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Reptile Remains from Tiga (Tokanod), Loyalty Islands, New Caledonia

Reptile Remains from Tiga (Tokanod), Loyalty Islands, New Caledonia[1]

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Abstract: Archaeological excavations on Tiga provide the first vouchered herpetological records for this small island between Lifou and Maré in the Loyalty Islands. Eighty-three skeletal elements from four sites yielded material assignable to skinks (*Emoia loyaltiensis, Lioscincus nigrofasciolatus*), geckos (*Bavayia crassicollis, B.* sp., *Gehyra georgpotthasti, Nactus pelagicus*), and a boid snake (*Candoia bibroni*) all known from elsewhere in the Loyalties, as well as undetermined material consistent with these and other Loyalties lizards. Diagnostic features of geckos versus skinks for elements commonly recovered from archaeological sites and from owl pellets are discussed. *Gehyra georgpotthasti* has a limited distribution in the Loyalties and its occurrence on Tiga clarifies its range. The boid snake is the only reptile likely to have been harvested by human inhabitants of Tiga. The presence of gekkonid geckos in pre-European times is confirmed and contrasts with the situation of Grande Terre fossil sites, where only diplodactylid geckos have been recovered. Although it is anticipated that all species recovered from archaeological sites are still present on the island, a modern herpetofaunal survey is needed.

THE LOYALTY ISLANDS lie on the Norfolk Rise in a line roughly parallel to the long axis of the Grande Terre of New Caledonia, separated from it by about 110 km across the Loyalty Basin, which has a maximum depth of approximately 2,000 m. The Loyalties (Figure 1) extend from Ouvéa (160 km²), at the northwest extent of the chain, through Lifou (1,150 km²), Tiga (10 km²), and a series of smaller islands, Maré (650 km²), and on to Ile Walpole (2 km²), approximately 160 km southeast of the main chain. All of the islands are relatively low lying. Their raised rims are uplifted coral reefs, whereas the lower elevation interior regions are uplifted lagoons or reef flats, probably emergent only since the Pleistocene (Paris 1981). The highest point (138 m) in the chain is on Maré, where basaltic outcrops represent the emergent portions of the volcanic base underlying the Miocene reef (Paris 1981, Kroenke

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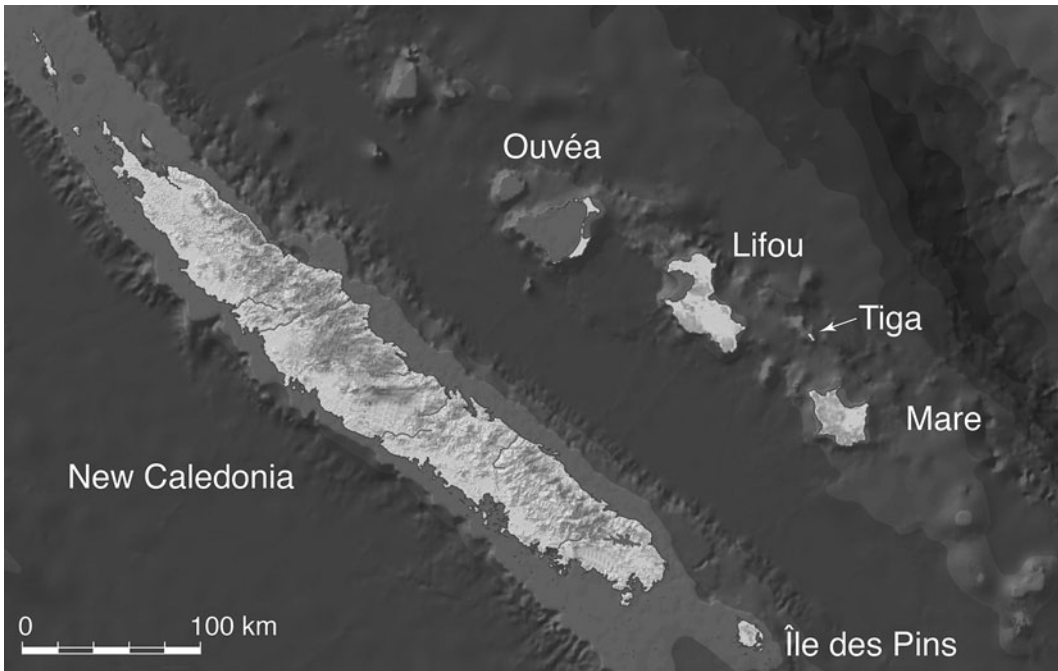[8] Corresponding author (e-mail: aaron.bauer@villanova.edu).

FIGURE 1. Location of Tiga Island in the Loyalty Islands archipelago.

1984). Rainfall is relatively low on the Loyalties, ranging from 1,700 mm per annum in northern Lifou to under 1,300 mm on Ouvéa (Sautter 1981), and the vegetation is highly depauperate relative to mainland New Caledonia, with <400 plant species (Jaffré 1993), consisting largely of coastal strand vegetation similar to that on the mainland and inland humid forests (Däniker 1931, Schmid 1981).

The herpetofauna of the Loyalties has been relatively little-studied, although its overall species composition is believed to be well known (Sadlier and Bauer 1997, Bauer and Sadlier 2000). The nineteenth-century Marist missionary Xavier Montrouzier (1820–1897) first noted the presence of the Loyalty Island boa, which he referred to as *Boa australis* (Montrouzier 1860). Bavay (1869), who catalogued the fauna of New Caledonia, describing many of the endemic species, was based on the Grande Terre, but he did obtain snakes from E. Dubois, who collected in the Loyalty Islands. In 1911–1912, Fritz Sarasin and Jean Roux traveled through much of the

Grande Terre, visited Maré and northern Lifou, and stopped briefly on Ouvéa. Roux's (1913) resulting monograph summarized the entire terrestrial and marine herpetofauna of New Caledonia and the Loyalty Islands. Subsequently, very little herpetological research has been conducted (material evaluated by Sadlier and Bauer [1997]). Virtually all research has been conducted on the three main islands of the group. Very recently, the largest gecko in the Loyalties, long considered conspecific with *Gehyra vorax* Girard, 1858, of Fiji, has been described as new based partly on material from Île Dudun, a small satellite off of northern Maré (Flecks et al. 2012), but other small islands, most notably Tiga, have not been explored herpetologically and are represented by no material in museum collections. Interestingly, however, both Tiga and remote Walpole have been sites of some paleoherpetological work on the extinct meiolaniid turtles (Gaffney et al. 1984, Balouet 1991).

Although the herpetofaunal tally of the Grande Terre continues to grow as more and

more microendemic geckos and skinks are discovered, chiefly at higher elevations (Bauer and Sadlier 2000, Bauer and Jackman 2006, Sadlier 2010), the herpetofaunal inventory of the Loyalty Islands has remained quite stable and has actually decreased. Sadlier and Bauer (1997) and Bauer and Sadlier (2000) reported 20 terrestrial squamates. One of these has since been recognized as synonymous with another on the list, leaving only 19 species. Six of these are widespread throughout much of the Pacific, including New Caledonia, and several of these are known or suspected to have reached the region through human agency. Another six are regional endemics, restricted to New Caledonia s.l. (one, *Caledonis-cincus atropunctatus* [Roux, 1913], also occurs in southern Vanuatu) and three species— *Gehyra georgpotthasti* Flecks, Schmitz, Böhme, Henkel, & Ineich, 2012; *Emoia cyanura* (Lesson, 1826); and *Candoia bibroni* (Duméril & Bibron, 1844)—occur elsewhere in the western Pacific but are absent from the Grande Terre. The remaining four species appear to be Loyalties endemics. Two of these have long been recognized as such, *Emoia loyaltiensis* (Roux, 1913) and *Ramphotyphlops willeyi* (Boulenger, 1900). Recent molecular phylogenetic research (Bauer and Jackman 2006), however, has also revealed that the diplodactylid gecko *Bavayia crassicollis* Roux, 1913 (previously believed to occur on other islands in the New Caledonian region) is a Loyalties endemic and that specimens of *B. sauvagii* (Boulenger, 1883), from Maré actually represent an undescribed endemic species.

Although the reptile species composition of the Loyalties may be considered well established, the same cannot be said of intra- and interisland distribution patterns. A few species appear to be restricted to Maré (*Bavayia* aff. *sauvagii*) or to Maré and its outliers (*Gehyra georgpotthasti*, although there is a single vouchered record from Lifou—ZFMK 70455), but sampling has been insufficient to confirm this or to determine whether other species with patchy distributions may, in fact, be ubiquitous. Any additional sampling in the region would be desirable, but Tiga stands out as an especially glaring gap. Not only is it the fourth

largest island in the Loyalties, but it also lies immediately north of Maré and may be expected to help resolve the distributional limits of the Maré area endemics.

We here report on the herpetological findings of an archeological study on Tiga carried out by the Institut d'archéologie de la Nouvelle-Calédonie et du Pacifique in collaboration with the University of Queensland and the Centre National de la Recherche Scientifique in Paris. The study focused on the integration between indigenous Kanak knowledge about Tiga's past and classic survey/excavation studies around the island. The first phase of the fieldwork concentrated on recording oral traditions and locating the traditional sites that local people were ready to share with us. In the second phase, a classic archaeological study was conducted. Over 160 different sites were recorded, from rockshelters to walled enclosures, from traditional burial grounds to mythical sites, and from horticultural sites to caves where people collected fresh water. An unexpected number of rock art sites have been recorded. Excavations done in different types of sites have shown that Tiga was first settled by humans around 2,950 yr ago on the low coastal plain facing the northwestern lagoon of the island. A rapid movement inland, concentrating on the fertile central plateau and surrounding areas, took place in the centuries following first settlement. A movement to marginal zones of the island is identifiable later in the sequence. This sequence is characterized by fluctuating exchanges with surrounding islands, demonstrated, for example, by the presence of ceramics and stone remains from the Grande Terre. But the main dynamics in terms of intensification of production and cultural changes were internal, with oral traditions showing the late political influence of incoming groups from surrounding islands (Sand et al. 2010).

We here report on the reptile remains found in association with the archeological sites investigated. Because there are no vouchered modern specimens from Tiga, this report constitutes the first list of the reptiles of the island.

MATERIALS AND METHODS

Sampling and Excavation of the Sites

The collection studied here comes from four 1 m² excavation pits, located at three different sites on Tiga (see Sand et al. [2010] for a summary). The letter after each site number designates a pit. Excavations were made by hand, mostly in artificial 5 cm or 10 cm spits. All the soil was sieved in water through 2.8 mm mesh and the remaining sediment sorted by hand. Site LTD-14, called Hari, is a small rock-shelter located on the west coast of Tiga, about 50 m inland and approximately 2 m above sea level. The excavation reached the beginning of human occupation at 100 cm deep, with an initial date of use of 1,630 ± 40 yr B.P. (Beta-227979). A total of four other dates range from 650 ± 40 yr B.P. (Beta-227977) at 70–75 cm, to 240 ± 40 yr B.P. (Beta-227972) at 15 cm, showing regular use of the site mainly during the middle of the second millennium A.D.

Site LTD-02A, in the center of the present-day village of Tiga, is a nearly filled rock-shelter on the northwest coast of the island, about 70 m from the present shore. Excavations reached 190 cm deep and demonstrate that until possibly the second half of the first millennium A.D., the site opened directly to the sea. It was only with the building of a raised sand dune and the movement of the coast toward the west that the shelter became usable to humans. In its first stage, between the end of the first millennium A.D. and the middle of the second millennium A.D., the shelter was used only episodically; thin lenses of ash being separated by thick lenses of sterile sand, indicating the proximity of wave action. It is only from about 530 ± 40 yr B.P. (Beta-227967), starting with layers at a depth of 65 cm, that continuous use of the shelter is apparent.

Site LTD-18, called Dréné, is a rock-shelter located on the first cliff face of the uplifted coral platform of Tiga, at the rear of the buildings of the Tiga chiefdom. This site was used until recently for shelter during cyclones. Three test-pits were opened in the low-ceilinged shelter (Figure 2), reaching the in situ prehuman base at a depth of approxima-tely 65 cm, with complex stratigraphies indicating multiple reuses of the site. The oldest date comes from test-pit LTD-18C, with a result of 2,530 ± 50 yr B.P. (Beta-227-996) at a depth of 55–65 cm. The other dates indicate a continuous occupation of Dréné, but with the main use of the rock-shelter occurring between the end of the first millennium B.C. and the first millennium A.D.

