Amphibians and Reptiles of Vanuatu (Melanesia)

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Ivan Ineich
Muséum National d'Histoire Naturelle

The Natural History of Santo

edited by
Philippe Bouchet, Hervé Le Guyader, Olivier Pascal

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AMPHIBIANS AND REPTILES

Ivan Ineich

• • • A brief history of herpetological collections from Vanuatu

The oldest known vertebrate collection from Vanuatu took place during the explorations of Captain James Cook. He discovered Tanna in 1774. That volcanic island was covered with thick forest and the naturalist Forster discovered a pigeon there, *Gallicolumba ferruginea*. The only specimen known in the world is the one he killed on 17 August 1774 and that his son illustrated. Subsequent searches have not found the species again.

Herpetological collections from Vanuatu are located in several European museums among which those in London (BMNH, Natural History Museum, UK), Paris (MNHN, Muséum national d'Histoire naturelle, France) and Basel (NMBA, Naturhistorisches Museum Basel, Switzerland) are the most important. Other European museums holding such collections included Geneva (MHNG, Muséum d'Histoire Naturelle de Genève, Switzerland), Bonn (ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Germany), Hamburg (NHMH, Naturhistorisches Museum von Hamburg, Germany) and Frankfurt-am-main (SMF, Senckenberg Museum von Frankfurt-am-Main, Germany).

••• The Natural History Museum, London (BMNH)

The Natural History Museum (London) possesses several specimens collected around 1865 by J.L. Brenchley (six lizards) who visited several Vanuatu islands (Anatom, Tanna, Erromango, Efate and Vanua Lava in the Banks), but not Santo. This historically important collection contains several geckos forming the type series of *Gymnodactylus multicarinatus* (recently revalidated as *Nactus multicarinatus*) described by Günther in 1872. During the 1940's

Edgar Aubert de la Rüe was born in Geneva on 7 October 1901. In 1924 he obtained his geological-engineering diploma from the Institute of Applied Geology of Nancy in France. He later made 15 field trips as a geological-engineer for the French Ministry of Colonies and later French Overseas Ministry, visiting Africa, North and South America, the Indian and Pacific Oceans as well as Antarctica. He was named correspondant of the Muséum national d'Histoire naturelle (Paris) in 1934 and associate researcher on 20 December 1951. By 1963, he had authored about 263 scientific publications.

Philippe François was born in Saumur (France) on 22 November 1852. He studied in different cities according to the military postings of his father. He obtained a Licence in Natural Sciences in 1882 at Poitiers. He achieved a Ph.D. in science in 1885, with his thesis dealing with the nervous system of hirudine flat worms. The same year he was named "Maître de conférences de zoologie" at the University of Rennes. In 1888, he made a trip to the Pacific Islands to study the development of coral reefs on the Great Barrier Reefs of Australia. He was also put in charge of representing France at the Universal Exposition of Melbourne in Australia. He left on 1st August 1888 and returned to Paris only on 1st May 1891. After arriving in Noumea in 1888 he spent a total of eleven months (five different trips) in Vanuatu. François left New Caledonia on 2 August 1894 and visited Vanuatu, including Banks and the Santa Cruz group in the Solomon Islands before returnning through Port Vila on 3 January 1895. He died from a liver infection on 13 March 1908 at Paris.

J.R. Baker (1947) made important collections under the Percy Sladen Expedition, including 238 lizards and 21 snakes. He studied the reproduction of some common skinks (*E. cyanura sensu lato* and *E. caeruleocauda*) at Hog Harbour, Santo. That work was based on data obtained during the Oxford University Exploration Club (1933-34), a trip financed with funds from the Royal Society, the Percy Sladen Memorial Found, the University of Oxford and the New College of Oxford. Miss Evelyn L. Cheesman made collections around 1929 and from 1954 to 1955, totalizing 46 lizards and one snake. Later, in 1971, the Royal Society/Percy Sladen Expedition allowed the Earl of Cranbrook (formerly Lord Medway) and A.G. Marshall to make additional herpetological collections comprising 15 frogs, 345 lizards and four snakes. That expedition also collected an introduced typhlopid snake (not previously reported from the archipelago), and a new skink (*Emoia*). Islands visited were Anatom, Tanna, Erromango, Efate, Malakula and two satellite islets (? Ouri and Suaro), Santo and two satellite islets (Malo and Aore). All herpetological specimens were deposited at BMNH. Several smaller herpetological collections from Vanuatu have been deposited at BMNH among which that of J. MacGillivray (*HMS Herald*) from Anatom, Mr Cuming (around 1860, two lizards), W. Wykeham Perry Esq. (around 1875-1876, five lizards), Dr Corrie (around 1878, one lizard and one snake), "Challenger" collections (around 1882, 14 lizards), E.L. Layard, consul of Noumea (around 1886, three lizards and six snakes), D. McNabb (or MacNab), surgeon of the Royal Navy (around 1892, one lizard and three snakes), R.A. Lever from the Department of Agriculture of Fiji (two lizards). Finally Noel L.H. Krauss made a gift of reptiles from Vanuatu to several world museums (Hawaii, Paris, six lizards given in 1987 to the Univerity of Hamburg, Germany) including the BMNH.

••• Muséum national d'Histoire naturelle, Paris (MNHN)

Even though the New Hebrides was a British-French condominium, herpetological collections from that area are few in the Paris MNHN collections. Angel (1935) first published about a collection made in Vanuatu by Aubert de la Rüe (62 lizards and four snakes) (see above). Later, during his visit to Paris, Lord Medway (1974) examined that collection but also the François collection from Vanuatu. The later collection comprised one crocodile, 35 lizards and 13 snakes (some lizards and snakes were destroyed) but also included specimens from the Loyalty Islands (see above). The François collection was registered in 1894 and later in 1973-1974 (14 lizards and four snakes). Several smaller herpetological collections from Vanuatu were also deposited at MNHN among which are those of Dr Cailliot (six snakes), Deshouillères (one snake) and Dr Joly (four lizards).

••• Other European collections

Dr Félix Speiser spent several years in Vanuatu from 1910 to 1912 and collected many specimens that he send to the Switzerland Natural History Museum of Basel (NMBA). That collection was later studied by Roux in 1913 and comprised two new species of skink, *Emoia nigromarginata* and *Emoia speiseri*, the second being later considered a synonym of the first during a revision of the genus by Brown in 1991. The Speiser collection was re-examined by Lord Medway in 1975. The Natural History Museum of Geneva in Switzerland (MHNG) possesses two major collections from Vanuatu, one made by H. Larsen during the summer of 1958 on Ambrym and Vanua Lava in the Banks (28 lizards and eight snakes) and another made in June 1976 by A. de Chambrier. The Bonn Natural History Museum in Germany (ZFMK) possesses one collection made in Vanuatu in February 1975 by H. Meier. The Senckenberg Natural History Museum of Frankfurt-am-Main in Germany (SMF) has the famous Bregulla unregistered collection, which is unfortunately in a bad state and is of only limited interest.

••• Non European Vanuatu collections

Other important herpetological collections made in Vanuatu are located in the USA. The most important of these are deposited at the American Museum of Natural History (AMNH, New York), United States National Museum, Smithsonian Institution (USNM, Washington), California Academy of Sciences (CAS, San Francisco) and Bernice P. Bishop Museum at Hawaii (BPBM). Minor collections were also deposited at the Field Museum of Natural History (FMNH, Chicago), Museum of Comparative Zoology (MCZ, Harvard University), and University of Michigan (UMMZ, Ann Arbor).

The Whitney South Sea Expedition yielded a huge set of herpetological specimens giving rise to several important scientific publications. That collection was deposited at the American Museum of Natural History and later examined by Lord Medway. Another important collection was recently made on numerous Vanuatuan Islands by George R. Zug and colleagues and deposited at USNM (Washington). Collections deposited at the California Academy of Sciences were made in Vanuatu by Robert N. Fisher (November-December 1988) on Efate and some of its satellite islets (Emao). The Bernice P. Bishop Museum at Hawaii possesses some specimens given by Noel L.H. Krauss and collected from December 1986 to January 1987. Collections deposited at the Field Museum of Natural History of Chicago were made during the years 1952 to 1958. The most important collections were obtained through A.G. Marshall and Elizabeth Laird (August 1952) and B. Malkin (July 1958). The most important collections from Vanuatu held by the University of Michigan at Ann Arbor were made by R. Kuntz in August 1944 on Santo, and by Craig Moritz in 1986 on Efate and Tanna.

Other important herpetological collections from Vanuatu are located at Sydney in Australia (AMS) and at the Auckland Museum and Institute in New Zealand (AMI). The Australian Museum of Natural History (AMS) has several specimens from Vanuatu from collections made by Prof W.A. Haswell (1903), R.J. Etheridge (1910), W.W. Frogatt (1921), A.J. Marshall (1934), R.H. Pickering (1982), L. Gibson and his collaborators (1990), P. German (1992), and McAfee, E. Jacquier, Capt. Braithwaite among others. One other collection was made by Ross Sadlier in August 1983. There is also one more recent collection made in May 1990. The most important Vanuatu collections of that museum were made by Harold G. Cogger from 1983 to 1994. The Auckland Museum and Institute in New Zealand possesses some specimens of reptiles collected on Santo (e.g. AMI 1675).

Including our most recent collections from the SANTO 2006 and the Torres 2007 expeditions, there are certainly about 3000 specimens of reptiles and amphibians from Vanuatu preserved in world museums. Among those MNHN should now possess one of the most important collections.

Biodiversity of the herpetofauna of Vanuatu

Our actual knowledge of the Vanuatu herpetofauna is based on scattered published papers dealing with some of the collections cited above or parts of them, either totally devoted to Vanuatu or partial reports in more general revisions. *Naika*, the Journal of the Vanuatu Natural Science Society (Efate, Port Vila), was published from 1981 to 1993 [numbers 1-42]. David Dickerson was President of that society in 1982 and Richard Pickering chief-editor, both being authors of herpetological notes published in that journal. New Caledonia, Solomon Islands, Fiji and Hawaii have one or more field guides or monographs devoted to their herpetofauna, but there is unfortunately no such book for Vanuatu.

Several Pacific island reptiles are still undescribed and numerous are known from a few specimens or even considered as extinct or severely endangered. Thus any attempt to make an analysis of that biodiversity is still fragmentary and remains only partial. The Pacific Ocean occupies about one third of the Earth's surface (larger that all continents together). Together there are more than 12 000 islands in the area totaling less than 2% of the earth's landmass. In 1996, Allison counted 672 amphibians and terrestrial or dulcaquicolous reptile species on Pacific islands. The six species of marine turtles are present in the whole area and thus do not carry much biogeographical information. There are also about 30 seasnake species in the area but knowledge on their distribution and even taxonomy is still fragmentary. New Guinea alone occupies more than 80% of the Pacific landmass and possesses at least 472 species totalizing 2/3 of the tropical Pacific herpetofauna. The New Guinean herpetofauna derives from the Oriental region but also to a lesser extent from Australia.

