 confirm the distinctiveness of the Loyalty Island populations in having fewer midbody scale rows than New Caledonian populations (32–36 versus 36–42, respectively), but other differences are minor and any formal taxonomic recognition of these populations will require a more thorough analysis of all available material.

Phoboscincus garnieri (Bavay, 1869)

MATERIAL EXAMINED: Lifou Island: NHMB 7139 (6).

REMARKS: In addition to the single specimen

examined, *P. garnieri* has also been observed from the vicinity of the lighthouse on the Cap des Pins, Lifou (locality 12). Bavay (1869) observed a large skink, probably *P. garnieri*, at Mouli on Ouvéa Island.

Elsewhere in the region, *P. garnieri* is now known from seven widely separated localities across both the north and south of New Caledonia itself, and also from small offshore islands (de Vosjoli 1995). Our observations indicate that *P. garnieri* is extremely secretive and when disturbed seeks shelter beneath debris or under rocks. It is probable that it occurs on all three major islands in the Loyalty group, but confirmation of this will be difficult because of its secretive nature and possible rarity.

Family TYPHLOPIDAE

Ramphotyphlops willeyi (Boulenger, 1900)

MATERIAL CITED IN LITERATURE: Lifou Island: The type specimen, BMNH 1946.1.10.80 (formerly BMNH 1900.5.29.1), derived from Lifou (Boulenger 1900). Maré Island: Roux (1913) listed a specimen from Netché on Maré; McDowell (1974) listed AMNH 62687 from Maré.

REMARKS: McDowell (1974) reviewed the status of *R. willeyi*. He assigned a single specimen (BYU 7448) from Guadalcanal, Solomon Islands, to this species, but did note that this specimen differed from his Loyalty Islands specimen.

Ramphotyphlops braminus (Daudin, 1803) was recorded from the Loyalties by Bauer and Vindum (1990) on the basis of local reports, but no specimens were obtained. This species, which was introduced into New Caledonia no later than 1974 (Ineich and Bauer 1992), is easily transported and is probably established in the Loyalty Islands, although perhaps only locally.

Family BOIDAE

Candoia bibroni (Duméril & Bibron, 1844)

MATERIAL EXAMINED: Ouvéa Island: AMS R125500 (1).

REMARKS: This species was first reported from the Loyalty Islands from Point Gatcha, an unidentified locality on Lifou, by Bavay (1869). We collected a single specimen from Fayaoué, Ouvéa Island. The specimen was located by day beneath debris in a native garden surrounded by a coconut plantation.

Roux and Sarasin in 1911–1912 collected numerous specimens (Maré, n=11; Lifou, n=7; Ouvéa, n=4) (Roux 1913). McDowell (1979) analyzed geographic variation between the islands in the Loyalties group using the data on scalation from Roux (1913) and American Museum of Natural History specimens (n=4). He noted significant interisland variation in midbody and ventral scale rows.

Candoia bibroni once played an important role in the life of Loyalty Islanders. It was widely used as food, but decreasing snake populations and changing traditions have decreased its cultural significance (Delauw 1990).

DISCUSSION

The Loyalty Islands are a group of three relatively small islands (Ouvéa, 160 km²; Lifou, 1150 km²; Maré, 650 km²) of low relief in comparison with adjacent island groups of Vanuatu (12 major islands and numerous lesser islands with a total area of 14,763 km² and Fiji (Vanua Levu, 5535 km²; Viti Levu, 10,384 km²) or with New Caledonia (16,750 km²). Despite this, the Loyalty Islands have a species richness of lizards (17 species) approaching that of Fiji (21 species [Zug 1991]) and Vanuatu (19 species [Medway and Marshall 1975, Cranbrook 1985, Zug 1991]), but only one-third that of adjacent New Caledonia (50+ species [Bauer and Sadlier 1993. Sadlier and Bauer 1996]). The Loyalties lack representatives of numerous New Caledonian endemic genera (e.g., Rhacodactylus, Eurydactylodes, Geoscincus, Sigaloseps, morosphax, Graciliscincus, Simiscincus), some of which require habitat types not present in the Loyalty Islands. Some, such as Rhacodactylus spp., however, appear to be absent because of the independent geological histories of the two areas. At least four species of Rhacodactylus occur on small (152 km²), low-lying (maximum elevation 262 m) Île des Pins (Bauer and Sadlier

1994, de Vosjoli 1995), apparently reflecting its former connection to the New Caledonian mainland.