Morphological Comparisons

Because our material is <3,000 yr old, we assume that it represents a fauna similar to that of the Loyalty Islands today. Megafaunal reptiles are known to have survived until relatively recent times and undescribed, apparently extinct species of lizards have been identified in mainland New Caledonian sites of comparable age (Anderson 1925, Buffetaut 1983, Balouet and Buffetaut 1987, Balouet 1989, 1991, Balouet and Olson 1989, Bayless and Naclerio 1993, Mead et al. 2002, Anderson et. al. 2010, Kennedy 2011). However, we found no evidence of extinct lineages in our material. Material from Tiga was compared with reference specimens representing species widely distributed in the Pacific as well as those known to be part of the extant fauna of the Loyalty Islands. In addition, specimens belonging to some taxa documented only from the Grande Terre of New Caledonia were also compared (see Bauer and Sadlier 2000) (Appendix 1). The New Caledonian regional herpetofauna is largely unique, with the exception of a few widespread, sometimes human-dispersed taxa (e.g., *Nactus pelagicus* [Girard, 1858]; *Hemiphyllodactylus typus* Bleeker, 1860; *Hemidactylus garnotii* Duméril & Bibron, 1836; *H. frenatus* Duméril & Bibron, 1836; and *Lepidodactylus lugubris* [Duméril & Bibron, 1836]). All lizards known from the region are either skinks (Scincidae) or geckos (Gekkonidae, Diplodactylidae). We used diagnostic characters previously employed to distinguish related groups of geckos and skinks in fossil localities of New Zealand and Tonga (Gill 1985, Worthy 1987, 1991, Pregill 1993, Lee et al. 2009), as well as additional characters based on published osteological studies (Wellborn 1933, Kluge 1962,
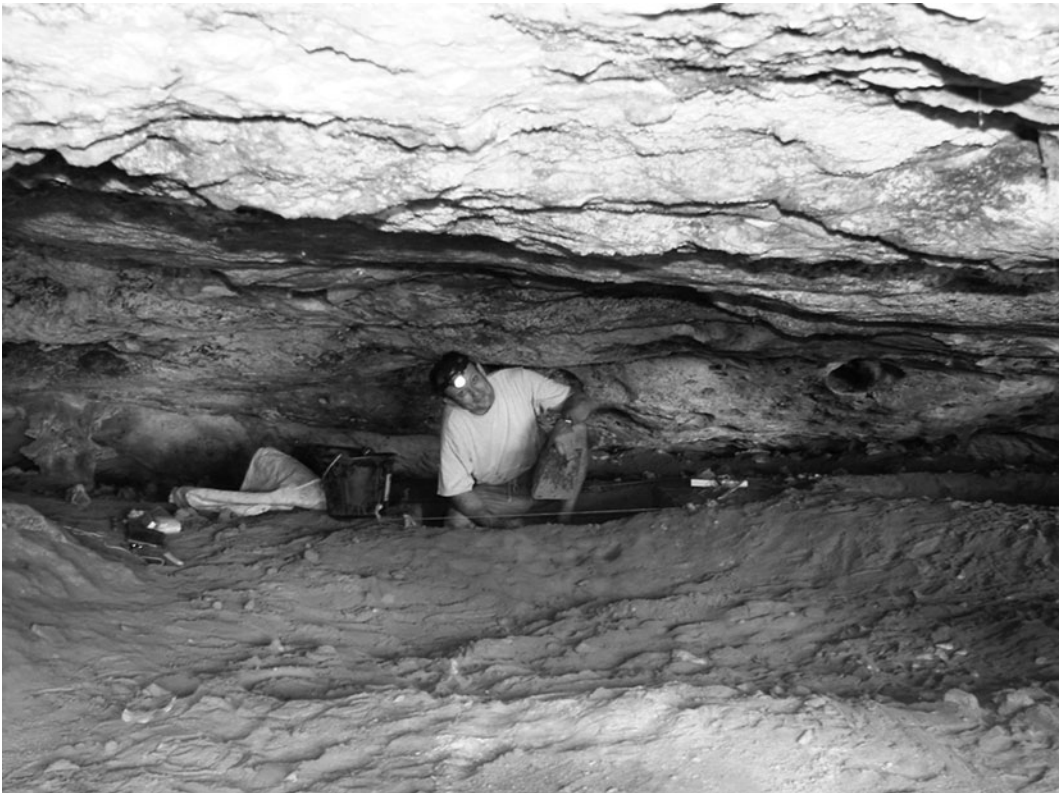
Figure 2. View of a test-pit excavation underway at site LTD-18 at Dréné, Tiga, showing the low ceiling of this shelter site.

Häupl 1980, Bauer 1990*a*, Abdala 1996, Conrad 2008, Daza 2008, Daza et al. 2008, Evans 2008, Gelnaw 2011, Kennedy 2011, Gauthier et al. 2012, Jerez 2012) and new observations to identify the taxa present in our archeological samples. It is not currently possible to use an apomorphy-based approach to diagnose the two resident gekkotan families (Diplodactylidae and Gekkonidae) from one another as they exhibit plesiomorphic and/or convergent osteological characters, at least with respect to the elements preserved in the Tiga material; therefore, we have focused on characters that are variable at the generic and species level for all of the lizard material from Tiga. Herein we use the term "gecko" synonymously with "limbed gekkotan" (i.e., nonpygopodid gekkotans), although in some instances we comment on pygopodids in a comparative context.

Terrestrial snakes in the Loyalty Islands are represented by two families, Boidae and Typhlopidae (Sadlier and Bauer 1997). Typhlopids occurring in the southwest Pacific are all very small and unambiguously identifiable osteologically at the familial level. As no typhlopid elements were present in our sample, our ophidian comparisons were restricted to relevant boids, although laticaudine elapids were also taken into account, as the four species in this group occurring in New Caledonian waters (*Laticauda colubrina* [Schneider, 1799], *L. frontalis* [de Vis, 1905], *L. laticaudata* [Linnaeus, 1758], *L. saintgironsi* Cogger & Heatwole, 2006) regularly come onto land and may be found at some distance inland (Ineich and Laboute 2002).

Descriptive osteological terms follow Daza et al. (2008, 2012) and Evans (2008). In this

paper we use the term "seam" (sensu Jones et al. [2011]) to refer to the boundary between bones in articulation as distinct from "suture," referring to the entire joint including the articulating surfaces of participating bones and the associated connective tissue, if any, between the seams.

Observations were made on Leica MZ6 and Nikon SMZ1000 dissecting microscopes (Leica Microsystems, Buffalo Grove, Illinois), the latter equipped with a digital camera (Nikon DS-Fi1) and the image acquisition software NIS Elements D (ver. 3.1, Nikon Corporation, Tokyo, Japan). All photographs were created using the Extended Depth of Focus application, which creates an all in-focus image from a series of Z-axis images. Images were assembled and measured on Adobe Illustrator CS3 software (Adobe Systems Incorporated, San Jose, California).

High-resolution X-ray computed tomographies of extant species were obtained at the Digimorph facility of the University of Texas at Austin and the American Museum of Natural History in New York with an Xradia microXCT scanner (Xradia Inc., Pleasanton, California; 200 kV and 100 µA) and 2010 GE phoenix v| tome|x s240a microfocus system (General Electric, Fairfield, Connecticut; 80 kV and 170 µA), respectively. Digital radiographs of some specimens were obtained at the U.S. National Museum of Natural History at the Museum Support Center using a Kevex PXS10-16W X-ray source (Thermo Electron Corporation, Scotts Valley, California) and Varian Amorphous Silicon Digital X-RayDetector PaxScanH 4030 (Varian Medical Systems, Inc., Palo Alto, California).

Fossil material examined is housed in the collection of the Institut d'archéologie de la Nouvelle-Calédonie et du Pacifique in Nouméa. Comparative material was examined from the collections of the American Museum of Natural History, New York (AMNH); Australian Museum, Sydney (AMS); California Academy of Sciences (CAS); James Ford Bell Museum, University of Minnesota, St. Paul (JFBM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); and The Natu-

ral History Museum, London (NHMUK). Institutional abbreviations for comparative material follow Sabaj Pérez (2013).

To estimate the snout-vent lengths (SVLs) of fossils, we multiplied individual fossil element lengths by (SVL/element length) derived from X-rays of adult specimens of 60 extant Pacific skinks and limbed gekkotans of comparable size (see Appendix 1). The estimated size for fossils was compared with maximum SVLs of candidate squamate species (Bauer and Sadlier 2000, Meiri 2008) for Tiga.

RESULTS

Osteological Comparisons between Geckos and Skinks

A total of 83 bones were recovered from four sites (Figure 2, Appendix 2). The most common elements in the combined sample of lizards and snakes were vertebrae (25.3%), lizard femora (18.1%), lizard dentaries (12.0%), lizard humeri (10.8%), lizard frontals (9.6%), and lizard maxillae (6.0%). The lizard material recovered includes both geckos and skinks of several species each, but snake material recovered represents a single species.

MAXILLA: Five maxillae were found, two from geckos, representing two species, and three from skinks, representing a single species. This bone has a very distinct morphology in both groups (Figure 3), especially with respect to the shape of the facial process (Worthy 1987), which, unfortunately, is very delicate and easily lost in small fossils (see Estes [1983]). Another variable part of this bone is the posterior process, which in some skinks bifurcates into a superior and inferior posterior processes (Gill 1985), but is always single in gekkotans. Tooth morphology can also be used to differentiate these groups; skinks tend to have blunt, chisel-shaped tooth crowns, whereas crowns are rounded and conical in most gekkotans, although in a few groups, these can also be recurved (Patchell and Shine 1986, Bauer and Russell 1990, Nikitina and Ananjeva 2009). Skinks may bear some striations on the lingual side of the crown (Kosma 2004), which are not present in gekkotans. The labial foramina are also variable in size (large in skinks and small
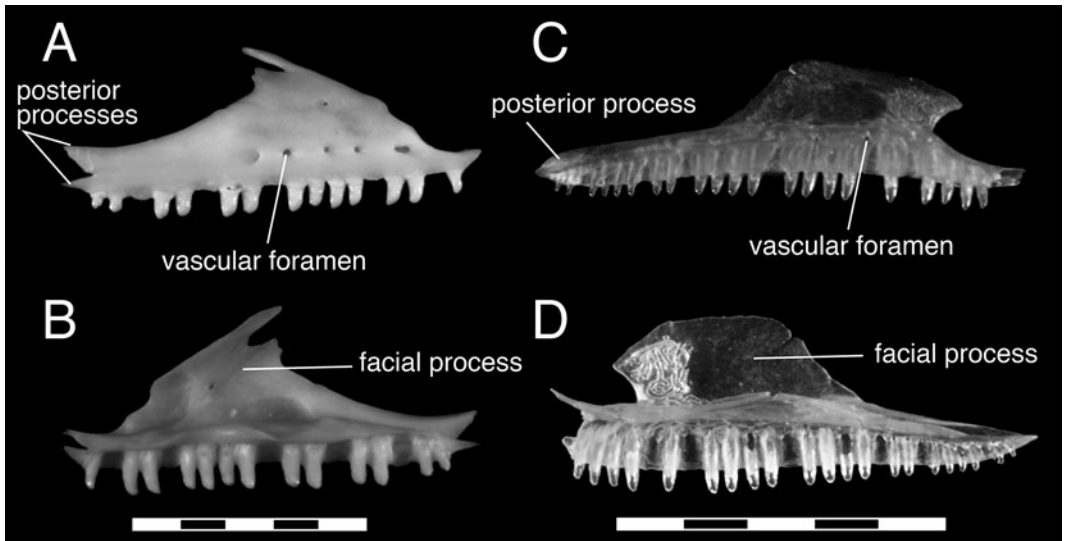
Figure 3. Maxillae: (*A*, *B*) *Lioscincus nigrofasciolatus* (MCZ A-27345), (*C*, *D*) *Bavayia robusta* (MCZ A-27347). (*A*, *C*) Lateral and (*B*, *D*) medial views of right maxilla. Scale bar equals 5 mm.
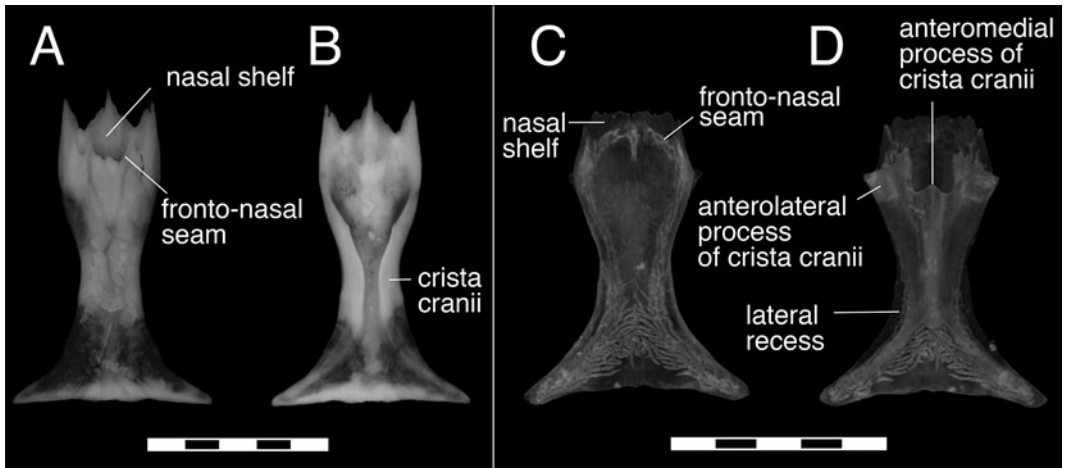
Figure 4. Frontals: (*A*, *B*) *Lioscincus nigrofasciolatus* (MCZ A-27345), (*C*, *D*) *Bavayia robusta* (MCZ A-27347). (*A*, *C*) Dorsal and (*B*, *D*) ventral views. Scale bar equals 5 mm.