Gekkota (pygopods, diplodactylids, and gekkonids) and scincid lizards are the most visible elements of the herpetofauna on Pacific islands, and to a lesser extent hydrophiine elapids (sea kraits, seasnakes and Melanesian terrestrial elapids) and boids, marginally typhlopid worm snakes, among snakes. The Melanesian herpetofauna serves as the source for the colonisation of islands located north and east by natural trans-oceanic dispersal that began at least during the mid-Miocene. Species diversity clearly decreases eastwards from New Guinea to Easter Island and that decrease is even stronger east of Fiji. Curiously, the Pacific islands have only a low influence on the composition of the New Caledonia herpetofauna, which is mostly related to an Australian fauna of Gondwana origin (e.g. diplodactylid geckos). Note however that the Loyalty Islands, located just beneath New Caledonia, possess a clearly distinct herpetofauna more closely related to that of the eastern tropical Pacific Islands (e.g. Vanuatu and Fiji) rather than to New Caledonia. Gondwana fragmentation began

150 million years ago. Fijian endemic iguanids of the genus *Brachylophus*, Pacific boas of the genus *Candoia*, and numerous Pacific plants show South American affinities that also agree with the dispersion hypothesis that they originated in the neotropics. Distribution patterns of the boid genus *Candoia* are however similar to that of most Melanesian skinks and geckos; this could however be an artifact related to food requirements of the snake needing large lizards for its diet prior to the arrival of the rat. Actual herpetofaunal distribution patterns in the tropical Pacific Ocean are thus a mixture of vicariance and dispersal events, natural dispersion but also accidental and voluntary human introductions.

The description of the 672 Pacific species listed by Allison in 1996 began with the European colonisation of the area. Before 1800, only nine species from the area were described, mostly species also living in Southeast Asia. During the 19th century, 276 additional species were described, and again 371 more during the 20th century. Numerous species with wide distributions in the area are classically considered as recent arrivals, often through man mediated travel. Most herpetologists agree with such an explanation, generally based on weak biological, ecological, biogeographical and even molecular data. In 1985 Gibbons showed that between islands, dispersal could have been largely facilitated during maximal glaciation periods giving rise to important additional exposed land areas. His map shows that 18 000 years ago exposed areas and island numbers were about double the present situation. Allison also reported 49 amphibian and reptile species from the islands located east of the Solomon Islands, including two endemic frog species of the genus *Platymantis* from Fiji. The most diversified tropical Pacific island genera are lizards of the genera *Emoia* (Scincidae) and *Lepidodactylus* (Gekkonidae).

Concerning Vanuatu, Medway and Marshall noted in 1975 that the relatively high number of species that they reported from Efate could be related to a higher collection intensity and more frequent external contacts related to the geopolitical position of that island (hosting the capital Port Vila); the only known specimen of the gecko *Gehyra mutilata* from Vanuatu could have arrived there by boat. The herpetofauna of Efate is as diverse as that of Santo and that island does not show the north-south rarefaction observed for birds and mammals in the archipelago. They also noted that two geckos, *Gehyra oceanica* and *Lepidodactylus lugubris*, were never collected in non-anthropic habitats and that on Santo, the number and diversity of lizards decreases considerably with elevation; on Nokovula at 1 100 m a.s.l, the skink *Emoia caeruleocauda* is the only registred species. Local people however mention a green lizard (probably the green forest skink *Emoia sanfordi*?) and that no geckos (locally called "big eye") occur at such elevations. This is not accurate since I often observed *Nactus multicarinatus* on Santo at around 900 m elevation.

Some reptile species were reported from Vanuatu as cryptozoological animals. They have not yet been collected and their existence is not confirmed. However these animals are locally reported in folklore and tales about them often exist; local observations and reports could be based on real animals and observations, but sometimes also on the wrong interpretation of an observation. In New Caledonia, a beach stranded banded lizard with short legs was interpreted as a cross between a sea krait (that lizard was found in sea water on the beach and was banded like the snake) and a lizard... It was in fact a nearly dead juvenile of Bocourt's terrific skink (*Phoboscincus bocourti*) that had probably fallen from the claws of a raptor. In 1994, Whitaker and Whitaker mentioned a flying gecko and an arboreal skink with a blue tail reported by some local people from the Matantas area on Santo. Such reports have of course to be considered as serious and attention has to be given to them. It has been noted that on Malakula, in the Uripiv language, there are four different words for lizards: "*mokoblab*" for *Gekko vittatus*, "*mob*" for other geckos, particularly *Gehyra oceanica*, "*negel*" for the green skink (*Emoia sanfordi*) and "*wejur*" for all other skinks. The biodiversity of the herpetofauna of Vanuatu was long considered as impoverished compared to islands north of it (Solomon Islands), south of it (New Caledonia) and east of it (Fiji). The most commonly accepted hypothesis to explain this situation are geologic events that I will discuss at the end of this paper. There is no known extinct species of reptile from Vanuatu. However giant skinks like those of the genera *Tachygyia* (Tonga, extinct?) or *Phoboscincus* (New Caledonia) could possibly have been present in Vanuatu or could still exist. Local people in Vanuatu also mentioned particular snakes from Malakula but they could correspond to uncommon color morphs of *Candoia bibroni*.

• • • The Herpetofauna of Vanuatu, with special focus on Santo

••• Seaturtles from Vanuatu

Several species of sea turtles were reported from Vanuatu and all of them can be encountered in Santo waters: *Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata* and *Dermochelys coriacea*. *C. caretta*, a carnivorous species, is very uncommon in Vanuatu.

Nesting sites of *C. mydas* have been reported from Vanuatu, and the species is considered as one of the most common sea turtles in the area. *C. mydas* is herbivorous and feeds on seagrasses and seeweed, thus implying active migration from feeding to reproduction areas (beaches). *C. mydas* sometimes concentrates on collective egg laying sites (rookeries).

E. imbricata is considered to be the second most common sea turtle of Vanuatu but its reproduction has never been attested to there, despite it reproducing in New Caledonia, Solomon and Fiji. *E. imbricata* is easy to observe by divers in the reef areas of Vanuatu where it feeds on invertebrates, sponges and soft coral. Egg laying sites of *E. imbricata* are more dispersed than those of *C. mydas*. The occurrence of *D. coriacea* in Vanuatu was confirmed by a specimen from South West Bay, Malakula, caught in a fisherman's net and eaten; the occurrence of that species remains however very unusual in Vanuatu.

D. coriacea is known from Fiji and Solomon. Its shell can reach 2 m and weigh nearly 650 kg. That marine turtle is present in deep water but occasionally occurs along coasts. It is the typical marine turtle of subtropical and temperate waters and feeds almost entirely on jellyfish. It lays its eggs from November to January in the southern hemisphere, generally on isolated beaches with low human disturbance, which are subjected to strong waves and slope steeply into deep water.

Lepidochelys olivacea could be present in Vanuatuan waters but that has never been confirmed. Note that in some parts of Vanuatu local chiefs prohibit the taking of marine turtles and the consumption of their eggs, as I have noted for fishes in some rivers. Shells of the different marine turtle species of Vanuatu are illustrated on the cover of number eight of the Vanuatuan journal *Naika* issued in 1982.

••• Amphibians from Vanuatu – FROGS

Platymantis Günther is a ceratobatrachid genus present in the Philippines, Palau, New Ireland, New Britain, Solomon Islands, with two endemic species from Fiji. The Solomon Islands also possess several endemic ceratobatrachid genera: *Batrachylodes* Boulenger, *Ceratobatrachus* Boulenger, *Palmatorappia* Ahl, and *Discodeles* Boulenger which is a regional endemic also present in the Bismarck Archipelago and the Admiralty Islands. That endemic stock has clearly an ancient Oriental origin, pre-dating the Australo-Oriental collision. Curiously, none of those species or genera, or even a related one, are present in Vanuatu where native frogs are completely absent. Eggs of *Platymantis* have direct development and such a characteristic was classically used to explain its successful colonisation of the area. In Vanuatu, the absence of native amphibians was often explained by the presence of porous volcanic soils that do not retain surface water and thereby prevent most amphibians from laying their eggs. Such an assumption is wrong, as the recent successful introduction (see below) of an Australian frog to Vanuatu has shown. The introduced species adapt to local conditions and some populations now reach considerable densities. *Platymantis* is suspected by some experts to have been transported by man but if that is true, the reason for its absence from Vanuatu is unclear. A recent geological hypothesis for the former position of Vanuatu is now more in accordance with such an absence. Vanuatu is geologically younger than Fiji and the Solomon Islands and the archipelago was previously located north/northeast of Fiji (see discussion). *Platymantis*, as well at least one *Eleutherodactylus* species, another insular frog genus from the West Indies, is suspected to have internal fertilisation and a single gravid female can give birth to a new insular population; note however that internal fertilisation has never been confirmed for *Platymantis*. Despite such presumed adaptations, native frogs never reached Vanuatu.

AMPHIBIA, HYLIDAE
Litoria aurea

The Green and Golden Bell Frog, *L. aurea*, is a hylid frog from coastal areas of New South Wales in Australia where it is paradoxically considered a threatened species. It has been introduced by humans to New Zealand, New Caledonia and Vanuatu. Its introduction to New Zealand dates from 1867-1868 from where it was introduced to New Caledonia. The first New Caledonian report dates from 1926. It was also introduced to Hawaii around 1920 but without success. The introduction to Vanuatu was most probably made from New Caledonia by planters around 1960, ostensibly to control mosquitoes. In 1975, Medway and Marshall reported that: "*There are no amphibians native to the New Hebrides, and none was taken by Dr Felix Speiser who collected herpetological material in these islands in 1910-1912*". The first published report of that frog for Vanuatu was made in 1967 by Fischthal and Kuntz in their study of amphibian and reptile parasites. In Vanuatu, the frog is presently known from Efate, Malakula and Santo, which are among the largest islands of the archipelago, and therefore the ones that are best able to retain fresh water for long periods. Note however that the species also exists on the small island of Aore off Santo. On Santo it is encountered as high as 1 132 m a.s.l. It was reported from Santo in 1975 by Medway and Marshall and by Challacombe in 1986. I have observed that frog in the most favourable habitats of Santo, particularly in taro plantations.

The colonization and spread of introduced populations was rapid on Efate, thus showing that habitats on Vanuatu are favourable for amphibian life, contrary to what was formerly believed. The absence of native amphibians on Vanuatu therefore remains a biogeographical mystery that is probably best explained by former geological and tectonic events.

Figure 204: Some specimens of *L. aurea* show a light green dominant colouration that is typical of the species. A typical dark band runs from anterior eye border to the nostril. Matantas, Santo.

Figure 205: Typical colouring is variable in *L. aurea* and not all specimens are light green, some being dark green or even nearly completely brownish. Santo.

Figure 206: *L. aurea* is common in flooded taro plantations. Tasmate, Santo.

The Green and Golden Bell Frog shows a high body size and colour variability. Colour is generally greenish on the back with brown or golden variable sized marks, particularly on the limbs. A distinct light band is seen on the sides of the head extending along the body, often with a fine black band below, mostly visible in front of the eyes. Eyes are goldenish with a horizontal dark colored band typical of the genus. The belly is granular and white. Snout end is sometimes turquoise blue. Some frog sightings, erroneously recorded as unknown endemic frogs, almost certainly refer to unusual color morphs of *L. aurea*.

L. aurea lives mostly in or around water, and is an excellent swimmer often seen where aquatic vegetation is well-developed. When disturbed, the frog dives and swims under water to escape. *L. aurea* is often active and singing after rain.