A few lizard species are shared between the Loyalty Islands (see Table 1) and Vanuatu (six species) and with Fiji (seven species). Based on their total Pacific distribution, there are two groups of species shared between these island groups. One group comprises species distributed throughout much of the Pacific region: Hemidactylus frenatus, H. garnotii, Hemiphyllodactylus typus, Lepidodactylus lugubris, Nactus pelagicus, and Emoia cyanura. All of these, with the exception of E. cyanura, also occur on New Caledonia. The second group comprises the lizard species Gehyra vorax and Emoia loyaltiensis. In the Loyalties both are known only from Lifou and Maré Islands. Elsewhere G. vorax occurs only in the Melanesian islands of Vanuatu, Fiji, and New Guinea and its satellite islands (Beckon 1992), whereas the Emoia samoensis group to which E. loyaltiensis belongs has an overall distribution restricted to a region of the southwestern Pacific that includes the Solomon Islands, Vanuatu, Fiji, Samoa,

Tonga, and the Cook Islands (but not New Caledonia [Brown 1991]). The snake *Candoia bibroni* also occurs in the Solomons, Vanuatu, Fiji, and Samoa, as well as the Loyalties, but is absent from the New Caledonian mainland (McDowell 1979).

Zug (1991) in discussing zoogeographic patterns among Fijian lizards initially divided these into native and exotic species, the latter defined as those whose colonization was aided by humans and coincided with or postdated human arrival. Zug recognized several species, including *H. frenatus*, *H. garnotii*, and *L. lugubris*, as exotic species to Fiji using criteria such as documentation of recent arrival, occurrence predominately as human commensals, or limited local but widespread extralimital distribution as exotic to the region.

In both New Caledonia and the Loyalty Islands *H. frenatus*, *H. garnotii*, and *L. lugubris* all occur as human commensals; although in New Caledonia *H. garnotii* has also been recorded in primary habitat distant from, and not associated with, human activity, and in both New Caledonia and the Loyalty Islands *L.*

TABLE 1
TERRESTRIAL SCINCID AND GEKKONID LIZARD SPECIES PRESENT IN THE LOYALTY ISLANDS

TAXA	VANUATU	FIJI	LOYALTY ISLANDS	ÎLE DES PINS	NEW CALEDONIA
Gekkonidae					
Bavayia crassicollis			X	X	X
Bavayia cyclura			X	X	X
Bavayia sauvagii			X	X	X
Gehyra vorax	X	X	X		
Hemidactylus frenatus	X	X	X	X	X
Hemidactylus garnotii		X	X		X
Hemiphyllodactylus typus		X	X		X
Lepidodactylus lugubris	X	X	X	X	X
Nactus pelagicus	X	X	X	X	X
Scincidae					
Caledoniscincus atropunctatus	X		X	X	X
Caledoniscincus austrocaledonicus "striped"			X		X
Caledoniscincus austrocaledonicus "plain"			X	X	X
Cryptoblepharus novocaledonicus			X	X	X
Emoia cyanura	X	X	X		
Emoia loyaltiensis			X		
Lioscincus nigrofasciolatum			X	X	X
Phoboscincus garnieri			X		X

NOTE: Species shared with Vanuatu, Fiji, New Caledonia, and the Île des Pins marked with an X. Data for Vanuatu derived from Medway and Marshall (1975) and Cranbrook (1985), for Fiji from Zug (1991), for New Caledonia from Bauer and Sadlier (1993), and for the Île des Pins from Bauer and Sadlier (1994) and de Vosjoli (1995).

lugubris occurs in a variety of natural shoreline habitats. In contrast, Hemiphyllodactylus typus, which Zug believed to be a native species in Fiji, was only recorded from the Loyalties either as a commensal or in disturbed habitat associated with human activities; as such, in the Loyalty Islands and possibly also New Caledonia, it appears to be an introduction. It is of interest to note that several widespread Pacific species, Gehyra oceanica (Lesson), Gehyra mutilata (Wiegmann), and Lipinia noctua (Lesson), known from both Vanuatu and Fiji do not occur in the Loyalty Islands or in New Caledonia.