in geckos) (Estes 1983, Greer 1989, Evans 2008). Number of tooth loci is also informative, but these vary with age and size (Arnold 1980, Bauer and Russell 1990), and this variation must be evaluated.

FRONTAL: One skink frontal and seven gecko frontals, the latter assignable to three species, were identified. Although the frontals are unpaired in the majority of gekkotans and in lygosomatine skinks (Greer 1970, 1989, Abdala 1996, Evans 2008, Skinner et al. 2011), this bone can be easily differentiated on the basis of the crista cranii. In skinks and many other lizards, the crista cranii are two ventral downgrowths that do not meet ventrally (Conrad 2008, Evans 2008, Gelnaw 2011, Gauthier et al. 2012) (Figures 4*A*, *B*); whereas in gekkotans they fuse

ventrally forming a subolfactory process that completely encloses the olfactory nerve (Wellborn 1933, Kluge 1962, Bauer 1990*a*, Daza et al. 2013) (Figures 4*C, D*).

PARIETAL: One skink parietal was found. Parietals of gekkotans and skinks are similar but they can be distinguished easily because skinks have a parietal foramen, fused parietals, and a well-developed parietal fossa, whereas in gekkotans, the parietal foramen is missing (Gill 1985, Estes et al. 1988, Daza et al. 2013), and the parietals are typically unfused (there are exceptions, e.g., the pygopodid *Lialis* and some species of the gekkonid genera *Gekko* and *Luperosaurus*, in which partial or complete fusion occurs in large specimens, but not among diplodactylids or insular Pacific gekkonids).

QUADRATE: One skink quadrate was found. The quadrates of limbed gekkotans and skinks have a similar deep concave conch, a relatively narrow central pillar, little medial expansion, and a small pterygoid lappet (Evans 2008). Despite these similarities, the quadrate of skinks differs from that of gekkotans in its type of suspension; whereas in skinks the squamosal and supratemporal contribute to the suspension by contacting this bone dorsally, in gekkotans the suspension is almost exclusively through articulation with the otooccipital (or paroccipital abutting) (Rieppel 1984), via a synchondrosis (Sensu Payne et al. [2011]). Although suspension cannot be directly assessed in disarticulated and fragmentary material, the differences in the degree of ossification of the posterolateral part of the cephalic condyle of the quadrate can help to distinguish these groups. In many limbed gekkotans, this area appears irregularly notched in the dried skull (Rieppel 1984), while cleared-and-stained preparations reveal the notch to be filled by cartilage, often with a small imbedded ossification (Daza et al. 2012, Daza pers. obs.). Among skinks, the posterolateral part may have only a slight notch or an apical foramen at the confluence of the tympanic crest, medial pillar, and the cephalic condyle (Evans 2008, Gelnaw 2011).

BRAINCASE: One gecko basicranium was found, and it can easily be differentiated from those of skinks by several characters. Some

of the most conspicuous differences are the presence of a foramen prootico for cranial nerve V instead of an incisura or notch (although there is a notch in pygopodids and a few limbed geckos, e.g., *Gekko gecko* [Linnaeus, 1758], *Coleonyx variegatus* [Baird, 1858]), longer basipterygoid process of the parabasisphenoid forming an obtuse angle (acute in skinks and elongated in pygopodids), lack of basal spines or vertical laminae that flare out anteriorly from the crista alaris and that overlie the basipterygoid stalks (some limbed geckos have a clinoid process in this position, but this structure is wider than a narrow spine), presence of a well-developed crista prootica (lacking in pygopodids and reduced in some gekkonids, e.g., *Matoatoa*), and a bicipital occipital condyle (single in *Lialis*).

DENTARY: Ten dentaries were found, seven are from geckos, representing three taxa, and three from skinks of a single species. These two groups typically have a closed Meckelian canal (Kluge 1967, Greer 1989, Shea 1999, Evans 2008) (Figure 5), although some skinks retain an open Meckelian groove, but they can be easily differentiated by the mandibular symphysis. Geckos generally have a reduced intermandibular articulation, tapering laterally away from the midline and giving the joint a ∧ shape (Holliday et al. 2010). The ventral border of the dentary in skinks is strongly curved (Figures 5*A, B*), whereas in geckos this edge is generally straight (Figures 5*C, D*); the dentary is also strongly curved mediolaterally in skinks (Gill 1985). Geckos also have a shelf for the anterolateral process of coronoid on the labial side, whereas in skinks the dentary has an upwardly directed coronoid process that prevents the extension of the coronoid onto the labial surface of the dentary (Figure 5). Additional characters from tooth morphology can be used to differentiate dentaries among these groups.

COMPOUND BONE: Three compound bones were found, two are from geckos and one from a skink, representing one taxon each. Geckos and skinks both experience fusion among some postdentary bones. In gekkotans, the fusion of the articular and prearticular and the partial fusion of the surangular are common. The angular has

FIGURE 5. Dentaries: (*A*, *B*) *Lioscincus nigrofasciolatus* (MCZ A-27345), (*C*, *D*) *Bavayia robusta* (MCZ A-27347). (*A*, *C*) Lateral and (*B*, *D*) medial views. Scale bar equals 5 mm.
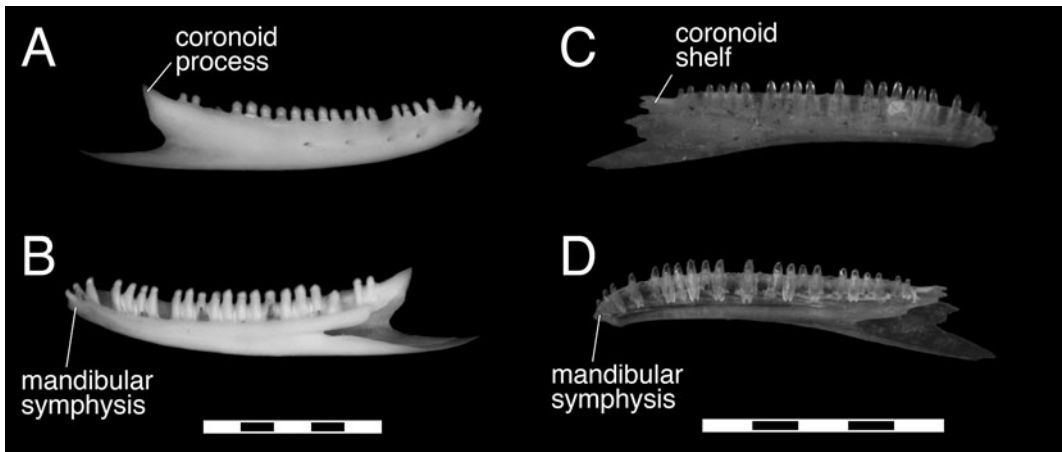
only been reported in a few species of eublepharid geckos and in the genus *Teratoscincus* (Kluge 1962; Arnold 1977; Grismer 1988; Evans 2008). Among skinks, fusion of the articular (articular complex, i.e., articular and prearticular) and angular is also common (Evans 2008), but the angular is reduced, being either persistent or absent in some lygosomines (Greer 1970, Gelnaw 2011). Although the morphology of the retroarticular process is somewhat convergent between skinks and gekkotans, these two groups can easily be differentiated because gekkotans have a unique lateral notch that forms a waist proximally (Estes et al. 1988) and a spoon-shaped retroarticular process (rod-like in pygopods), whereas skinks have a narrower retroarticular process with only a narrow, shallow cup (Kluge 1976, Hutchinson 1997, Evans 2008).

VERTEBRAE: Twenty-two procoelous vertebrae were found, 5 are from skinks, representing two taxa and 17 from a single snake species. Gekkotan vertebrae, with the exception of the majority of New World sphaerodactyls, are characterized by amphicoelous vertebrae (Hoffstetter and Gasc 1969, Kluge 1967, 1995).

PELVIC GIRDLE: Five innominate bones were recovered, three from skinks and two from geckos. These two groups can be differentiated because the pubis in skinks is more elongated, thus defining a more elliptically shaped, rather than a cordate ischiopubic fenestra of some geckos (Kluge 1962, Bauer 1990b, Daza et al. 2012). The acetabular area is also proportionally larger in geckos than in skinks (Daza et al. pers. obs.).

APPENDICULAR ELEMENTS: Nine humeri were recovered, four from skinks and five from geckos. When limbs are not reduced, the humerus is proportionally longer in skinks than in gekkotans. Another difference lies in the shaft, which is more cylindrical and straight (Figures 6*A*, *B*) in skinks, in comparison to geckos in which the preaxial tuberosity and ectepicondyle eminence are considerably more well developed (Figures 6*C*, *D*). Another difference is that the radial condyle is twice as large as the ulnar condyle is in geckos, whereas in skinks the radial condyle is only slightly larger than the ulnar condyle (Daza pers. obs.).