••• Amphibians from Vanuatu – TOADS

AMPHIBIA, BUFONIDAE
Bufo marinus

In 1985 Challacombe reported in the local newspaper *Vanuatu Weekly* the collection of a specimen of the toad *Bufo marinus* [sometimes also called *Rhinella marina*]. It has been widely introduced on tropical Pacific islands and Australia, where its spread has been spectacular. No other observation of that toad has since been reported from Vanuatu. That observation could also correspond to an undescribed (endemic?) species but that is unlikely; more probably it refers to unusual color morphs of *Litoria aurea* that could have been mistakenly confused with a "large brown toad". The same paper also reported a small green arboreal frog. The absence of endemic amphibians in Vanuatu seems to be confirmed by recent collections, however it cannot be excluded that additional field collections will discover such an undetected endemic animal.

••• Reptiles from Vanuatu – CROCODILES

CROCODYLIA, CROCODYLIDAE
Crocodylus porosus

A dwarf fossil crocodile, *Mekosuchus kalpokasi*, has been described from Efate. This recently extinct species was most likely exterminated through human predation since fossil remains are dated about 3 000 BC. The absence of rigorous pre-quaternary and quaternary dating of fossil vertebrates from New Caledonia, Vanuatu and Fiji does not allow us to establish colonisation routes for mekosuchine crocodiles in the south Pacific but they most likely derive from an Australian dwarf crocodile stock.

Crocodylus porosus reaches its eastern distribution limit in Vanuatu. The species is present from southwest India to northern Australia and New Guinea, Micronesia, the Solomon Islands and Vanuatu. The occurrence of occasional specimens on New Caledonia and the Loyalty Islands is confirmed. The species reaches more than 7 m total length and is typical by its nuchal scalation and its bone crest above each eye extending at mid-length on the snout. Commercial exploitation has decimated many populations, except those of New Guinea and Australia that are still exploited under the control of strict management programmes. *C. porosus* is present in marshes and coastal areas but is not exclusively associated with saltwater.

The species was still common at some places on Vanua Lava (Banks, northern Vanuatu) before 1972 and its population was estimated at about 200 specimens at that time. That crocodile was responsible for a significant predation of pigs and cattle. The largest known specimen from Vanuatu reached 5.5 m. The 1972 hurricane was particularly violent and subsequent floodings can certainly explain the elimination of those crocodile populations, either by washing them away or by the destruction of their habitats and nests on the island. Sightings still take place but their frequency is now low. No human attack cases are known from Vanuatu.

Dickenson reported an estimation of the Vanua Lava population at 50 individuals [Ministry of Lands]. Hunting is uncommon but hunters coming from the Solomon Islands around 1973 killed seven individuals and in January 1980 an additional individual of 4.8 m length was killed by an Australian. Dickenson demanded the strict protection of the Vanua Lava populations of Silver River through the creation of a National Park or a Nature Reserve. In 1993, the species was still considered as facing extinction on Vanua Lava. (See: http://www.flmnh.ufl.edu/natsci/herpetology/act-plan/cporo.htm). No specimen of that species from Vanuatu is present in the BMNH collections. That crocodile has been reported from Vanuatu by several authors. The species was reported from the Santa Cruz Islands, Solomon, not far from northern Vanuatu by Roux. A jaw of that species from Vanikolo (Solomon; sometimes called Vanikoro) is present in MNHN collections (François collection). Several reports also exist from Tikopia (Solomon) not far from northern Vanuatu. When Baker visited Santo in 1927, he observed a large crocodile track near the mouth of Yoro River but did not see the animal that was regarded as rare on the island. Dickenson reported some crocodile observations from Santo and Malo around 1980-1981. It seems likely that the species is now extinct on Santo and other Vanuatu islands and now only survives on the Banks archipelago. However occasional observations of vanished specimens can still be possible on Santo but occurrence as established populations is excluded.

••• Reptiles from Vanuatu – LIZARDS (Iguanidae)

SQUAMATA, IGUANIDAE, IGUANINAE
Brachylophus bulabula

Fiji is considered to have originated from a volcanic geological event dating at least 45 million years ago. Iguanas arrived through floating rafts from South America. However it is also thought that Madagascar iguanids originating from an older lineage arrived before the Gondwana landmass breakup (50-70 million years ago). Iguanine ancestors of that endemic Fijian/Tongan lizard group have formerly travelled more than 8 000 km, which is one of the longest known dispersal events by large terrestrial vertebrates via natural rafting. Among central Pacific island iguanas, two genera and five species are recognised among which two species are extinct, *Lapitiguana impensa* from the Fijian late quaternary, and *Brachylophus gibbonsi* from the Tongan late Holocene. Both were probably eaten to extinction after the arrival of humans about 2 800 years ago.

A recent study has shown that existing species comprise *Brachylophus vitiensis* in northeast Fiji (dry forest), a new species in the centre of Fiji, *B. bulabula* (moist forest), and *B. fasciatus* in the southeast of Fiji (Lau group, dry). Vanuatuan populations have been shown to belong to *B. bulabula*. Tongan populations were also introduced from the Fijian Lau group and they belong to *B. fasciatus* (type locality).

Brachylophus bulabula, which was collected for the first time on Vanuatu in 1976, seems to be a recent introduction originating from different Fijian stocks. It is now established in Vanuatu in the southwest of Efate Island. This population is recent and the first wild individuals were caught in the vicinity of Mele Maat. It is believed that they came from a small zoo on top of Klehm Hill and were relased into the nearby forest sometime prior to 1980 when the zoo closed. Gibbons noted that a German reptile collector named Heinrich Bregulla (who deposited an important reptile collection at the Senckenberg Museum of Frankfurt-am-Main; see above) lived on Efate. H.L. Bregulla authored a field guide on the Birds of Vanuatu (ed. Anthony Nelson) in 1991. He left Fiji, where he was based, for Efate in Vanuatu at the end of the 1960s. It has been suggested that H. Bregulla took the Vanuatu founding stock from Fiji to Efate in the late 1960s. Banded iguana specimens were exhibited at a tourist zoo on Efate. After about 10 years of captivity and public display, the animals were released. The first wild *B. bulabula* was collected on Efate only three months after the departure of Bregulla. The species is now well established in the area of Klemms (or Klem's) Hill on Efate (near MeleMart) and it is the only area on the archipelago where it has been reported. The species is abundant around the waterfall and is sometimes carried by children on their shoulders to attract tourists. Their actual distribution extends at least to Pango. Horrocks considered Vanuatu populations to be expanding. This seems to still be the case.

B. bulabula incubation can last as long as 8-9 months, a long time compared to most other lizard species. Such an incubation period explains the colonisation capacity and raft transport potential for its ancestors' arrival from the neotropics. Hatchlings can survive a long time without eating, living on their fat reserves. Males are larger than females and their white bands are more obvious. In the sun, green dominant coloration rapidly darkens and the white marks become more visible. Only males have dorsal light bands whereas females are nearly uniform green. This species can vary its coloration in a spectacular way according to its physiological state (stress, sexual displays…). This faculty has been attributed to the presence of cutaneous receptors rather than nerve connections to the vision system. Adults as well as juveniles possess functional nasal salt glands. Such glands could have permitted that lizard to undergo its trans-oceanic travel allowing its colonization of Fiji.

In captivity, banded iguanas readily eat *Hibiscus* sp. flowers. They feed mostly on plants but their food sources can vary from completely vegetarian to almost totally insectivorous. Females lay 3-4 eggs (40 x 30 mm) that are deposited in a hole dug in the soil. In the laboratory, at 30 °C, incubation time was 17-23 weeks (119-161 days). Hatchling body size is 65 mm whereas adult size is about 160 mm, males being larger than females. Tail length is about three times body size.

Fijian iguanas (three endemic species) are particularly threatened by the recent introduction of the mangoose *Herpestes auropunctatus* on numerous islands, and by other introduced mammals like cats, pigs, and goats. Note that all iguana species in the genus *Brachylophus* are on the CITES appendix I list and live specimens can reach a very high price in both the legal and illegal pet trade. However it is possible to obtain live specimens on Efate for only a few euros! Local authorities need to take care on the attractiveness of that species for smugglers; the Vanuatu price makes them particularly competitive… However, the occurrence of *B. bulabula* in Vanuatu is problematic because of its CITES status. In Vanuatu it is clearly an alien species and as such has no conservation significance or value. In fact, it could be validly argued that it should be eradicated to protect the local biota. However, because of its present situation in Fiji, where it is seriously threatened by a wide variety of anthropogenic factors, the eradication of the population in Vanuatu would be controversial and certainly make it hard to argue against export for science or the pet trade. Live animals from the Mele population are frequently on sale in the market place in Vila, as pets and not for food.

No specimen of that species from Vanuatu is present in BMNH or MNHN collections. Two specimens from Efate are present in CAS collections.

••• Reptiles from Vanuatu – LIZARDS (Gekkonidae)

SQUAMATA, GEKKONIDAE
Gehyra mutilata

The gecko *Gehyra mutilata* is widespread and broadly distributed in the tropical Pacific and Indian oceans, as well as on the Asian mainland. The Indian Ocean populations, which are generally attributed to that species, certainly belong to a

Figure 207: *Gehyra mutilata* from Toga Island, Torres. Specimens from this population are highly contrasted and patterned. They typically have narrow white rings on their tail and a dark band bordered with white behind their eyes. They can easily lose their skin when handled.

different taxa and the name *Gehyra peroni* should be applied to them. In the same way *Gehyra insulensis* should be applied to the Pacific populations, as the morphology and ecology of both populations are different. The status of geographically intermediate Asian populations has to also be carefully clarified since the type locality (Philippines) of *G. mutilata* is located there. The species is widespread on Pacific islands but generally not abundant.

Only one immature specimen was collected in Vanuatu from Efate by J.R. Baker in 1924 or 1925. The species is considered to have been recently introduced to Vanuatu. Fieldwork by Medway and Marshall on Efate did not locate the species. The only occurrence on Efate seems to be linked to a recent introduction of the species on the archipelago. Note that in 1980 McCoy reported the species from Santa Cruz, southern Solomon, not far from northern Vanuatu.

Our recent surveys on Santo did not succeed in locating this gecko. However, during a follow-up expedition to the Torres Islands I collected numerous specimens of *G. mutilata* in the main village of Toga island (November 2007). The species was collected on house walls in sympatry with another gecko, *Lepidodactylus lugubris*, where both were common. *G. mutilata* was certainly recently introduced to that village and was not found anywhere else on the Torres Islands. Moreover another introduced snake, *Ramphotyphlops braminus* was also collected for the first time in this island group and in the same village. Thus I suspect a recent introduction of both species to this village, probably not from Vanuatu because *G. mutilata* had not been collected there previously. The colour pattern (narrow white bands on tail and back), rapid and significant loss of skin when handled and small size of *G. mutilata* link the Toga population to Asiatic ones rather than other Pacific populations or even those in the Indian Ocean. The absence of natural populations of that widespread species on Vanuatu remains a mystery. It has been proposed that *G. mutilata* has an ecology on Pacific islands that is consistent with human-mediated dispersal, in support of the conclusions of its genetic data. I do not agree with such conclusions since the ecology of *G. mutilata* is not more reliant on a human-mediated dispersal than the ecology of *G. oceanica*, which is considered as a potential natural colonist of those islands. *G. mutilata* is not a typical forest species on Pacific islands and most frequently occurs along coastal plains and on atolls such as those in French Polynesia.