The distribution of species between the main islands of the Loyalty Islands group is remarkably uniform, with the majority of species recorded from all three islands. Of the widespread, or moderately widespread, Pacific species found on the Loyalties, nearly all occur on all three islands, and nearly all also extend into New Caledonia. The notable exceptions are Gehyra vorax and Emoia loyaltiensis, which do not occur on Ouvéa Island or extend to New Caledonia. Bauer (1989, Bauer and Vindum 1990) proposed that the relatively recent tectonic movement by parts of Vanuatu (Chase 1971), in conjunction with the Pleistocene emergence of the Loyalties, might explain the presence of taxa shared between these two island groups but absent from New Caledonia. Further, existing current systems would promote colonization of the Loyalties from Fiji or Vanuatu (Gibbons 1985), whereas the prevailing Southern Tropical Countercurrent would tend to promote colonization of the Loyalty Islands from New Caledonia but retard colonization of New Caledonia proper by propagules from the Outer Melanesian Arc islands. The absence of species from Ouvéa may be artifactual but could be related its very low physical relief and less diverse vegetation.

The occurrence in Vanuatu of the otherwise New Caledonian/Loyalty Islands species *Caledoniscincus atropunctatus* is problematic. It is widespread in New Caledonia in mainly closed forest habitat, but is otherwise only known from the Loyalties and certain islands in Vanuatu (Medway and Marshall 1975, Bauer et al. 1992). Because it is known from four islands in Vanuatu, it does not fit the criteria proposed by Zug (1991) for recognition as an exotic species in Vanuatu. Bauer (1989) expressed the view that

it may have dispersed from New Caledonia to Vanuatu via the Loyalties in the Quaternary.

Nine species of lizards are shared between New Caledonia and the Loyalties that do not occur outside this region (if C. atropunctatus is included). These are species with generally widespread distributions throughout New Caledonia and tend to be either habitat generalists or forest-edge dwellers (e.g., the geckos Bavayia cyclura and B. crassicollis and the skinks Caledoniscincus austrocaledonicus "plain," C. austrocaledonicus "striped," Lioscincus nigrofasciolatum, and *Phoboscincus* garnieri). Exceptions to this are C. atropunctatus and B. sauvagii, which both occur mainly within closed forest habitat, and Cryptoblepharus novocaledonicus, which inhabits rocky foreshores. The Loyalty populations of two species, B. sauvagii and C. austrocaledonicus "plain," have their most similar counterparts in the south of New Caledonia, though both species belong to species complexes currently under review and believed to be composite.

Gehyra vorax appears to have specialized habitat preferences on the Loyalties, and its possible presence on Ouvéa cannot be entirely ruled out; however, it is considered unlikely that E. loyaltiensis has been overlooked on Ouvéa. Suitable habitat exists on Ouvéa for both species, and the most likely explanation for their absence is historical.

Of the 14 species shared with New Caledonia, nearly all occur on all three of the main islands in the Loyalties. In this instance the notable exception is Bavayia sauvagii, which occurs on Maré Island only, perhaps because of a paucity of appropriate daytime retreats (Bauer 1990, Bauer and Vindum 1990). At this point in time the absence of Bavayia crassicollis from Ouvéa is considered most likely due to inappropriate searching for this species. Recent discoveries (e.g., Sadlier 1986, Sadlier and Bauer 1996) and rediscoveries (e.g., de Vosjoli 1995) of lizards on both New Caledonia and the Île des Pins indicate that even well-surveyed areas within the region may yet yield herpetological novelties. This suggests that the species list for the Loyalty Islands may be incomplete. Nonetheless, the basic interpretation of the Loyalties as an integral part of the New Caledonian faunal region, albeit the only part of that region with notable

Outer Melanesian Arc influences, is not likely to be altered.

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