Seventeen femora were recovered, 10 from skinks and 7 from geckos. Femora of skinks and geckos can be identified because skinks exhibit a well-defined U-shaped notch between the femoral head and the internal trochanter (Figure 6; see also Worthy [1991: fig. 8]). Morphological variation at the genus or species level is subtler, and here we limit ourselves to size comparisons, although in many cases the bones recovered did not exhibit epiphyseal terminal fusion, therefore skeletal maturity cannot be assumed.
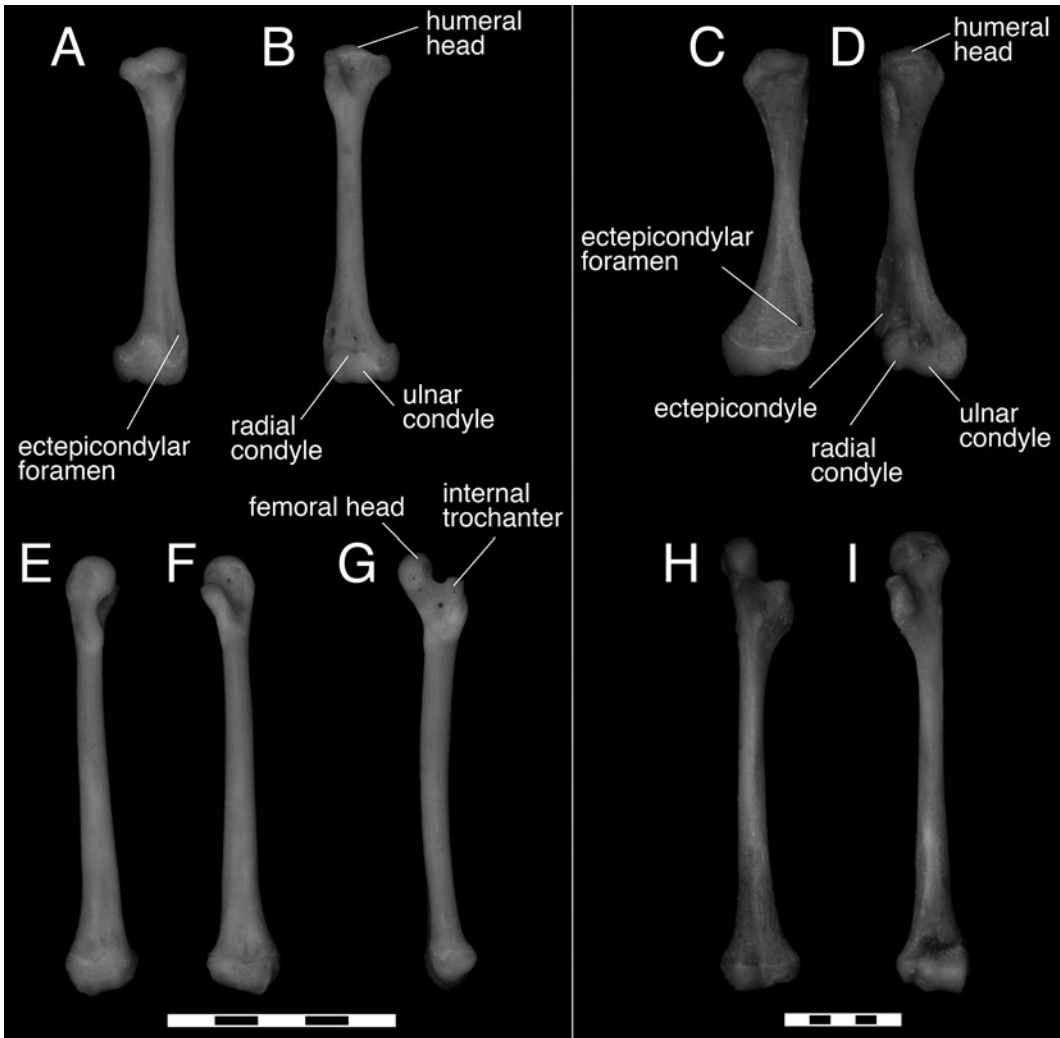
Figure 6. Humeri (*A–D*) and femora (*E–I*). (*A, B, E–G*) *Marmorosphax tricolor* (MCZ A-27320); (*C, D, H, I*) *Correlophus ciliatus* (JFBM 15825). (*A, C*) Anterodorsal view of right humeri; (*B, D*) posteroventral view of right humeri; (*E, H*) anterior view of right femora; (*F, I*) posterior view of right femora; (*G*) posteroventral view of right humerus. Scale bar equals 5 mm.

Species Identification

SCINCIDAE

Emoia loyaltiensis (Roux, 1913), Loyalty Islands *Emoia*.

DISTRIBUTION IN NEW CALEDONIAN REGION: Recorded only from Ouvéa, Lifou, and Maré (Sadlier and Bauer 1997, Bauer and Sadlier 2000).

MATERIAL: Maxillae (*n* = 3) (Figures 7*A, C*) and compound bone (*n* = 1) (Figures 7*D, E*). Using the length of two complete maxillae and a compound bone, we estimate SVL values between 66.5 mm and 68.5 mm. The maximum SVL for this species is 83.2 mm (Zug and Ineich 1995).

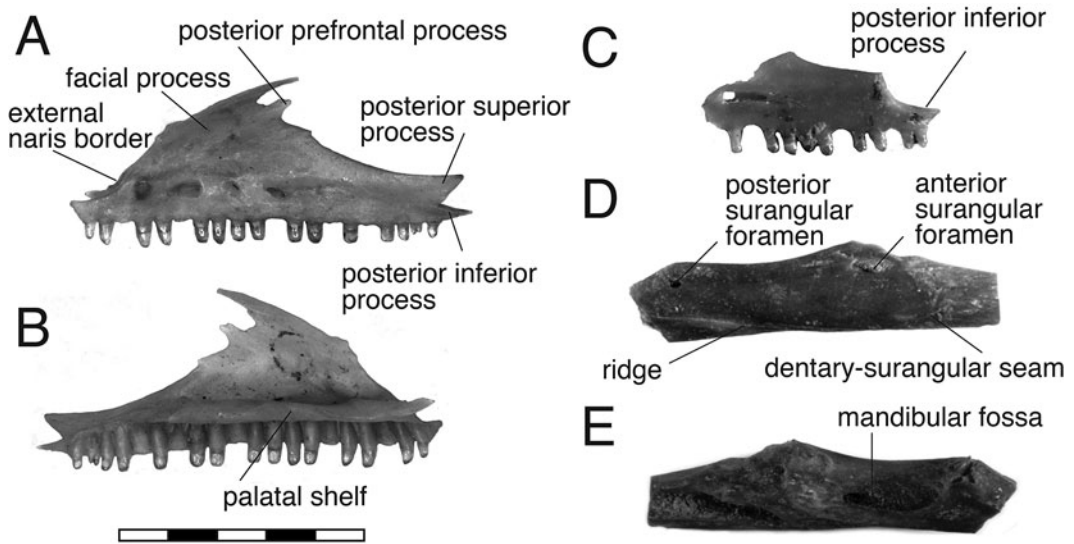Figure 7. Material identified as belonging to *Emoia loyaltiensis:* (*A–C*) maxilla (LTD-14A 65–70 cm, LTD-18C 55–65 cm); (*D*, *E*) compound bone (LTD-18C 55–65 cm). (*A*, *C*, *D*) Lateral view; (*B*, *E*) medial view. Scale bar equals 5 mm.

REMARKS: One left (Figure 7*A*, *B*) and one right complete maxilla and a fragment of the posteromedial portion of a left maxilla (Figure 7*C*). The most complete element measures 8.6 mm and bears 20 tooth loci. Teeth have slightly expanded tooth bases and chisel-shaped crowns. The facial process bends dorsomedially. The facial process slopes gradually from the posterior edge of the external naris and ends in a pointed process. There is a well-defined triangular depression medial to the external border of the naris, this depressed area is defined by two ridges, the crista lateralis, which is perpendicular to the labial margin of the maxilla, and the crista transversalis, which extends from the dorsal area of the maxillary lappet to the border of the nares. Below the junction of these two ridges there is a triangular transverse wall that is pierced by a foramen that opens anteriorly and corresponds to the anterior alveolar foramen (Smith and Gauthier 2013). The posterior margin is mainly concave but also has a short prefrontal posterior process. The posterior process above the tooth row is bifurcated, the superior projection forms a posterolateral triangular process, and the maxilla contacts the ventral and labial surfaces of the jugal. The palatal shelf is irregular and somewhat folded ventrally (forming a thick labial edge for the tooth row, being deeply troughed).

The compound bone is from the right side and is incomplete (Figures 7*D*, *E*), lacking the anterior process of the surangular portion and the totality of the retroarticular process, but the outline has no indication of a proximal waist as in geckos. This bone is compressed mediolaterally, the labial surface with an equal anterior tapering dentary-surangular seam, the anterior surangular foramen oval and more than four times the diameter of the posterior surangular foramen, a longitudinal ridge ventral to the posterior surangular foramen, and an oval but elongated mandibular fossa.

COMPARISONS: The fossil maxilla has four vascular foramina, but some of these are very enlarged and seem to be confluent as result of compact bone erosion. Five and six vascular foramina were observed in comparative material *Lioscincus nigrofasciolatus* and *E. loyaltiensis,*

respectively, although the number of foramina may be intraspecifically variable.

Lioscincus nigrofasciolatus (Peters, 1869), Green-bellied tree skink.

DISTRIBUTION IN NEW CALEDONIAN REGION: Widespread on the Grande Terre; Ile des Pins and its satellite islands; and on Ouvéa, Lifou, and Maré (Bauer and Sadlier 2000, Geneva et al. 2013).

MATERIAL: Frontal (*n* = 1) (Figures 8*A*, *B*), parietal (*n* = 1) (Figures 8*C*, *D*), quadrate (*n* = 1) (Figures 8*E*, *F*), dentary (*n* = 3) (Figures 8*G*, *H*), and innominate bone (*n* = 2) (Figure 8*I*), and vertebrae (*n* = 3) (Figure 8*J*). Using the length of complete frontal and parietal, we es-

timate SVL values between 98.1 mm and 108.9 mm. The maximum adult SVL for this species is 112 mm (Bauer and Sadlier 2000).

REMARKS: The frontal bone, measuring 7.7 mm in length, is almost complete (Figures 8*A*, *B*). Similarities with the frontal of the comparative material from this species includes dorsal sculpturing and a broad nasal shelf indicating that nasal bones covered most of the anterior portion.

The parietal (Figures 8*C*, *D*) shows significant interspecific variation among some skink species (Worthy 1987, 1991). This bone was found associated with the frontal and an innominate bone, and they might correspond to the same individual. The main body of this bone (excluding the posterolateral process) is
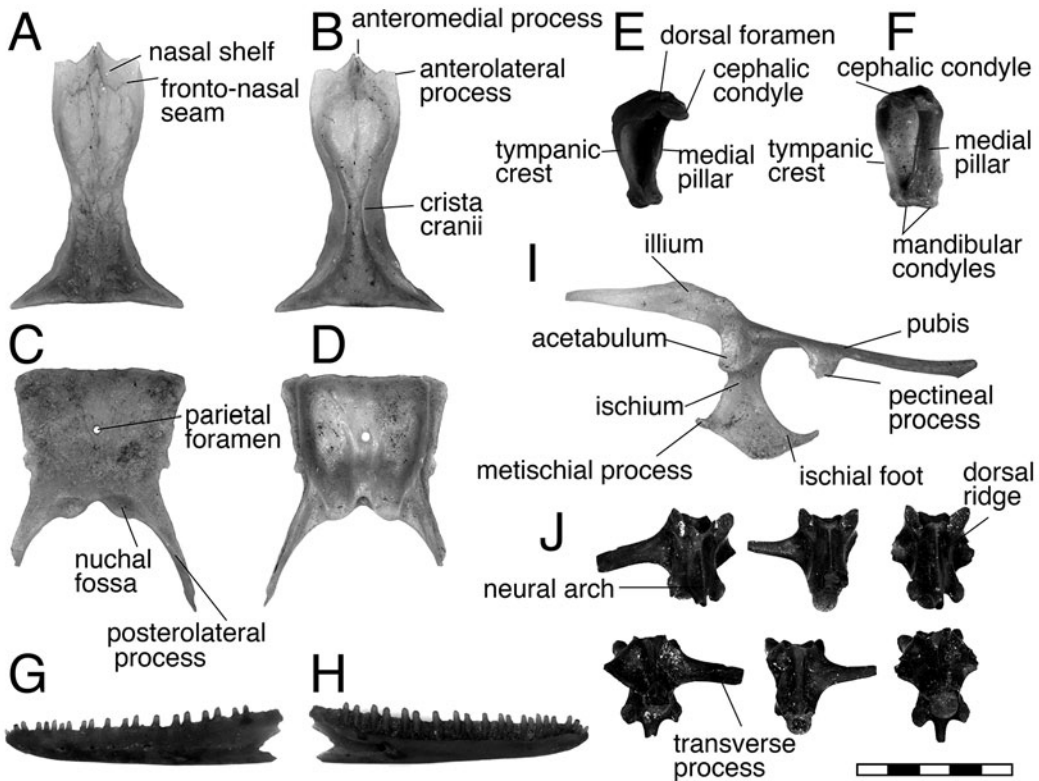
FIGURE 8. Material identified as belonging to *Lioscincus nigrofasciolatum*: (*A*, *B*) frontal (LTD-14A 70–75 cm); (*C*, *D*) parietal (LTD-14A 70–75 cm); (*E*, *F*) quadrate (LTD-18C 55–65 cm); (*G*, *H*) dentary (LTD 18C 45–55 cm); (*I*) innominate bone (LTD-14A 70–75 cm); (*J*) vertebrae, pygal series (LTD-02A 60–70 cm). (*A*, *C*) Dorsal view; (*B*, *D*) ventral view; (*E*) posterior view; (*F*, *H*) medial view; (*G*, *I*) lateral view; (*J*) dorsal (above) and ventral (below) views. Scale bar equals 5 mm.

almost rectangular (7.5 mm long ×5.5. wide) and the parietal foramen is located in the anterior half as in other skinks (Greer 1970, Gelnaw 2011). The lateral margins are almost straight with a small lateral projection anterior to the posterolateral processes. In ventral view, the posterior margin has a ∩-shaped notch with no posteromedial process, defining the posterodorsal margin of the parietal fossa.