SQUAMATA, GEKKONIDAE
Gehyra oceanica

This gecko *Gehyra oceanica* has a nearly continuous distribution from northern Australia (occurrence not confirmed) and New Guinea, Mariannas and Palau to Easter Island. *G. oceanica* is curiously absent from Hawaii. According to Bauer and Henle, that species occurs in nearly the whole of Vanuatu. Roux and McCoy reported the species from Santa Cruz and Reef Islands, southern Solomon. The species was sometimes mixed with *G. vorax*. According to scale characters (mostly the number of toe lamellae and femoral pores), Beckon recognized three morphotypes, respectively located in Micronesia, Solomon (Bougainville) and other parts of Oceania; he suggested that these forms could correspond to three distinct species but no recent study has confirmed that point of view.

G. oceanica has 13-20 lamellae on the fourth toe, 12-50 preanal and femoral pores, a snout-vent length varying from 27-102 mm (52-102 mm for


Photo I. Ineich

Figure 208: *Gehyra oceanica* is a common gecko of Vanuatu. It is most frequently found in and around houses but also in cultivated areas. However the species is present but rare in forest where favourable habitats are uncommon. The species is more common in small rural villages than in towns like Luganville.

Table 22: Egg size and mass for *G. oceanica* from Tonga, Viti Levu (Fiji) and Rotuma (Fiji), compared to our data for Santo and French Polynesia. **MES**: mean egg size (mm). **MEW**: mean egg weight. * n = 88.

Locality	n	MES	Range	MEW
TONGA	7	12.4 x 14.0	12-13 x 12-15	1.25
FIJI (Viti Levu)	4	12.3 x 14	12-13 x 13-15	1.18
FIJI (Rotuma)	10	12.5 x 13.5	11.8-13.1 x 12.6-14	1.26
VANUATU (Santo)	26	12.4 x 13.6	11.4-13.3 x 12.2-15.2	/
FRENCH POLYNESIA (Moorea)	55	11.6 x 13.1	10.8-12.4 x 12.2-14.9	1.06*

Table 23: Hatchling size and mass for *G. oceanica* from Tonga and Rotuma (Fiji), compared with Moorea Island (French Polynesia). **MHS**: mean hatchling size (mm). **MTL**: mean tail length (mm). **MHW**: mean hatchling weight (g). * n = 62. ** n = 55.

Locality	n	MHS	Range	MTL	Range	MHW
TONGA	7	33.7	33-35	29.7	28-32	0.83
FIJI (Rotuma)		33.6	33.1-34.2			
FRENCH POLYNESIA (Moorea)		30.7*	28-33			0.76**

Table 24: Egg size for *G. oceanica* from two localities on Santo, Peavot village on the east coast of Cape Cumberland and the mangroves of Palikoulo. **MES**: mean egg size (mm).

Locality	n	MES	Range
Peavot	11	12.77 +/- 0.37 x 13.82 +/- 0.38	12.21-13.33 x 13.37-14.59
Palikoulo	12	12.01 +/- 0.33 x 13.30 +/- 0.87	11.38-12.52 x 12.24-15.18


Photo I. Ineich

Figure 209: *G. oceanica* is a massive gecko with a large head and heavily built limbs allowing it to easily climb large trees. Adult snout-vent length varies from 60-90 mm and the tail is nearly equal to body size.


Photo I. Ineich

Figure 210: *G. oceanica* has enlarged finger and toe pads, the terminal portion of each digit arises from the middle of the enlarged pad and each digit terminates with a well-developed claw. The pinkish band on the posterior part of thigh and leg is typical of the species.

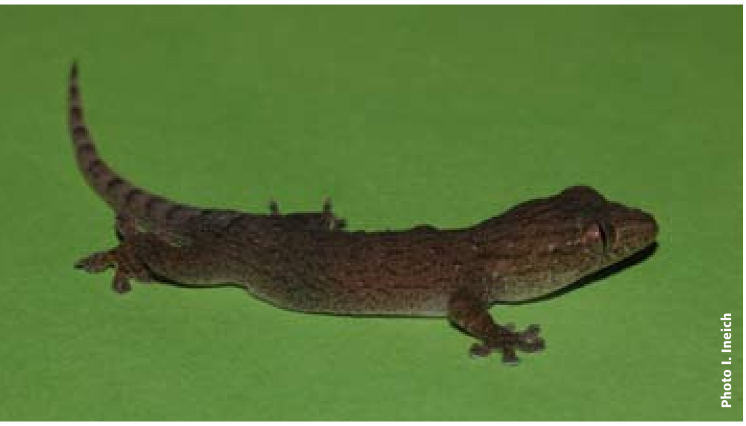
Photo I. Ineich

Figure 211: Hatchlings of *G. oceanica* are strongly patterned. Their tails are dorsally annulated with dark and light rings.


Photo I. Ineich

Figure 212: *G. oceanica* hatchlings typically have a pinkish wash around the eye. Total length is about 60-70 mm with a nearly equal body and tail length.

Figure 213: Ventral colouration of *G. oceanica* is either lemon yellow (that image) or greyish white; there are no intermediates. Colour polymorphism is not related to sex, is present in both hatchlings as well as adults, and has as yet no explanation.

mature males with femoral and preanal pores). The species occupies a wide spectrum of habitats, including mangroves, inhabited areas, cultivation and to a lesser extent primary forest, where suitable habitats are rare (dead and/or old trees) and generally occupied by a larger species of the genus, *Gehyra vorax*. *G. oceanica* lays its eggs in communal egg laying sites which can sometimes hold more than 40-50 eggs together (each female lays two eggs). Such egg concentrations can be found under the loose bark of live coconut trees or even dead trees and all development stages are present at the same time, including hatched empty eggs.

Data in table 22 clearly shows that the Vanuatu populations of *G. oceanica* have egg sizes similar to those of Tonga and Fiji. There are however significant differences between all of these and those of French Polynesia as shown in tables 22 & 23. Such differences correspond to the significant live colour differences between French Polynesian populations and others and are not in agreement with Beckon's biogeographical separation of potentially distinct species. French Polynesian specimens are less coloured (often uniform greyish) and less patterned, they also have less orange-pinkish colours on their body, even as hatchlings, compared to Melanesian and Tongan specimens. The tails of hatchlings are often ventrally pinkish orange like in other populations. The differences observed between French Polynesia and other islands (Tables 22 & 23) cannot be related to habitat choice since the differences are very low between French Polynesian populations when comparing eggs on atoll and more humid high altitude islands. They really should correspond to a specific or subspecific differentiation between populations.

In the same way if I consider populations from two different habitats on Santo:

- An east Cape Cumberland population from the village of Peavot on Santo,
- The mangrove population of Santo (Palikoulo, 15.498° S, 167.251° E);

the differences are also relevant (Table 24) but slight, and not to the same extent as between French Polynesia and other populations (Tables 22 & 23).

Gehyra oceanica has a wide distribution in Vanuatu. It is reported from Torres and Banks in the north, and to the south on most if not all other islands until Anatom in the extreme south of the archipelago. The species was reported from Santo by Medway and Marshall in 1975. Specimens from Santo are present in several museum collections: AMS, BMNH, MNHN and UMMZ. Some recent

Figure 214: Adult males of *G. oceanica* are easily distinguished from females by the presence of a large swelling on each side at the base of the tail (red arrow), cloacal spurs and a typical V shaped row of femoral and preanal pores (white arrow).

data are consistent with the hypothesis that *G. oceanica* was naturally dispersed across the Pacific, prior to the arrival of humans.

SQUAMATA, GEKKONIDAE
Gehyra vorax

For about 75 years after its original description, *G. vorax* was regarded as a valid species, distinct from *G. oceanica*. In 1932, Burt and Burt placed it in the synonymy of *G. oceanica*. That concept was accepted until 1984 due to new data from Gibbons and Clunie. The revision of Beckon in 1992 showed that this species has clear differences from *G. oceanica* in terms of habitat, behavior, and ecology, but also morphology.

G. oceanica has lamellae on about half the toe pad whereas in *G. vorax* lamellae occupy two thirds of the pad. The pad is also distinctly larger. Furthermore *G. vorax* has a mottled pattern and a greater number of subdigital lamellae (more than 18 (19-34) vs 12-15 in *G. oceanica*). For *G. vorax*, Beckon indicated 26-90 pores, a snout-vent length of 35-156 mm and 90-156 mm for mature males with pores. *G. vorax* is less common in collections than *G. oceanica*. I have also noted that even as a hatchling and juvenile, *G. vorax* can easily be distinguished from *G. oceanica*. The former has only about 5-6 dark dorsal tail bands whereas the later has at least 9-10 such bands.

According to external morphological characters (toe lamellae and preanal/femoral pores), three morphotypes are distinguished in *G. vorax*: Fiji, Vanuatu and New Guinea. Fijian and Vanuatuan specimens do not share the same coloration and can easily be distinguished. The morphotype from New Guinea looks very closely like *G. oceanica* (the later species being absent from there) and could correspond to *Gehyra membranacruralis*. *G. vorax* does not occur in New Caledonia where it is replaced by *Rhacodactylus* sp. It is however present on the Loyalty Islands. Reports from Tonga seemed to be valid but the species is now considered to be extinct on that island group, but of course might still occur there. Beckon supposed the extinction of *G. vorax* on Tonga arose through habitat perturbation or destruction but such a hypothesis is not

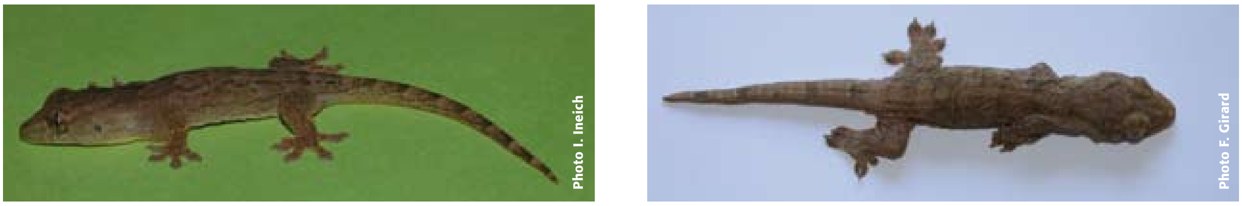

Figure 215: In contrast to hatchlings of *G. oceanica* (left), those of *G. vorax* (right) have only 5-6 dark dorsal tail bands. Santo.

Figure 216: Adult male of *G. vorax* on a giant banana trunk at Butmas, Santo.

Figure 217: Red morph (female) of *G. vorax*. Butmas, Santo.

Figure 218: Eggs of *G. vorax* (numbers 3 and 6) can easily be distinguished from smaller ones of *G. oceanica* (numbers 1 and 10) and also from all other species of Vanuatu by their size and circular shape. Santo.

acceptable since primary forests are still present on several islands like 'Eua. A fourth morphotype from the Moluccas could also represent another distinct species. Thus the available biogeographic and morphological data seem to agree with multiple species in the *G. vorax* complex.