The left quadrate recovered (Figures 8*E*, *F*) measures 5.0 mm long and has an expanded posterior concavity with stout medial pillar. On the dorsal surface, this quadrate of this species has a large quadrate foramen or this may perforate the margin of the bone to form a small notch.

One of the dentaries is nearly intact (Figures 8*G*, *H*). The Meckelian canal is fused but remains open up to the 11th last tooth. The most complete one is a left bone with 35 tooth loci, 5 mental foramina, measuring 9.5 mm in length.

The innominate bones are from the left and right sides (Figure 8*I*). These bones are identified as *L. nigrofasciolatus* based on size and morphological characters, including a short and wide pectineal process, an anteromedially oriented metischial process, and an expanded boot-like ischial foot.

The vertebrae are procoelous and are all from the caudal region. Each measures about 3 mm long (Figure 8*J*). They have single transverse processes with expanded bases; this marks the division between a wide anterior part and a narrow posterior part. They are nonautotomic and have no hemal arches; therefore, we identify these as part of the pygal series using two previous definitions of this vertebral segment (Holder 1960, Russell 1967). Although the most proximal caudal vertebrae are similar in all lizards (Etheridge 1967), these vertebrae have variable transverse processes that may be used to identify their position. We identify as the first pygal vertebra (Figure 8*J*, left) an element that retains a posterolaterally directed left transverse process that is wide and long (1.5 times centrum length) and does not taper laterally. Another vertebra (Figure 8*J*, middle) exhibits a left transverse process that is narrower and is almost laterally directed,

corresponding to the third or the fourth pygal. The third vertebrae has both transverse processes broken, therefore it is not possible to infer its position. The neural arch in all of these vertebrae is moderately high and has marked dorsal ridges on the neural arch lamina, although in comparison with the material of *L. nigrofasciolatus*, these ridges tend to be somewhat abraded.

COMPARISONS: The frontal resembles both *Lioscincus nigrofasciolatus* and *Emoia loyaltiensis* in the degree of nasal overlap and surface sculpturing. However the frontonasal seam in the comparative material of *L. nigrofasciolatus* (Figure 4*A*) is characterized by a less well-defined superficial median projection of the bone. The bifurcation of the anteromedial process of the frontal is well defined, as in the comparative material of *Lioscincus* and *Emoia*. The two prongs are asymmetrical in *L. nigrofasciolatus* and subequal in *E. loyaltiensis*. The fossil frontal seems to have subequal prongs, but it is possible that one of the sides is incomplete; therefore, this difference cannot be used conclusively. Additionally, although characters from the anterior margin of the frontal may be used to compare different species, these characters in skinks should be used with some reserve because it has been demonstrated that in *Oligosoma* (as *Cyclodina*) this structure varies with degree of ossification (Worthy 1987).

Scincidae, *incertae sedis*

MATERIAL: One dentary, one innominate bone, five presacral and three caudal vertebrae, four humeri, and seven femora.

REMARKS: The innominate bone is from the right side and is associated with an 8 mm femur; it is tentatively identified as belonging to *Emoia cyanura*. The innominate bone is somewhat similar to that of *Marmorosphax tricolor*, but is smaller in size. The pectineal process is broken and the metischial process is digit-like in shape and more posteriorly directed than in *M. tricolor*, where this process is more laminar and slightly bent anteriorly. The ischial foot is rectangular, but the terminus of this structure seems to be broken.

The presacral vertebrae are very fragmentary and measure about 4 mm each. These elements cannot be identified beyond familial level based on previous descriptions (Hoffstetter and Gasc 1969).

The lack of diagnostic features at species level limits the precise allocation of the appendicular elements. Using known lengths of bones from disarticulated specimens and the maximum SVL size for candidate species, we were able to provide tentative identifications.

The four humeri recovered were mostly complete. The estimated SVL interval for the lizards associated with these bones is 55.8 mm to 76.9 mm. This falls within the size range of adult *Emoia loyaltiensis* or subadult to small adult *Lioscincus nigrofasciolatus*. The much larger *Phoboscincus garnieri* (Bavay, 1869) (to 200 mm SVL) has been recorded from Lifou and Ouvéa (Sadlier 1987, Bauer and Sadlier 2000), and it is also possible that the larger humeri and femora could represent juvenile material of this species.

Seven femora were recovered, and the estimated SVL interval for the lizards associated with these bones is 44.9 mm to 76.8 mm. Within this range some of the likely species are *Caledoniscincus atropunctatus*, *C. haplorhinus* (Günther, 1872), or *C. austrocaledonicus* (Bavay, 1869), all of which attain maximum sizes of 57 mm or less, or *Emoia cyanura* (maximum 56 mm SVL), and *Emoia loyaltiensis* (maximum 83 mm SVL). The larger femora are also consistent with juvenile or subadult *Lioscincus nigrofasciolatus*.

DIPLODACTYLIDAE

Bavayia crassicollis Roux 1913, Strand *Bavayia*.

DISTRIBUTION IN NEW CALEDONIAN REGION: Although previously thought to be present on the Ile des Pins as well as at least one near-coastal islet off the northeast Grande Terre (Bauer and Sadlier 2000), ongoing molecular phylogenetic studies reveal that *B. crassicollis* is restricted to Lifou and Maré (its absence from Ouvéa may be an artifact of poor sampling), except for probable accidental translocations to the Ile des Pins region (Geneva et al. 2013).

MATERIAL: Dentary ($n = 1$) (Figures 9*A*, *B*), maxilla ($n = 1$) (Figures 9*C*, *D*), frontal ($n = 1$) (Figures 9*E*, *F*), and compound bone ($n = 2$) (Figures 9*G*, *H*), and innominate bone (incomplete, $n = 1$) (Figure 9*I*). The estimated SVL using the most complete bones are frontal (72.7 mm), dentary (66. 7 mm), maxilla (68.1 mm), and compound bone (74.3 mm). The maximum SVL for this species is 86 mm (Bauer and Sadlier 2000).

REMARKS: The dentary (Figures 9*A*, *B*) is nearly complete. It is robust and has relatively stout teeth in 28–30 tooth loci. The number of tooth loci in adult specimens of *B. crassicollis* over 70 mm SVL is usually approximately 35, so the low number in the Tiga specimen is consistent with the estimated size of the specimen since tooth loci increase with size intraspecifically (Bauer and Russell 1990).

The single left maxilla lacks most of the facial process. The piece of bone measures 8.5 mm and has 34 tooth loci and six vascular foramina (Figures 9*C*, *D*). Features we tentatively consider diagnostic of *B. crassicollis* include similar tooth locus counts and a similar transverse shelf of the premaxilla (straight, between a short anterolabial process and the maxillary lappet).

The frontal is incomplete, lacking the anterodorsal part. The preserved part measures 7 mm in length (Figures 9*E*, *F*). This bone has a dorsal surface that is slightly furrowed, large distally expanded anterolateral processes of the crista cranii, short anteromedial process of the crista cranii, posterior margin of the crista cranii transverse instead of V notched, a broad recess lateral to the tubular portion of the bone, and a constricted posterolateral process of the frontal to fit the postorbitofrontal.

The compound bone (Figures 9*I*, *J*) lacks most of the retroarticular process and the medial margin of the mandibular fossa. It is 10–11 mm in length, has a dentary-surangular seam with rounded outline, and lacks an anterior surangular foramen.

The innominate bone lacks the distal portions of pubis and ischium and exhibits the iliac blade shape and acetabular contour typical of this species (Figure 9*K*). The more incomplete elements can only be assigned with cer-
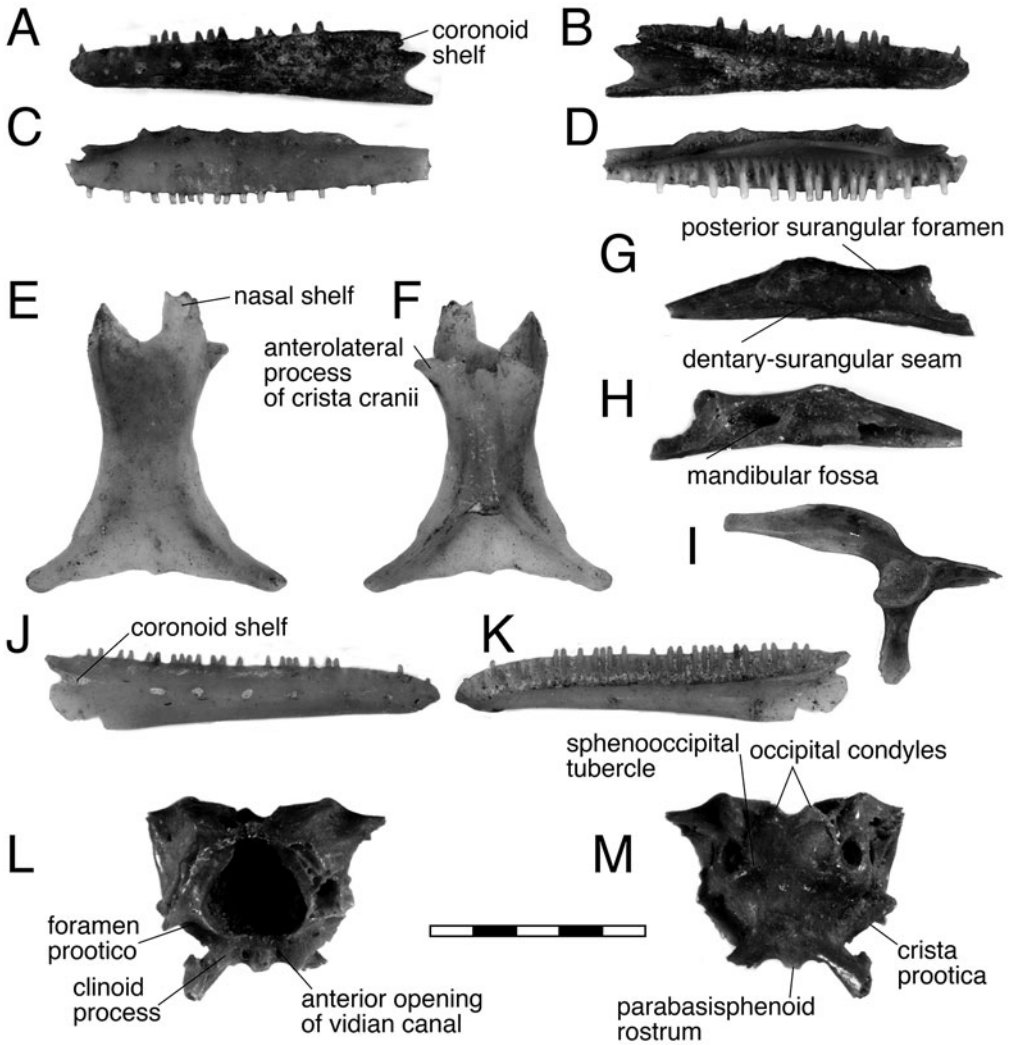
FIGURE 9. Material identified as belonging to *Bavayia crassicollis* (*A–I*) and *B.* sp. (*J–M*): (*A, B*) dentary (LTD 18C 55–65 cm); (*C, D*) maxilla (LTD-18C 55–65 cm); (*E, F*) frontal (LTD-14A 60–65 cm); (*G, H*) compound bone (LTD-18C 55–65 cm); (*I*) innominate bone (LTD-14A 70–75 cm); (*J, K*) dentary (LTD 18A 50–55 cm); (*L, M*) braincase (LTD-18C 55–65 cm). (*A, C, G, J, I*) lateral view; (*B, D, H, K*) medial view; (*E, L*) dorsal; (*F, M*) ventral. Scale bar equals 5 mm.

tainty to the *B. cyclura* complex, but their specific allocation is highly probable.

COMPARISON: The frontal of *B. crassicollis* and other members of the *B. cyclura* group has more pronounced anterolateral processes of the crista cranii and broader lateral recesses than *B. sauvagii*. The Tiga frontal implies a SVL of ~73 mm, which is substan-

tially larger than the largest known *B. sauvagii* (~62 mm SVL). The more robust dentary and larger, less numerous teeth also distinguish *B. crassicollis* from this species.

The posterior surangular foramen location, medial offset of the articular, quadrate groove, and anterodorsal inclination of the articular surface are also similar to other large-bodied

members of the *B. cyclura* group, including *B. robusta* Wright, Bauer, & Sadlier, 2000.

Bavayia sp.

MATERIAL: Dentary (*n* = 3) (Figures 9*J*, *K*) bones, braincase (*n* = 1) (Figures 9*L*, *M*). Using the length of the most complete dentary and the braincase, we estimate SVL values of 69.3 mm and 50.3 mm, respectively.

REMARKS: The dentary is represented by two incomplete left rami and one nearly complete right ramus (Figures 9*J*, *K*). These bones have numerous slender teeth (total tooth loci ranges of 38–44, which are consistent with counts from living specimens). The braincase (Figures 9*L*, *M*) has a marked suture between the parabasisphenoid and the basioccipital anterior to the sphenooccipital tubercles and the sphenooccipital tubercle partially covering the lateral aperture of the recessus scalae tympani in ventral view.

COMPARISONS: The dentary differs slightly from the comparative material of *Bavayia sauvagii* in having a lower height and a very well-defined lateral shelf for the coronoid posterior to the tooth row. The slender dentition somewhat resembles the larger, extralimital species *Oedura marmorata* Gray, 1842. The braincase strongly resembles comparative material of *Bavayia*. It is too large to be referable to *Lepidodactylus lugubris* (maximum SVL 47 mm), to which it also bears some similarity. The paroccipital process is long and slender as in *Bavayia*, *Gehyra*, and *Nactus*, but differs from the latter two in the extent of the sella turcica, being small in *Bavayia*, intermediate in size in *Gehyra*, and broad and elongated in *Nactus*.

Bavayia sauvagii was previously thought to be widespread on the Grande Terre as well as on the Ile des Pins and on Maré (Bauer and Sadlier 2000); however, ongoing molecular phylogenetic studies reveal that *B. sauvagii* is a complex of microendemic cryptic species (Bauer and Jackman 2006). The form occurring on Maré appears to be restricted to this island and perhaps other islands in the southern Loyalties. The maximum size of *B.* aff. *sauvagii* is 62 mm SVL (Bauer and Sadlier 2000). Thus the braincase, which shows rela-

tively little intrageneric variation in *Bavayia*, may be attributable to either this species or *B. crassicollis*. At least the largest of the dentaries implies a size greater than that reached by *B.* aff. *sauvagii*, but is more similar to this species than to *B. crassicollis* in morphology.

GEKKONIDAE

Gehyra georgpotthasti Flecks, Schmitz, Böhme, Henkel & Ineich, 2012, Vanuatu giant gecko.

DISTRIBUTION IN NEW CALEDONIAN REGION: This species is known from Maré, Dudun, and a single individual from Lifou, as well as from Malakula, Pentecost, Epi, Espiritu Santo, Ambae, Erromango, and Efate in Vanuatu (Hamilton et al. 2009, Ineich 2011, Flecks et al. 2012). Two specimens from Fakarava, Tuamotu Archipelago, are certainly the result of human introduction (Flecks et al. 2012), and we consider a record from Norfolk Island (Boulenger 1885) to be in error.

MATERIAL: Maxilla (*n* = 1) (Figures 10*A*, *B*), dentary (*n* = 3) (Figures 10*C*, *D*), innominate bone (*n* = 1) (Figure 10*E*). The estimated SVL values using the most complete bones are: dentary (137.5 mm), and maxilla (123.8 mm). The maximum known SVL for this species is 142 mm (Flecks et al. 2012).

REMARKS: The maxilla is one left incomplete bone without most of the facial process and preserving the entire basal part including the palatal shelf (Figures 10*A*, *B*). The tooth row measures 16.5 mm, bears 33 tooth loci, and has nine vascular foramina.

Two dentaries from the left and one from the right were recovered; the ones from the left are the most complete ones (Figures 10*C*, *D*), whereas the one from the right is largely incomplete. The most complete dentary measures 21 mm and bears 34 tooth loci. The other more complete element measures 16 mm and bears 31 tooth loci, and the most incomplete element only preserves the anterior-most part of the tooth row and a splint of bone corresponding to the ventral margin of the dentary.

A fragment of a large right innominate bone (Figure 10*E*) preserves the ilium blade, acetabulum, and minor parts of ischium and pubis. On the pubic part, there is no indication of
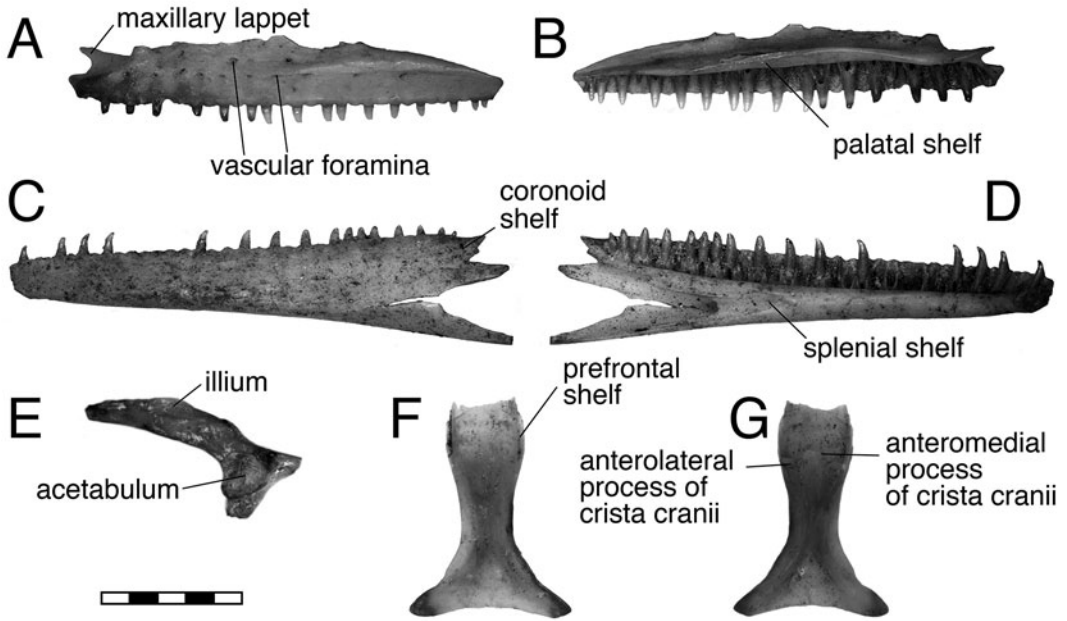
FIGURE 10. Material identified as belonging to *Gehyra georgpotthasti* (*A–E*) and *Nactus pelagicus* (*F, G*). (*A, B*) Maxilla (LTD-14A 45–50 cm); (*C, D*) dentary (LTD-14A 65–70 cm); (*E*) innominate bone (LTD-18C 55–65 cm); (*F, G*) frontal (LTD-14A 85–90 cm). (*A, C, E*) lateral view; (*B, D*) medial view; (*F*) dorsal view; (*G*) ventral view. Scale bar equals 5 mm.

an obturator foramen right next to the acetabulum. The iliac blade tapers distally gradually.

COMPARISON: Although this material resembles both large-sized gekkonids and diplodactylids, we favored an identification of this material with *G. georgpotthasti* based on comparisons with museum material and distribution records of this species (Bauer and Sadlier 2000, Flecks et al. 2012), previously only known from Vanuatu and Lifou, Maré, and Dudun among the Loyalties (Ineich 2011, Flecks et al. 2012).

In terms of size and shape, the maxilla is also comparable to that of *Rhacodactylus auriculatus* (Bavay, 1869) and *R. trachyrhynchus* Bocage, 1873, including two rows of vascular foramina, a posterolateral margin slightly rectangular and not tapering markedly, middle teeth 3–4 times larger than the posterior teeth, palatal shelf with a shallowly troughed ventrally, palatal shelf anterior to the palatine suture straight with maxillary lappets forming an internal angle of about 140°. However, the dentition is moderately recurved as in *G. georgpotthasti* and *R. trachyrhynchus* and not strongly recurved as in *R. auriculatus*.

The dentaries also resemble *Rhacodactylus auriculatus* and *R. trachyrhynchus* although they differ from *Rhacodactylus* in having more tooth loci. The splenial extends as far anteriorly as the 10th tooth locus from the back. The mesial teeth are recurved and the posterior straight, but the anterior-most are not as procumbent as in *R. auriculatus*. There are seven mental foramina, the last one slit-like and having a markedly shallow furrow directed toward the anterior point of the labial coronoid shelf as in *Gehyra georgpotthasti* and *Rhacodactylus* spp. Ventral border of dentary is flattened, and bone surface is slightly rugose.

Nactus pelagicus (Girard, 1858), Pelagic gecko.

DISTRIBUTION IN NEW CALEDONIAN REGION: This unisexual species is widespread in the New Caledonian region, including

Ouvéa, Lifou, and Maré (Bauer and Sadlier 2000) and is widespread in southern Vanuatu, Fiji, and parts of Micronesia and Polynesia (Bauer and Henle 1994, Heinicke et al. 2010).

MATERIAL: Frontals (*n* = 5) (Figures 10*F*, *G*). The estimated SVL using the most complete frontal (7.8 mm) is 75.1 mm. The maximum SVL for this species is 86 mm (Zug and Fisher 2012).

REMARKS: The frontal (Figures 10*F*, *G*) has a smooth, flat dorsal surface and wide anterior end (Pregill 1993). The nasofrontal seam is W-shaped, and the anterior and dorsal part of the frontal remains unfused, defined anterolateral shelves for the prefrontal, anterior portion of the bone laminar with little or no indentation (i.e., no discrete anteromedial and anterolateral process), slightly concave frontoparietal suture, posterolateral processes terminate in broad, slightly posteriorly angled flanges, anterolateral process of the crista cranii triangular and poorly developed, with a longer process in between (i.e., anteromedial process).

COMPARISONS: Diplodactylids and *Hemidactylus frenatus* possess a relatively broader interorbital region of the frontal. The posterolateral processes of the frontal (which reaches a maximum SVL of only 47 mm) in *Lepidodactylus lugubris* taper to a fine point.

Gekkota, *incertae sedis*

MATERIAL: Six humeri and seven femora.

REMARKS: Using the size of the elements recovered to infer the SVL, the six humeri (range 6.5–7.0 mm) and seven femora (range 7.0–9.0 mm) recovered imply SVLs of 48.2–58.4 mm, and 47.1–60.7 mm, respectively. These could belong to any of several candidate gekkonid or diplodactylid species (*Bavayia crassicollis*, *B.* aff. *sauvagii*, *Nactus pelagicus*, *Hemidactylus garnotii*, *H. frenatus*, *Lepidodactylus lugubris*) except *Gehyra georgpotthasti* or *Hemiphyllodactylus typus*, which can be excluded on the basis of size.

BOIDAE

Candoia bibroni (Duméril & Bibron, 1844), Pacific boa.

DISTRIBUTION IN NEW CALEDONIAN REGION: This snake has been recorded from Ouvéa, Lifou, and Maré (Bauer and Sadlier 2000) and is the only reptile previously reported in the literature from Tiga (Oliva and Talon 1996). It is otherwise widely distributed from the eastern Solomon Islands to American Samoa (Smith et al. 2001).

MATERIAL: Procoelous trunk vertebrae (*n* = 17) (Figures 11*A*, *D*). No exact estimations of the size are possible with the isolated vertebrae, but the sizes of these vertebrae are comparable to the skeletons of the comparative material.

REMARKS: All the vertebrae have the diagnostic characters of boine snakes such as the presence of paracotylar fossae and foramina and the vaulted, biangled posterior margin of the neural arch (Head et al. 2006, Head et al. 2009). *Candoia bibroni* is the only boine known from the Loyalty Islands (Bauer and Sadlier 2000, Noonan and Sites 2010).