G. vorax is poorly represented in world museums and its biology is only poorly known. It is the second largest gecko in the southern Pacific; on Fiji, its total length reaches nearly 25 cm. The body is heavily built with strong muscles; fingers and toes are widely enlarged. Locals fear the species due to the way it mimics vegetation, its capacity to produce sounds, its adherence to human skin associated with its developed subdigital lamellae, strong claws able to cause injuries, and also its capacity to lose skin when handled. I have observed a green muscle colour under the lost skin in one specimen from Butmas on Santo. In Fiji, some specimens show a dorsal colour pattern comprising an alternate brown and grey-blue or greenish bands sometimes causing confusion with endemic iguanas of the genus *Brachylophus*; such colouration was not observed in Vanuatu. In that area the gecko is named the "lizard that barks like a dog" and its cry can be confused with that of the pigeon *Ptilinopus luteovirens*. Its diet is based on fruits and in captivity it readily eats papaya. It is mostly a forest species but it can also be seen on breadfuit trees or even large banana plants, *Pandanus* sp., coconut trees, large palm trees, mangroves, sometimes not far from human habitation. Contrary to *Gehyra oceanica*, it never enters human habitation. *G. vorax* is an arboreal species showing a clear tendency to avoid man, contrary to *G. oceanica*. I suspect that species to be naturally less anthrophilous than *G. oceanica* and not to avoid humans as a secondary adaptation to its fear of being predated for meat. *G. vorax* is hunted for food in Fiji and also on Vanuatu where *G. vorax* is often active during day time. Its skin perfectly matches tree trunks covered with lichen, and it can change its coloration from light green to grey or dark chocolate brown. On Vanuatu, sexual colour dimorphism occurs: adult females are rather brownish and adult males greyish to greenish. The species is difficult to collect or observe in the field since it often lives high on tree trunks and even in the canopy, mostly in primary forest. When sympatric with *G. oceanica*, *G. vorax* is found higher up towards the canopy. *G. vorax* is less common in coastal forest and highly disturbed habitats than in deep humid forests.

Eggs of *G. vorax* are clearly larger than those of *G. oceanica* with which it was long confused. Gibbons and Zug measured two eggs from Fiji (Viti Levu Island) with a mean size of 18 x 20 mm and a mass of 3.9 g. The mean size for three eggs from Santo is 17.57 x 19.24 with ranges of 16.59-18.11 x 18.59-19.75 mm.

G. vorax is particularly sensitive to two threats, deforestation and the international pet trade. The species is regularly and easily available on the internet from where several colour morphs can be obtained from Vanuatu ("red morph", "ornate morph").

G. vorax was reported from several islands of Vanuatu: Erromango, Efate, Epi, Malakula, Pentecost, Aoba and Santo. Specimens from Santo are present in AMS and MNHN. The species was never reported north of Santo and south of Erromango and seems limited to the largest islands of the archipelago.

SQUAMATA, GEKKONIDAE
Gekko vittatus

G. vittatus is present in the Indo-Australian archipelago from Java (Indonesia) to New Guinea, Palau [probably a distinct species], Admiralty, Bismarck Archipelago, and as far as the Solomon Islands (Santa Cruz Group) and northern Vanuatu. The species was reported from Santa Cruz (southern Solomon) by Roux based on one specimen from the Speiser collection (NMBA). He stated: "*C'est, à l'est, le point de dispersion le plus extrême connu pour cette espèce. Notre exemplaire n'appartient pas à la var.* bivittatus *D.B.*", thus indicating observed

Figure 219: *Gekko vittatus* is an arboreal species living on small branches of small trees and shrubs. Torres Islands.

Figure 220: Like all lizards, *G. vittatus* sheds its skin in pieces. Torres Islands.

differences with *Gekko bivittatus* from New Guinea. McCoy also reported the species from the Santa Cruz Islands, Southern Solomon. Cranbrook and Pickering reported the species from the Banks: Vanua Lava, Mota Lava and Gaua (nowadays Santa Maria). Bauer and Henle stated: "*A single, questionable record from the main islands of Vanuatu*". Burt and Burt considered the species unable to migrate south of a limit fixed by Banks and Santa Cruz, a statement that seems correct.

This relative large gecko can be distinguished from other geckos from Vanuatu by the lack of claws on its fifth toe and finger and its flattened and elongated body. The MNHN specimen from southern Solomon (Vanikolo) shows a snout-vent length of 98 mm, tail length 96 mm, 12 supralabials, 10 infralabials, and 23 lamellae on the fourth toe. It shows larger granules on the back separated between them by smaller scales. The throat is covered by enlarged separated granules and followed by true scales on chest and belly, without granules. The legs show enlarged scales anteroventrally, followed by distinctly smaller granules in the posteroventral area. Postmental scales are asymmetric and median. Four successive larger scales lie behind the mental plate. The mouth is elongated by a dermal fold going up to just below the ear. The tail cross-section is typically circular. According to my observations, the Vanuatu and southern Solomon specimens clearly differ from Indonesian populations and might represent a separate taxon.

In Vanuatu, the species was reported from the northernmost islands: Torres Islands (Hiu, Tegua, Loh, Toga) and Banks Islands (Mota Lava, Vanua Lava, Santa Maria) where it is common. It was also recorded southernly, from Malakula by McKerras but its occurrence there has not been reconfirmed. Our research on Santo and Torres did not confirm its presence south of Banks. Locals consider the species to live in deep forest, which is wrong. It is sometimes eaten by the local people. On Torres Islands, the locals told us that children often use that lizard to make scarifications (tattoos). They get the lizard to bite them on body parts like the arm, then toss it away to produce injuries that later give rise to a kind of "V" shaped scarification. That gecko is the main prey of Barn Owls on the Torres Islands.

Figure 221: *G. vittatus* females deposit two adhesive eggs under bark or more generally under vegetation, like here in the axil of a *Pandanus* sp. leaf. Torres Islands. Detail: Eggs of *G. vittatus* have nearly the same size as those of *G. oceanica* but can be distinguished because they are adhesive.

Figure 222: In this gravid female of *H. frenatus*, eggs are visible through the body wall. Matantas, Santo.

Figure 223: Head of *H. frenatus*. In Vanuatu, geckos (Gekkonidae) can be distinguished from skinks (Scincidae) by the presence of small granules on top of the head in the former and large symmetrical head plates in the later. Matantas, Santo.

SQUAMATA, GEKKONIDAE
Hemidactylus frenatus

The gecko *Hemidactylus frenatus* is a recent colonist in Vanuatu where it arrived most likely around 1980 through man-mediated introduction. *H. frenatus* presently occurs on almost all tropical and subtropical areas of the Indo-Pacific. It naturally occurs in South and Southeast Asia but also on part of the Indo-Australian archipelago. It is an invasive species particularly adapted to human dispersal. It is generally believed to compete with indigeneous species and displace them. Such species interactions were noted as early as 1985 by Gibbons on Fiji, where populations of *H. garnotii* seem to suffer from such competition. In Vanuatu, the species is common in many villages and towns where it is often syntopic with *Lepidodactylus lugubris* and as yet has not replaced the latter.

Figure 224: *H. frenatus* is only active at night and does not hesitate to come to electric lights to capture the attracted insects on which it feeds.

Figure 225: *H. frenatus* can be distinguished from the other house gecko *Lepidodactylus lugubris*, by its larger adult size, the lack of deep black symmetrical spots on the back, and regular rings of erected granules around the dorsal tail vs only lateral small spines in *L. lugubris*. Luganville, Santo.

This introduced gecko was only reported from Efate and Espiritu Santo in 1994 and more recently (2008) from Malakula. Specimens from Santo are present in the Australian Museum (Sydney) and MNHN. AMS collections have specimens from Luganville (Santo) and Port Vila (Efate) collected in 1984. BMNH does not possess any specimens of this species from Vanuatu.

SQUAMATA, GEKKONIDAE
Hemidactylus garnotii

The gecko *Hemidactylus garnotii* has a broad distribution including the entire tropical Pacific, from New Guinea to French Polynesia. It occurs in India and mainland Southeast Asia through Indonesia to the Philippines. It is apparently absent from most of Melanesia and Micronesia. The species is, however, poorly represented by voucher specimens because it is relatively rare.

H. garnotii is a parthenogenetic species. It has a flattened appearance and an entire tail with only lateral spines but no dorsal spine rings. The ventral part of the tail is often coloured reddish pink in juveniles and subadults.

The species has not been previously reported from Vanuatu, but its absence is certainly an artifact, as is the case for *Gehyra mutilata*. *H. garnotii* is confirmed by a voucher at BMNH from Anatom, collected by Miss Cheesman but this record most likely constitutes a wrong identification. During the Santo 2006 expedition, I collected two specimens from the village of Tasmate, on the western coast of Cape Cumberland; these represent the first records of the species from Santo and the first vouchers for Vanuatu. It is certainly just a rare species that is difficult to locate.

Gibbons and Zug (1987) provide some data on eggs and hatchling from ‘Eua Island (Tonga): one egg size was 9 x 10 mm, mass 0.6 g; three hatchlings had a mean snout-vent length of 27.3 mm (range of 27-28), a tail length of 20 mm (range 19-21) and a mass of 0.31 g (range 0.28-0.36).

SQUAMATA, GEKKONIDAE
Hemiphyllodactylus typus

The gecko *Hemiphyllodactylus typus* has a wide distribution extending from South Asia to the Mascarenes, through Indonesia, Philippines and the whole tropical Pacific to French Polynesia. In Oceania, the species is represented by only a few records. This poor representation is the result of its rarity. It has not been reported from Vanuatu, but its absence is unlikely, and it will certainly be discovered in the coming years. It is a small gecko with a typical elongated body and short enlarged toe pads. It can be present in forest as well as around human habitation but is not attracted to lights on houses.

SQUAMATA, GEKKONIDAE
Genus *Lepidodactylus*

In his PhD thesis, Russell considered the genera *Gekko*, *Pseudogekko*, *Luperosaurus*, *Ptychozoon*, *Lepidodactylus*, *Hemiphyllodactylus*, *Gehyra* and *Perochirus* as belonging to the same relational group, the *Gekko* group of the subfamily Gekkoninae. Within the genus *Lepidodactylus*, he examined toe morphology and formulated an evolutionary hypothesis related to distal transformations, mostly a reduction of the number of subdigital lamellae, accompanied by a median division of some distal lamellae to form two rows. Later, Brown and Parker indicated that a more compressed tail and members habitus is parallel to that evolution. They distinguished three evolutionary lineages in the genus *Lepidodactylus*. Group I species (***pumilus-oorti* group**) still possess numerous undivided "*Gekko* like" lamellae at all digits. *L. manni*, a Fijian endemic, belongs to that group. Group II members (***guppyi-pulcher* group**) also have undivided lamellae but several terminal lamellae are divided. *L. gardineri*, a Rotuma endemic (north of Fiji) and *L. vanuatuensis* (see below), belong to this group. Tails of groups I and II are subcylindrical, without lateral fringes or spines. Group III species (***lugubris-woodfordi* group**) are characterised by a reduced number of subdigital lamellae but the terminal and some subterminal lamellae divide, associated with a depressed body and a more flattened and widened tail. Group I is considered as the most primitive of the genus. Species of that group are present from Indonesia to Papua New Guinea, Torres Straits islands, Solomon and Fiji, and on Christmas Island in the Indian Ocean. *L. listeri* from Christmas Island cannot be distinguished morphologically from *L. manni* of Fiji. Group II species are present over a smaller area from north New Guinea, Solomon, Vanuatu, Admiralty, Bismarck and Rotuma. Group III species are the most evolved species regarding their digital structures according to Russell’s hypothesis. Several distal lamellae,

Figure 226: *L. buleli* seems to be endemic from the west coast dry forests of Santo. It was only observed in myrmecophilous plants but it is unlikely that this represents its only habitat.

Photo V. Prié

Figure 227: *L. lugubris* is easily distinguished from other Vanuatu members of the genus by its dorsoventrally flattened tail with lateral indentations. This specimen has typical black marks of triploid clone B.

Photo I. Ineich

Figure 228: Diploid clone A is the most common clone of Vanuatu. That clone was recently (during World War II) introduced over most tropical Pacific islands. It is typical by its seven pairs of double symmetric fine black points from the neck to the base of the tail.

Photo I. Ineich

Figure 229: Ground colouration is variable in most geckos but black marks are always present in that species and do not disappear whether the gecko is active under light or under shelter in the dark during day time. Their size, number and position allow clonal attribution to each individual (diploid or triploid clones).

including the terminal one, are divided and lamellae are in more reduced numbers, with a clear tendency to disappear at the base of the finger; their tail is wider and more compressed dorsoventraly. These species have a wide distribution comprising several Indian Ocean islands and most tropical Pacific islands, reaching both sides of Central America where populations are generally considered to have been recently introduced by man.

SQUAMATA, GEKKONIDAE
Lepidodactylus buleli

The gecko *Lepidodactylus buleli* is known only from the Cape Cumberland west coast, in the forest around the village of Penaoru. It was discovered during the Santo 2006 expedition and is known from two specimens, one in bad condition and the second, the holotype, which arrived in Paris as an egg that was hatched and the juvenile grown to an adult, allowing it to be described. It is a typical group II *Lepidodactylus* (terminal lamellae entire) due to its cloacal spurs at base of the tail in males, its subcylindrical tail, yellowish lips and dorsal and head pattern.

This gecko has a unique habitat and lives in myrmecophilous plants hanging on tree trunks around 20 m high in primary forest of the dry west coast of Santo. It is however not unlikely that it occurs in a wider range of habitats that only such kind of plants.

SQUAMATA, GEKKONIDAE
Lepidodactylus lugubris

L. lugubris is widely distributed from the Indian Ocean to South Asia (India and Sri Lanka) through Southeast Asia, Indonesia, Philippines and almost all tropical Pacific islands. Most authors consider that the species owes its broad occurrence to accidental transport by man; even if the genetical structure of the populations referring to that species reflect a long evolutionary history in the Pacific. The species occurs throughout Vanuatu and was reported from there already since a long time.

The species is common around human habitation and does not hesitate to visit the interior of houses. It occurs in most habitats from mangroves, cultivated areas, villages and cities, and also in forest at low elevation. The populations of Vanuatu are unisexual and females reproduce clonally through parthenogenesis. Males have never been reported in Vanuatuan populations. At least three clones are present in Vanuatu, diploid recently-introduced

Figure 230: *L. vanuatuensis* is typical by its yellowish anterior eye border, short and rounded snout and purple brownish colouration.

Figure 232: This male *L. vanuatuensis* has a swollen tail base that allows easy sex recognition for adults. Tasmate, Santo.

Figures 231: Other diagnostic features of *L. vanuatuensis* are enlarged dark dorsal symmetric blotches and a roundish tail section. Females (this image) do not have a swollen tail base.

Figure 233: Hatchlings of *L. vanuatuensis* are smaller than those of *L. lugubris*. They typically have large symmetric dark dorsal blotches, a rounded snout, and a round tail section without lateral fringes.

clone A, and triploid clones B and C which are rare. In Vanuatu, the species was reported from Torres and Banks groups, Espiritu Santo, Aore, Malo, Aoba, Tutuba, Malakula, Ouri, Ambrym, Tongoa, Efate, Emao, Erromango, Aniwa, Tanna, Futuna, Anatom. Specimens from Santo are present in numerous world collections: AMNH, AMS, BMNH, FMNH, MCZ, MNHN, UMMZ and USNM. The species was reported from Santo by Medway and Marshall in 1975.

Each female lays two adhesive eggs (adhesive to the substrate but also to one another). Eggs are often deposited in communal egg laying sites under the bark of upright living or dead trees. They can also be found in rock crevices or even in pompilid wasps nests. Hatchling snout-vent lengths from Santo vary from 19-21 mm (n = 13, mean 20.1 +/- 0.9) and tail length varies from 16-23 mm (n = 13, mean 19.6 +/- 1.8).

SQUAMATA, GEKKONIDAE
Lepidodactylus vanuatuensis

The recently described gecko *Lepidodactylus vanuatuensis* is a Vanuatu endemic and its type locality is located on Santo (holotype in USNM). It was reported from several Vanuatu islands: Santo, Efate, probably Tanna, and Anatom. Specimens from Santo are present in the following museum collections: AMNH, USNM, MNHN and AMS.

The species often lives in high numbers on the same tree, sometimes in complete syntopy with *L. lugubris*. It is present around villages not far from sea level or on the seashore, e.g. under tree bark like mango trees or *Casuarina* sp. It can be distinguished from *L. lugubris* by its round tail cross section, short and rounded snout and red brownish dorsal colouration with a yellow eye border.

Hatchling snout-vent length varies from 16-17 mm (n = 5, mean 16.6 +/- 0.5) and tail length from 12-15 mm (n = 5, mean 14.2 +/- 1.3). Eggs of this species are smaller than those of *L. lugubris*; they are laid in pairs, stuck together and onto the support were they are laid in communal egg laying sites.

SQUAMATA, GEKKONIDAE
Lepidodactylus guppyi

L. guppyi is a group II *Lepidodactylus* species. It was first reported by Burt and Burt in 1932 from Tinakula (Tinehula) in the Santa Cruz group. In 1980, McCoy recorded the species from Santa Cruz and Vanikolo Islands. I recently collected a single specimen of this species in northern Vanuatu (Hiu, Torres Islands) in November 2007. It is a forest arboreal species observed during the day under loose bark on a dead tree in a garden surrounded by deep forest.

SQUAMATA, GEKKONIDAE
Genus *Nactus*

Despite that some populations of *Nactus* were considered to be distinct species in the past, all populations were subsequently considered as a single, wide-ranging species, *Nactus pelagicus*,

Figure 234: *Lepidodactylus guppyi* (right) can be distinguished from *L. lugubris* (left) by its habitus and colouration. Torres islands.

until the revision by Zug and Moon in 1995. Schwaner found only females in Samoan populations, whereas most Australian and Melanesian populations are bisexual. In 1987 Moritz was the first to review this species complex. He examined 322 specimens from Vanuatu: Banks (Vanua Lava), Espiritu Santo, Aoba, Malakula ("Malekula") and Efate for the northern islands from which populations comprised males and females, Erromango, Tanna and Anatom for the southern islands from where populations only comprised females, except for Anatom. Chromosomal and enzymatic polymorphism analysis shows that bisexual populations are highly polytypic and probably comprised several species that could be separated into four geographic groups based on electrophoresis and cytogenetics. He made no nomenclatural decision to distinguish those morphologically similar populations. Unisexual populations are diploid, highly heterozygous but do not show a genetic segregation between them, thus suggesting parthenogenetic reproduction. The high heterozygosity of unisexuals indicate a probable origin through hybridization with one of both parental species genetically similar to the bisexual populations of northern Vanuatu and the second not identified but whose genetic characteristics could be predicted. Oceania (comprising the islands located east of a Philippines/New Guinea/Solomon/Vanuatu limit) and New Caledonia have only unisexual populations whereas Vanuatu possesses mixed populations — both unisexual and bisexual at the same time (mixed on Anatom in Vanuatu), whereas elsewhere in southwest Pacific populations are unisexual. Moritz also shows a scalation character concerning post-mentals allowing the separation of unisexual females (small post-mentals separated from infralabials) from bisexual females (enlarged post-mentals in wide contact with infralabials).

During a detailed analysis of populations until then attributed to the *N. pelagicus* complex, Zug and Moon in 1995 showed that north Vanuatu and Solomon populations have males and females, whereas elsewhere in Oceania and New Caledonia populations only comprise females, as in southern Vanuatu (except Anatom). Precloacal pores are only present in males; unisexual populations have a significantly larger size than bisexuals but that character, as with body size, and other statistical differences highlighted by Zug and Moon, do not allow a serious separation of unisexual and bisexual

Figure 235: *N. multicarinatus* is typical by the presence of dorsal lines of keeled enlarged granules and black and white striped lips.

Figure 236: *N. multicarinatus* is often heavy dark when disturbed during day time. Symmetrical black dorsal marks can however be seen on its back. Tail base is typical by the presence of enlarged granules forming a kind of lateral spine line. Torres Islands.

Figure 237: When disturbed and stressed, *N. multicarinatus* often curls up its tail. Note the typical black and white striped lips.

populations. Those authors noted however a clear tendency to a correlation between those variations with latitude, and explained that phenomenon by the influence of climatic factors affecting development. They suggest testing that hypothesis by analysing altitudinal variations on a sample from the same island. Moritz's hypothesis, which supposed that one of both parental species of the unisexual form would be the sexual form of Vanuatu and the Solomon Islands seems to agree with those results. According to Zug and Moon, the distinction of unisexual from bisexual specimens by the size of post-mentals as shown by Moritz is not always reliable; their work also shows that it is impossible to distinguish unisexual and bisexual females through morphology and scalation. The same authors proposed to distinguish Vanuatu bisexual populations at a specific level (*Gymnodactylus multicarinatus*) from Oceanian unisexual populations (*Heteronota pelagica*). Two binomen are available to name the Oceanian unisexual populations (*Arnouxii* and *pelagica*). The International Commision of Zoological Nomenclature validated *pelagica* with its type locality "Feejee and Navigator Islands". Zug and Moon (1995: 88) designated a lectotype and restrict the type locality to Ovalau, Fiji. The syntypic series of *Nactus multicarinatus* comprised six specimens coming from three different localities. Again, Zug and Moon designated a lectotype and restricted the type locality to Efate, Vanuatu. The electrophoretic and cytogenetical studies of Moritz, as well as the morpho-meristic study of Zug and Moon seem to show that unisexual populations are uniform and certainly arose from a unique hybridisation event between two bisexual species.

SQUAMATA, GEKKONIDAE
Nactus multicarinatus

The bisexual species *Nactus multicarinatus* occurs from the southern Solomon Islands to Vanuatu, except Tanna and Erromango. On Vanuatu, it has been reported from the Torres group, the Banks group (Vanua Lava, Santa Maria), Elephant Island (east coast of Santo), Santo, Malo, Aore, Aoba, Maewo Pentecost, Suwarro, Ouri, Ambrym, Malakula, Epi, Emao (off Efate), Niogriki Island (north coast of Efate), Efate, Anatom. Specimens from Santo are present in several world museums: AMNH, AMS, BMNH, MNHN and UMMZ.