FIGURE 11. Material identified as belonging to *Candoia bibroni*: (*A–D*) trunk vertebra of *Candoia bibroni* (18C 45–55 cm). (*A*) Dorsal; (*B*) ventral; (*C*) anterior; (*D*) posterior views. Scale bar equals 5 mm.

DISCUSSION

The boid *Candoia bibroni* is the only extant reptile to have previously been reported from Tiga, but without any vouchered specimens (Oliva and Talon 1996). The analysis of the present material, obtained from archaeological excavations, thus adds substantially to the known reptile fauna of Tiga. Of a total of 19 species previously recorded from the Loyalty Islands (Sadlier and Bauer 1997, Bauer and Sadlier 2000), we are able to infer the presence of six species with some surety, including two skinks and three geckos, and the boa. Another two species, *Bavayia* aff. *sauvagii* and *Emoia cyanura* are probably represented. On the basis of size, postcranial material is potentially consistent with up to six additional species (Figure 12). All of the confirmed species are present elsewhere in the Loyalty Islands and most are common where they occur. The most interesting records are *Gehyra georgpotthasti* and *Candoia bibroni*. The first of these species, very recently described based in part on Loyalty material previously assigned to *Gehyra vorax*, is the only gekkonid gecko endemic to the greater New Caledonian region (it is also present in Vanuatu). It has previously been recorded from Maré and Dudun, to the southeast of Tiga (Flecks et al. 2012), with only one record, without precise locality, from Lifou to the north. The confirmation of the presence of this species on Tiga helps to clarify its limited range in the Loyalties. Although the similarly sized *G. vorax* was traditionally consumed by humans in Fiji (Gibbons and Clunie 1984), there is no evidence of this practice in the Loyalties, so if the species is no longer present on Tiga today, it is likely that habitat alteration would be the underlying cause. *Candoia bibroni*, on the other hand, is known to have been regularly eaten by people in the Loyalties, and this practice has continued on a limited scale to the present, at least on Lifou (Delauw 1990). The species is now uncommon, at least in portions of its range in the Loyalties (R. Shine, pers. comm., Jan. 2014), although it is not known if this is associated with human hunting pressure, habitat modification, or introduced mammals, although all could play a role. The vertebrae recovered on Tiga confirm at least the historical presence of the snake on the island.

Both *Gehyra* and *Candoia* were found in deeper as well as more superficial layers of excavation (Appendix 2). Although the skeletal elements themselves have not been dated, it may be assumed that the most recent material corresponds to the historical period, whereas the older material extends well into the pre-European period of Tiga's occupation. Although most herpetologists have assumed that *Candoia bibroni* is native to the Loyalties, one published source has proposed that the snakes were introduced as food items by Polynesians in the sixteenth century (Logan and Cole 1997) and other theories propose its human-mediated introduction as a rat predator (Oliva and Talon 1996). Although Loyalties material was not included in a molecular study of variation in Pacific boas (Austin 2000), it does appear that there are deep divergences among populations of *C. bibroni* in Fiji and Samoa, and there is no reason to suspect that these snakes are not native to the region.

Previously *Bavayia sauvagii* was regarded as a widespread diplodactylid that occurred over much of the Grande Terre and its satellite islands as well as on Maré. Its absence in the other Loyalties was tentatively ascribed to a lack of suitable rocky substrates for diurnal refugia (Sadlier and Bauer 1997). However, recent investigations (Bauer and Jackman 2006) suggest that the *sauvagii*-like species on Maré are probably endemic to the Loyalties. Its occurrence on Tiga, suggested but not confirmed by material from archaeological sites, is of both biogeographic and conservation interest.

Interestingly, at least one species of gekkonid gecko, *Nactus pelagicus*, is present in both older and younger screenings (Appendix 2). Grant-Mackie et al. (2003) hypothesized, based on a small sample of reptile remains from owl pellets at Mé Auré on the west coast of the New Caledonian mainland, that gekkonid geckos may have arrived on the Grande Terre sometime during the period of human colonization, perhaps even after the arrival of Europeans. This hypothesis has received further support from much more extensive owl pellet sampling from Pindaï, where >5,000 lizard bones spanning the period before and
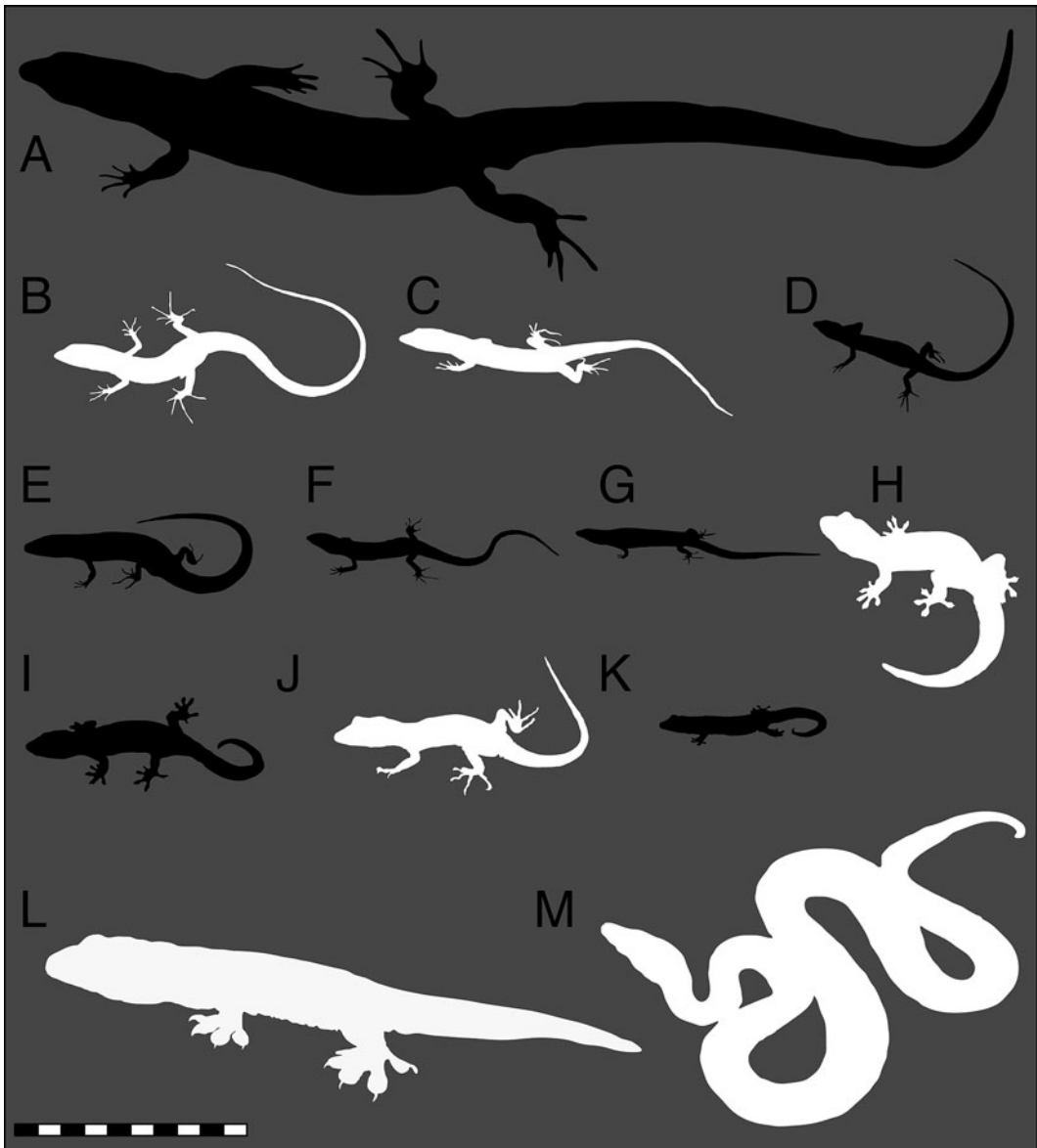
FIGURE 12. (*A–M*) Silhouettes of the candidate squamate species recovered from Tiga archaeological sites. All silhouettes are drawn at the same scale based on the maximum values for each species. Species shown in white are those confirmed to be present in Tiga archaeological sites; others may be present based on material identifiable only to higher order groups. (*A*) *Phoboscincus garnieri*, (*B*) *Lioscincus nigrofasciolatus*, (*C*) *Emoia loyaltiensis*, (*D*) *Emoia cyanura*, (*E*) *Caledoniscincus atropunctatus*, (*F*) *Caledoniscincus haplorhinus*, (*G*) *Caledoniscincus austrocaledonicus*, (*H*) *Bavayia crassicollis*, (*I*) *B.* aff. *sauvagii*, (*J*) *Nactus pelagicus*, (*K*) *Lepidodactylus lugubris*, (*L*) *Gehyra georgpotthasti*, (*M*) *Candoia bibroni*. Scale bar equals 100 mm.

after the arrival of the first Pacific Islanders and predating European settlement have revealed no gekkonid remains, only diplodactylids and skinks (Kennedy 2011). The data from Tiga demonstrate that at least in the Loyalties, *Nactus* does predate the European period. This parthenogenetic species has a broad distribution in the Pacific, much of which is certainly not human-mediated, so it is probable that this gecko is native to the Loyalties. Differences in the means of bone accumulation, habitat, and lizard community structure could all contribute to differences seen on the Grande Terre and in the Loyalties. However, the Loyalties, unlike the mainland, shares a number of lineages with other island groups of the western Pacific (Bauer 1989, Sadlier and Bauer 1997, Bauer and Sadlier 2000) and might be expected to have historically harbored species absent on the mainland.

Tiga presents an interesting case in that fresh samples of reptiles are unknown and archaeologically derived material provides the only evidence for the recent occurrence of lizards and snakes on the island. On the Grande Terre, reliable modern records provide a baseline against which subfossil remains can be compared and reveal that local and even island-wide extinctions have taken place since human occupation (Kennedy 2011). On Tiga, we start with the osteological material, which provides a hypothesis about what may be present today. Some taxa (e.g., *Lioscincus nigrofasciolatus*, *Caledoniscincus* spp.) are widespread throughout New Caledonia or on the Loyalties alone (*Emoia cyanura*, *E. loyaltiensis*) and have generalized habitat requirements allowing them to thrive in even disturbed habitats (Bauer and Sadlier 2000) and may certainly be expected to be present and locally abundant today. However, the requirements of *Gehyra georgpotthasti* for a more specialized forest habitat (Flecks et al. 2012) and the human harvesting of *Candoia bibroni* (Delauw 1990) leave the current status of these taxa on Tiga uncertain and call for a thorough herpetofaunal survey of the island.

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Appendix 1

Comparative Specimens Examined

Abbreviations for the type of preparation: EtOH = ethanol-preserved specimens, C&S = cleared and stained preparation, HRXCT = high-resolution X-ray computed tomography, Sk = dry skeleton, XR = X-rays.

DIPLODACTYLIDAE: *Bavayia crassicollis:* C&S, AMS R78285. *Bavayia cyclura* (Günther): C&S, AMS R78092, MCZ A-27309, XR, USNM 146331, USNM 515879. *Bavayia montana* Roux, 1913: C&S, AMS R77666, Sk, AMS R77665. *Bavayia robusta:* Sk, AMS R93710, MCZ A-27346–27348, 27356–27357. *Bavayia sauvagii:* C&S, AMS R-78350–78351, CAS 16590–16696, Sk, AMS R77661, CAS 80823. *Correlophus ciliatus* Guichenot, 1866: Sk, NHMUK 85.11.16.7, JFBM 15825. *Eurydactylodes vieillardi* (Bavay, 1869): HRXCT, CAS 231986. *Nebulifera robusta* (Boulenger, 1885): Sk, CAS 75675. *Oedura marmorata:* Sk, CAS 75405. *Rhacodactylus auriculatus:* C&S, CAS 165895–165902; HRXCT, CAS 205486; Sk, NHMUK 86.3.11.10, CAS 165891, CAS 165892. *Rhacodactylus trachyrhynchus:* Sk, NHMUK 86.3.11.4.