N. multicarinatus is very common and widespread on Santo. It is found in many kinds of habitats and can easily be observed during daytime under stones and logs at soil level. Its colouration is heavy dark brown to black when disturbed during the day. It lives mostly on the ground but climbs on to the bases of trees, generally less than one meter high at night. This gecko is easy to distinguish by its toes, which are not enlarged (no toe pads). *N. multicarinatus* is present above 900 m elevation on Santo were it was the only species found during the day under stones and dead fallen trees.

SQUAMATA, GEKKONIDAE
Nactus pelagicus

The unisexual gecko species *Nactus pelagicus* is present from Micronesia, New Caledonia to the east of Melanesia and Polynesia. In Vanuatu, *N. pelagicus* seems to occur only on Erromango and Tanna, perhaps on Anatom, but it is absent from Santo. The status of Anatom populations has to be checked.

Figure 238: Reproduction of the original plate of *Perochirus guentheri* by Boulenger (1885: pl. 12, fig. 4).

Gibbons and Zug indicated a mean egg size and mean mass for 5 eggs from Viti Levu (Fiji): 7 x 13 mm, range 6.5-8 x 12-14 mm, mass 0.44 g, range 0.39-0.49 g.

SQUAMATA, GEKKONIDAE
Perochirus guentheri

In 1976, W. C. Brown revised the genus *Perochirus* first described by Boulenger in 1885. He recognized three species all with restricted distributions, limited to one island or a small island group. *Perochirus scutellatus* is present in Micronesia on Tetau Island (Carolines) and Greenwich Islands (Kapingamarangi Atoll, State of Pohnpei). *Perochirus ateles* occupies the Truk Islands, Kapingamanrangi Atoll, Guam, Tinian, Ponape, Marcus and Cocos in Micronesia. *P. guentheri* is endemic to Vanuatu and the only species of the genus found outside Micronesia. *Perochirus* was erected by Boulenger with *Perochirus ateles* as the type species. It shows different characteristics including a first rudimentary finger, without a claw and a granular back. In 1954, Underwood placed that genus in Gekkoninae, principally based on its pupil shape. Later, in an unpublished manuscript, Russell considered the genus to belong to a group of genera including *Gehyra* and *Hemiphyllodactylus*. In fossil remains discovered on ‘Eua island (Kingdom of Tonga), Pregill noted in 1993 the occurrence of nine species among which two are extinct, one such gecko was placed in the genus *Perochirus* and a large extinct skink in the genera *Emoia* (not *E. trossula*), *Eugongylus* or *Tachygyia*. This endemic species seems to agree with the hypothesis that Vanuatu was formerly positioned north of its current location, near the putative center of origin of the genus in the Central Pacific, in the Micronesian area. However, fossil remains of *Perochirus* reported from ‘Eua (Tonga) by Pregill could also indicate that the group previously had a wider distribution. That author considered *Perochirus* to have been eliminated from Tonga by the most recent arrival of *Gehyra oceanica*. An illustration of *P. guentheri* is given in the early work of Boulenger published in 1885. Adult sizes vary from 61 to 71 mm snout-vent length and males possess 10 to 12 preanal and femoral pores extending to the lower thigh.

P. guentheri is a southern Vanuatu endemic. The species is known only from four specimens: two specimens from Erromango collected in 1859 or 1860 (type locality) by Cuming (BMNH) and a third one collected on the same island in August 1971 in Marshall’s tent, on the site of Nuangkau camp. Cranbrook considered however that origin to be uncertain and that it could have been transported during the expedition going from island to island. A fourth specimen from AMNH was collected on Anatom but was not reported by Medway and Marshall in 1975. Note however that a recent list of BMNH specimens from Vanuatu does not mention any BMNH *Perochirus* from Anatom. Thus the Anatom locality requires confirmation.

No data are available on the ecology of *P. guentheri*. *P. ateles*, a related species, occupies coconut palms on Kapingamarangi, and one specimen was collected on a bread fruit that had fallen onto a tree fern branch. *P. scutellatus* also was observed on coconut palms on Tetau Island. No data are available on reproduction.

••• Reptiles from Vanuatu – LIZARDS (Scincidae)

Most Santo lizards observed during the day are skinks (family Scincidae). They can be distinguished from geckos by the presence of symmetrical head plates and smooth overlapping scales. Some species are terrestrial and others arboreal.

SQUAMATA, SCINCIDAE
Caledoniscincus atropunctatus

The genus *Caledoniscincus* is a regional endemic comprising about 11 recognized species of which all except one are New Caledonia/Loyalty area endemics. The exception, *C. atropunctatus*, occurs throughout New Caledonia and the Loyalty islands, but also in the southern islands of Vanuatu. Its broad distribution in these latter islands suggest that it arrived in Vanuatu prior to humans; however, a human mediated introduction cannot be excluded since the species has probably also been recently introduced to Surprise Island off New Caledonia. The species is widely distributed in New Caledonia and its arrival in Vanuatu is sometimes considered to be recent. It occurs on Ouvéa, Lifou and Maré islands in the Loyalty Islands, and in Vanuatu it is restricted to forest on Erromango, Tanna, Aniwa, Futuna and Anatom. Bauer and Sadlier recently add Efate but that record arises from a misidentification referring to *Emoia* sp. There is no record of that species for Santo and it is clearly a southern Vanuatu skink species.

The species was present in Vanuatu before the Second World War and also occupies forest, thus arguing against a recent human mediated introduction. Medway and Marshall considered it to be restricted to forest; it however only occurs in dry open-canopy forest but is more abundant in larger patches of coastal forest or interior mixed hardwood forest. Its distribution in Vanuatu is however wide and encompasses native dry open-canopy forest, thus suggesting an older arrival.

I have examined MNHN specimens from Tanna which belong to that species. They are small skinks with three dorsal keels and 28 midbody scale rows. Their flanks are dark brown from nose to tail, the back is light brown with spots on a line corresponding to each scale line (like interrupted lines). The belly of both specimens show a pigmentation on each scale. There is a sexual dimorphism in coloration and both specimens are females. Supranasals are separated, prefrontals largely separated, the interparietal is large, and there is a single frontoparietal.


Photo I. Ineich

Figure 239: *C. novohebridicus* is a small skink less than 38 mm snout-vent length. Its eyes are covered by a fixed transparent eyelid thus explaining standard name of Vanuatuan snake-eyed skink. Santo.


Photo I. Ineich

Figure 240: Specimens of *C. novohebridicus* are usually dark and always possess a pair of lighter lateral bands. They are the only skink of Vanuatu lacking moveable eyelids. Santo.


Photo I. Ineich

Figure 241: *C. novohebridicus* is a typical littoral species that regularly forages on sandy beaches when stones and vegetation are nearby, sometimes in syntopy with *Emoia cyanura*. Santo.

SQUAMATA, SCINCIDAE
Cryptoblepharus novohebridicus

Burt and Burt regarded *Cryptoblepharus boutonii novohebridicus* (as it was originally named) as a synonym of *Cryptoblepharus boutonii poecilopleurus*. The taxonomy and systematics of the genus *Cryptoblepharus* have been recently reviewed for Indian Ocean as well as for Pacific Island populations by Horner. Fuhn in 1969 and Greer in 1974 considered *Cryptoblepharus boutonii* as a super-species with about 36 morphological and/or geographical types. Mertens in 1931 previously attributed a subspecific rank to all these 36 "forms". *C. novocaledonicus*, as *C. novohebridicus*, is now considered as a valid species. In 1931, Mertens recognized affinities between the faunas of New Caledonia and Vanuatu. He also noted affinities between *C. novohebridicus* and *C. virgatus* (northern Australia) from which the former could derive.

C. novohebridicus is a small species with a maximum snout-vent length of 37 mm. The species is sometimes present in mangroves but generally frequents upper sandy beaches covered with vegetation. Coastal populations usually occur on coral litter, palm trunks and dead timber and can display high densities in such habitats. It is also sometimes abundant in dry open forest areas a short distance (approximately 3 km) from the coast as I observed in the Penaoru area, Santo. However, that population was certainly accidentally introduced by the Santo 2006 expedition team from the sea shore to that area.

This species occurs throughout the entire Vanuatu archipelago. It was reported from Banks (Merig), Espiritu Santo, Malo, Aore, Aoba, Pentecost, Ambrym, Malakula, Efate, Emao (off Efate), Erromango, Tanna, Futuna, and Anatom. I confirmed its occurrence in the Torres Islands during a November 2007 trip. It was reported from Santo by Medway and Marshall but not found again. The species can be considered to be present over the whole of Vanuatu from the extreme north to the extreme south.

SQUAMATA, SCINCIDAE
Genus *Emoia*

The genus *Emoia* has numerous insular endemic species, as well as some widespread species. Many species remain to be discovered or described. For example, prior to 1980 Fiji had a single known endemic species. After that date, intensive fieldwork allowed the recognition of five additional taxa new to science in the genus from Fiji, most of them from the *E. samoensis* species group. The systematics of that species group is being clarified, including the Vanuatuan populations from which additional species remain to be described.

SQUAMATA, SCINCIDAE
Emoia aneityumensis

The skink *Emoia aneityumensis* is an Anatom endemic, in southern Vanuatu. It was described based on three immature specimens collected by Lord Medway during the 1971 Royal Society Expedition and three additional specimens collected by Miss Evelyn Cheesman on the same island and deposited in the BMNH collection. They were first catalogued as *Emoia nigra*. The material collected by Cheesman during 1954-1955 has no precise collection locality. Medway did not find additional specimens in the different collections he examined elsewhere (AMNH, BMNH, MNHN, Senckenberg Museum). The species belongs to the *Emoia samoensis* group comprising 14 described species among which 11 are geographically limited to the Vanuatu, Fiji, Tonga and Samoa subregion, one species is endemic to the Solomon Islands, one to Cook Islands, and another occupies nearly the whole of Melanesia.

The *E. samoensis* group comprises two species subgroups that seem to be closely related and three species with unclear affinities to other members of the group. It is the only group in the genus where females lay more than two eggs. *Emoia aneityumensis* belongs to the *Emoia concolor* subgroup, which comprises eight species (several more to be described): *Emoia campbelli* (Fiji), *Emoia concolor* (Fiji), *Emoia erronan* (Futuna, Vanuatu), *Emoia aneityumensis* (Anatom, Vanuatu), *Emoia loyaltiensis* (Maré, Loyalty, New Caledonia), *Emoia mokosariniveikau* (Vanua Levu, Fiji), *Emoia tongana* (Samoa and Tonga) and *Emoia nigromarginata* (Vanuatu). *E. aneityumensis* can be distinguished from *E. samoensis* by its higher number of medio-dorsal scales (40-42) and its lower number of subdigital lamellae (36-42); its coloration is identical to that of *E. nigromarginata* (but can be distinguished from the former by its larger size at sexual maturity (up to 92 mm SVL) and its increased number of eggs. Total length is about 2.74 times snout-vent length. Prefrontals are in weak contact and separate nasals from frontals. The interparietal is distinct. The 5th or 6th supralabial is the largest and located under the eye. Twelve specimens of *E. nigromarginata* from different localities in Vanuatu studied by Medway show 28-34 midbody scale rows,


Photo I. Ineich

Figure 242: *Emoia atrocostata freycineti* is a littoral species that prefers rocky shorelines. Torres Islands.

38-48 subdigital lamellae under the fourth toe, and a snout-vent length of 60-72 mm. *E. aneityumensis* is only known from Anatom and specimens are conserved at BMNH and FMNH.