GEKKONIDAE: *Gehyra australis* (Gray, 1845): XR, USNM 128538, USNM 203930. *Gehyra baliola* (Duméril, 1851): XR, USNM 167701. *Gehyra borroloola* King, 1983: XR, USNM 128537. *Gehyra brevipalmata* (Peters, 1874): XR, USNM 546190, USNM 546197, USNM 546203. *Gehyra georgpotthasti*: EtOH, AMS R3558, AMS R13256, AMS B3834, AMS R1158, AMS R6668, AMS R7244, AMS R7257. *Gehyra membranacruralis* King & Horner, 1989: XR, USNM 518565. *Gehyra mutilata* (Wiegmann, 1835): Sk, JFBM 15819, XR, USNM 584526, USNM 584527. *Gehyra oceanica* (Lesson, 1830): Sk, AMNH R-27048, CAS 50045 [434], XR, USNM 322415, USNM 322419. *Gehyra papuana* Meyer, 1874: XR, USNM 159828. *Gehyra variegata* (Duméril & Bibron, 1836): XR, USNM 570629. *Gehyra vorax:* Sk, AMS R179016. *Hemidactylus frenatus:* Sk, AMNH R-71551, AMNH R-71589, AMS R123990, JFBM 15817, CAS 21784. *Hemiphyllodactylus typus:* C&S, CAS 127969, Sk, AMS R125810. *Lepidodactylus christiani* Taylor, 1917: XR, USNM 305956, USNM 305957, USNM 305959. *Lepidodactylus lugubris:* Sk, AMS R26611, AMS R179020, MCZ A-27306–27308, XR, USNM 494236, USNM 494238, USNM 287039, USNM 287040, USNM 287045. *Nactus eboracensis* (Macleay, 1877): Sk, MVZ 77610, MVZ 77615, XR, USNM 561877, USNM 561882. *Nactus pelagicus:* Sk, AMS R179023, AMS (no number), XR, USNM 343831, USNM 343833, USNM 343836.

SCINCIDAE: *Caledoniscincus austrocaledonicus:* Sk, uncatalogued, MCZ A-27301–27305, XR, USNM 267845, USNM 515855. *Caledoniscincus festivus* Sadlier, 1987: Sk, AMS R116036. *Celatiscincus euryotis* (Werner, 1910): Sk, AMS R153990. *Cryptoblepharus egeriae* (Boulenger, 1888): Sk, AMS R83160. *Cryptoblepharus plagiocephalus* (Cocteau, 1836): Sk, AMS R142565, XR USNM 54063. *Cryptoblepharus virgatus* (Garman, 1901): Sk, AMS R85791. *Emoia adspersa* (Steindachner, 1870): Sk, AMS R2084, XR, USNM 322722, USNM 322723. *Emoia atrocostata* (Lesson, 1830): Sk, AMS R40833, MCZ R15080, XR USNM 195779. *Emoia caeruleocauda* (De Vis, 1892): Sk, AMS R25720, XR, USNM 122797, USNM 122857. *Emoia concolor* (Duméril, 1851): Sk, MCZR 16931, XR, USNM 333338, USNM 333340. *Emoia cyanogaster* (Lesson, 1830): Sk, MCZR15135, XR, USNM 533324, USNM 533332. *Emoia cyanura:* Sk, MCZ R-14582, R-72287, XR, USNM 28203, USNM 28204. *Emoia kordoana* (Meyer, 1874): Sk, AMS R64319, XR, USNM 499639. *Emoia longicauda* (Macleay): Sk, AMS R23905, USNM 336680, USNM 336681. *Emoia loyaltiensis* (Roux, 1913): HRXCT, AMNH R-60463. *Emoia maculata* Brown, 1954: Sk, AMS R80134, XR, USNM 121807. *Emoia nigra* (Jacquinot & Guichenot, 1853): Sk, AMS R138857, MCZR 72514, XR, USNM 215235. *Emoia pallidiceps* (De Vis, 1890): Sk, AMS R14834, AMS R127604, XR, USNM 166268, USNM 166276. *Emoia physicae* (Duméril & Bibron, 1839): Sk, AMS R60458, XR, USNM 567019. *Graciliscincus shonae* Sadlier, 1987: Sk, AMS R146534. *Kanakysaurus viviparus* Sadlier, Bauer, Smith & Whitaker, 2004: Sk, AMS R162921. *Lacertoides pardalis* Sadlier, Shea & Bauer, 1997: Sk, AMS R152644. *Lioscincus maruia* Sadlier, Whitaker & Bauer, 1998: Sk, AMS R149958. *Lioscincus nigrofasciolatus:* Sk, AMS R78348, AMS R93712, MCZ A-27345, MCZ A-27310. *Lioscincus novocaledoniae* (Parker, 1926): Sk, AMS R78349. *Lioscincus steindachneri* Bocage, 1873: Sk, AMS R153495. *Lioscincus tillieri* Ineich & Sadlier, 1991: Sk, AMS R148033. *Lioscincus vivae* Sadlier, Bauer, Whitaker & Smith, 2004: Sk, AMS R167230. *Marmorosphax tricolor:* Sk, AMS R93713, MCZ A-27319–27321. *Nannoscincus garrulus* Sadlier, Bauer & Smith, 2006: Sk, AMS R151502, AMS R151521. *Nannoscincus gracilis* (Bavay, 1869): Sk, AMS R77745, AMS R135195, XR, USNM 268764. *Nannoscincus greeri* Sadlier, 1987: Sk, AMS R149495, AMS R165974. *Nannoscincus manautei* Sadlier, Bauer, Whitaker & Smith, 2004: Sk, AMS R167225. *Nannoscincus mariei* (Bavay, 1869): Sk, AMS R146485, XR, USNM 515886, USNM 515887. *Nannoscincus rankini* Sadlier, 1987: Sk, AMS R149387. *Nannoscincus slevini* (Loveridge, 1941): Sk, AMS R135149. *Sigaloseps deplanchei* (Bavay, 1869): Sk, AMS R125837, XR, USNM 515889, USNM 525888. *Simiscincus aurantiacus* Sadlier & Bauer, 1997: Sk, AMS R164368. *Tropidoscincus variabilis* (Bavay, 1869): Sk, AMS R164374, uncatalogued specimen, XR, USNM 149680, USNM 268762.

BOIDAE: *Candoia bibroni:* Sk, MCZ R14516, MCZ R15018.

Appendix 2

Material by Excavation Site and Depth of Recovery

SVL* indicates the estimated size based on comparable elements of articulated specimens.

LTD-14A: Rock-shelter located on the west coast of Tiga, about 50 m inland. Human occupation starts at 100 cm below surface, dated to the middle of the

first millennium A.D. Most of the fill is dated to the second millennium A.D. 45–50 cm: *Lioscincus nigrofasciolatum*, dentary (1L, >9 mm, SVL* = 52.0 mm). *Gehyra georgpotthasti*, maxilla (1L, 16.5 mm, SVL* = 123.8 mm); 50–55 cm: *Nactus pelagicus*, frontal (1, >7 mm, SVL* = 67.3 mm). *Gehyra georgpotthasti*, dentary (1L, 16.5 mm, SVL* = 113.4 mm); 55–60 cm: *Nactus pelagicus*, frontal (1, 7.8 mm, SVL* = 75.1 mm); 60–65 cm: *Bavayia crassicollis*, frontal (1, >7 mm, SVL* = 60.8 mm), innominate bone (1L). Gekkota, femur (2L, >8.5 mm. SVL* = 57.2 mm); 65–70 cm: *Emoia loyaltiensis*, maxilla (1L, 1R, 8.6 mm, SVL* = 66.5 mm). Gekkota, humerus (1L, 1R, 7 mm, SVL* = 54.4), femur (1R, 7 mm, SVL* = 47.1 mm). *Gehyra georgpotthasti*, dentary (1L, 20 mm, SVL* = 137.5 mm); 70–75 cm: *Lioscincus nigrofasciolatum* frontal (1, 7.7 mm, SVL* = 108.86 mm), parietal (1, 7.5 mm length ×5.4 wide, SVL* = 98.13), innominate bones (1L, 1R). Scincidae, *incertae sedis*, humerus (1R, 10.5 mm, SVL* = 76.8 mm), femur (1R, 13 mm, SVL* = 76.6 mm). *Bavayia* sp., dentary (1L, >9 mm, SVL* = 67.4 mm). *Gehyra georgpotthasti*, dentary (1R, anterior portion only); 75–80 cm: Scincidae, *incertae sedis*, humerus (1L, 1R, 6.5 mm, SVL* = 55.8 mm; 1L, 11.1 mm, SVL* = 78.6 mm); 85–90 cm: Scincidae, *incertae sedis*, humerus (1L, 7.1 mm, SVL* = 57.2 mm), femur (1R, 6 mm, SVL* = 44.9 mm; 1L, 7.6 mm, SVL* = 49.2 mm). *Nactus pelagicus*, frontals (2, 7 mm, SVL* = 67.37 mm). Scincidae, *incertae sedis*, presacral vertebrae (2, ~4 mm).

LTD-18A: Rock-shelter located on the northwest Coast of Tiga. Human occupation in pit A starts at 65 cm below surface, dated to 2,100 yr B.P. Most of the fill is dated to the first millennium A.D. 50–55 cm: *Bavayia* sp. dentary (1R, 9.2 mm, SVL* = 69.33 mm); 65–70 cm: *Bavayia* sp., dentary (1L, >8.5 mm, SVL* = 64.06 mm).

LTD-02A: Rock-shelter located on the northwest coast of Tiga. Human occupation starts at over 190 cm below surface, dated to the second half of the first millennium A.D. The long-term occupation fill, concentrated in the upper 70 cm of the stratigraphy, is dated to the last 600 yr. 50–60 cm: Scincidae, *incertae sedis*, femur (1L, 13 mm, SVL* = 76.6 mm); 60–70 cm: *Candoia bibroni*, vertebra (3, ~5 mm). Scincidae, *incertae sedis*, femur (1R, 8 mm, SVL* = 50.8 mm; 1R, 12.5 mm, SVL* = 76.1 mm) and innominate bone (1), and caudal vertebrae (3); 100–110 cm: *Nactus pelagicus*, frontal (1, >8 mm; SVL* = 80.3 mm).

LTD-18C: Rock-shelter located on the northwest coast of Tiga. Human occupation in pit C starts at 65 cm below surface, dated to 2530 yr BP. Most of the fill is dated to the first millennium A.D. 0–15 cm: *Candoia bibroni*, trunk vertebra (2, ~5mm). Scincidae, *incertae sedis*, femur (1L, 11 mm, SVL* = 68.0 mm). Gekkota, femur (1L, 8 mm, SVL* = 50.5 mm); 15–25 cm: Gekkota, humerus (1R, 7 mm, SVL* = 48.2), femur (1R, 9 mm, SVL* = 60.7 mm); 35–45 cm: *Candoia bibroni*, trunk vertebra (2, ~5 mm). Gekkota, femur (1R, 8.5 mm, SVL* = 56.7). Two undetermined appendicular bones (incomplete). Scincidae, *incertae sedis*, presacral vertebra (3); 45–55 cm: *Candoia bibroni*, trunk vertebrae (8), ribs (3). Undetermined femur (1, >8.5 mm). *Emoia loyaltiensis*, dentary (1L, >9 mm, SVL* = 63.7), Gekkota, humerus (1R, 6.5 mm, SVL* = 58.4), femur (1L, 9 mm; SVL* = 60.7 mm); 55–65 cm: *Candoia bibroni*, trunk vertebrae (2, ~5mm). *Emoia loyaltiensis*, maxilla (1L, >5 mm), compound bone (1L, 8 mm, SVL* = 68.5 mm). *Lioscincus nigrofasciolatum*, quadrate (1L). *Bavayia crassicollis*, maxilla (1L, <8.5 mm, SVL* = 68.1 mm), dentary (1L, 8.9 mm; SVL* = 66.7 mm), compound bone (1L, 7 mm; 1R, 9 mm, SVL* = 74.3 mm). *Bavayia* sp., braincase (1, 4.6 mm, SVL* = 50.3 mm). *Gehyra georgpotthasti*, innominate bone (1). Two indeterminate appendicular bones; 65–75 cm: Scincidae, *incertae sedis*, dentary (1L, >9 mm, SVL* = 38.0 mm).