The coloration of the holotype (after 18 months preservation in alcohol), is dark brown on the back, with a discontinuous and irregular row of black spots and punctuations extending in the shape of a discontinuous dorso-lateral line from ear to tail base extending above legs and feet. Flanks are brownish, crossed and spotted by intrusions of the whitish ventral coloration. In three live juveniles the back was grey-brown or olive-brown, marked by a broken row of punctuations or black spots, mixed with Nile water flecks extending from the ear to the base of the tail. Flanks are olive-brown, crossed and spotted by the dirty white ventral colouration. The tail is the same brown as the dorsal colouration but regenerated tails are lighter. Medway supposed, according to Cheesman's description, that adults have a general grey blue coloration.

All available specimens originated from a disturbed and partially regenerated forest located about 1 mile northeast of Anelgauhat on Anatom. Medway erroneously considered two reported specimens of *E. samoensis* as valid for Erromango and thus allows for a competitive exclusion between *E. aneityumensis* and *E. samoensis* on Erromango and Anatom, but he excluded the possibility of considering them as subspecies of a same species.

SQUAMATA, SCINCIDAE
Emoia atrocostata freycineti

In 1913, Roux reported the occurrence of the lizard *Emoia atrocostata freycineti* from the Santa Cruz group, southern Solomon, and from Pentecost in Vanuatu (both NMBA collections). He noted: "*Elle n'avait pas encore été signalée aux Nouvelles-Hébrides*". In 1991 Brown distinguished three subspecies and refers Solomon and Vanuatu populations to *E. atrocostata freycineti*. The type locality of that subspecies is Vanikolo Island, Santa Cruz group, southern Solomon Islands. The nominal subspecies occurs in Micronesia (Mariannas, Carolines), Palau and in the Bismarck Archipelago along the Pacific and Australian plates west to New Guinea, Torres Strait islands, Indonesia, Christmas Island, the Malay Peninsula, Indochina, Borneo, Philippines, Taiwan and only one island south of the Ryukyus in Japan. The subspecies *E. atrocostata australis* only occurs in the Cape York area of Queensland, Australia. Cranbrook and Pickering noted that the species is known from Vanuatu by two specimens respectively from Malo and Pentecost.

It is a common specialised species but restricted to some habitats. It is mostly present on rocky

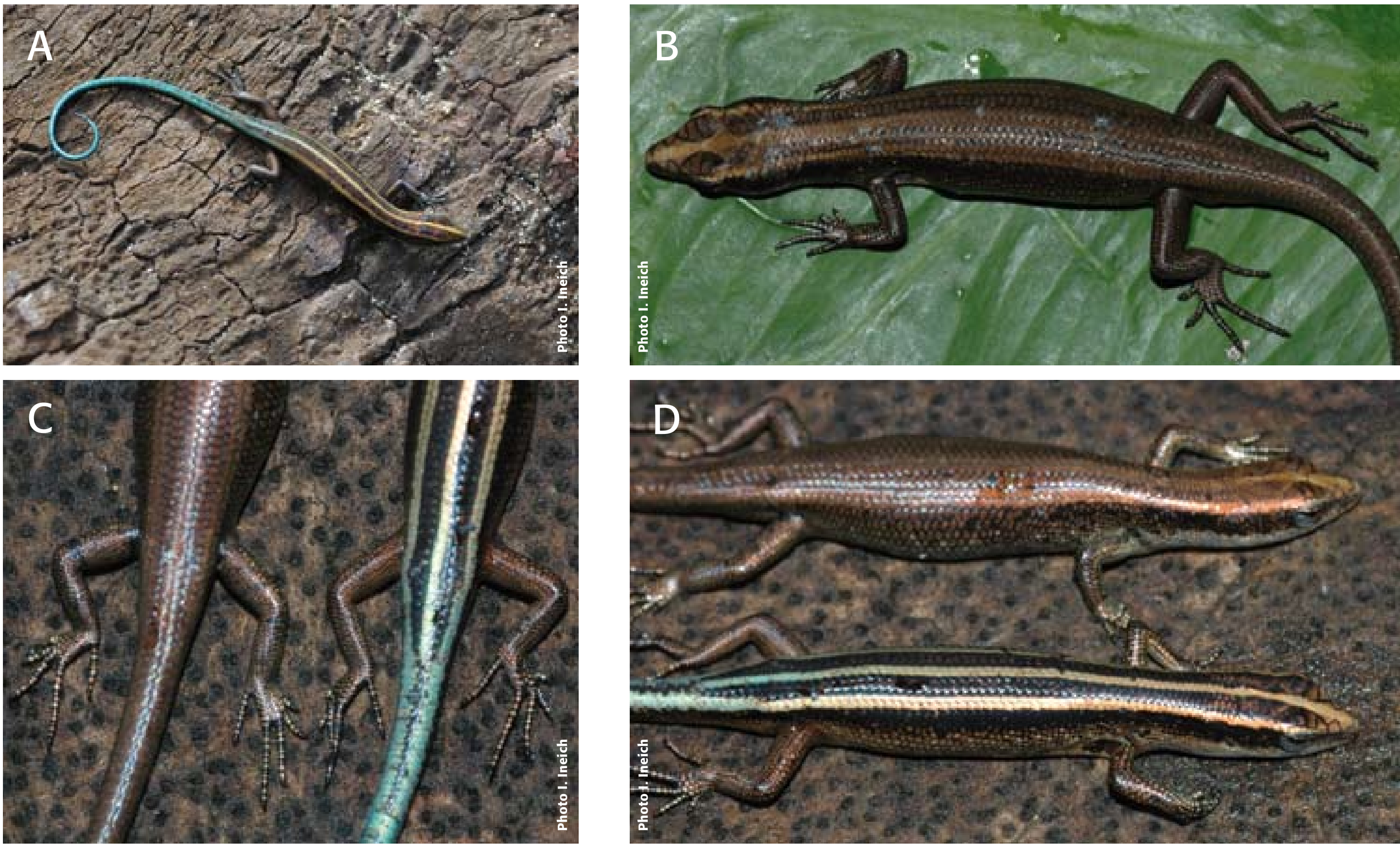

Figure 243: *E. caeruleocauda* has two color morphs in Vanuatu and elsewhere. They are not related to sex or age as classically believed. One morph is characterized by its emerald green tail and the other by its dark brown colour with more or less visible golden stripes on the back. Some specimens can sometimes be nearly completely melanistic.

Figures 244: The most useful character for easy recognition of *E. caeruleocauda* is the presence of a typical axilla black or darker spot. This trait has not been noted previously but it is really useful for identification in the field as in museum.

beach margins where densities can be high. It is an active and agile lizard, which does not hesitate to enter saltwater puddles at low tide to escape from predators. It can easily stay submerged for several minutes. It is active even in the wave-washed areas where it can maintain itself firmly on rocks with its strongly clawed fingers. It feeds in inter-tidal areas. In 1980, McCoy noted that two eggs are deposited on beach litter, under floating driftwood logs or in limestone rock cavities.

E. atrocostata freycineti was reported from several Torres islands, Aore, Malo, Espiritu Santo, Pentecost, Malakula, and Efate. Specimens from Santo were reported by Medway and Marshall in their general distribution table but later in their paper they noted that this report refers to Malo — a small peripheral island of Santo, and not to Santo itself; these authors however mention an observed specimen not collected by Medway on the reefs of Hog Harbour, Santo. One specimen from Santo is also deposited in the Australian Museum.

Figure 245: Like *E. impar*, *E. caeruleocauda* lack the black parietal spot of *E. cyanura* located at the posterior part of the frontoparietal head plate (see arrow).

SQUAMATA, SCINCIDAE
Emoia caeruleocauda

The skink *Emoia caeruleocauda* belongs to the *E. cyanura* group, and *E. caeruleocauda* subgroup. It was long confused with *Emoia cyanura sensu lato* (see below). Parker in 1925 was the first to provide clear characters to distinguish between them, mostly based on lamellae appearance and number. He called both the Vanuatu species respectively *Lygosoma* (*Emoa*) *cyanurum* and *Lygosoma* (*Emoa*) *lessoni*. The first taxon comprises the actual *Emoia cyanura* and *E. impar* and the second corresponds to *E. caeruleocauda*. Several wrong names were attributed to the Vanuatu populations of that species: *Lygosoma kordoanum* by Baker, *Emoia werneri* by Burt and Burt in 1932, Baker in 1947, Tanner in 1952, and Medway and Marshall in 1975, *Lygosoma* (*Emoa*) *Werneri* by Angel in 1935, *Emoia caeruleocauda* (= *E. werneri*) by Cranbrook and Pickering in 1981, *E.* [*moia*] *werneri* by Cranbrook in 1985, and finally *Emoia caerulocauda* [sic] by Goldberg and coauthors in 2005.

E. caeruleocauda, as presently defined, is widely distributed, although it certainly consists of a species complex. Its type locality is located on Sudest Island (formerly Tagula Island) in the Louisiade Archipelago, Papua New Guinea, but unfortunately its holotype is lost. The species is reported from the Mariannas, Carolines, Marshall, Palau, Fiji, Vanuatu, Solomon, Bismarck Archipelago, New Guinea, Moluccas, Sulawesi, northern Borneo and southern Philippines. Brown in 1991 and Zug in 1991 are certainly wrong when they state that the Fijian populations were recently introduced by man; I found them often in deep primary forest on Santo as well as on Fiji.

E. caeruleocauda is a terrestrial species even though some individuals can be seen on tree trunks or bushes, generally no more than one or two meters above ground. In Vanuatu, like on the Solomon

Islands and New Guinea, the species occurs in gardens, open areas and in deep forest; it is however most frequent in forested areas. In Papua New Guinea that skink is present from sea level to almost 1 500 m elevation but I did not observe it above 700 m on Santo.

E. caeruleocauda occurs as two colour morphs over most of its distribution: one emerald green tailed form and one completely dark brown form sometimes with one to three more or less visible golden dorsal back stripes. That later morph can easily be confused with *Emoia cyanura*. They differ however by toe lamellae and other scale counts. One practical way to distinguish between them in the field is the occurrence of a dark blackish axilla spot in *E. caeruleocauda* but absent in *E. cyanura* and other Vanuatu *Emoia* species. That useful character was never used before our study but it is really helpful and reliable. Anyway there is no relationship between colour pattern and sex in that species, contrary to what has often been stated in the past.

Gravid females usually bear two eggs. Eggs are deposited in soil debris and vegetation. In Vanuatu, reproduction is continuous all year round with a peak from November to February and a slower period from May to June. I suspect that rainfall rather than day length is the factor that causes the observed variations. Curiously Baker in his 1947 work does not report the occurrence of totally dark brown specimens and it is not clear under which binomen he considered them (*E. caeruleocauda* or *E. cyanura sensu lato*?).

Photo I. Ineich

Figure 246: *E. cyanogaster* is a slender species with an elongate body and tail. Such characteristics allow this lizard to move easily on small branches of shrubs and short trees, even on large leaves.

Photo I. Ineich

Figure 247: *E. cyanogaster* is typical by the strong dark/light colour contrast between the back and the light yellow belly. Four medio-dorsal scale rows are clearly enlarged.

Photo I. Ineich

Figure 248: *E. cyanogaster* has a typical uniform yellow light greenish belly.

In Vanuatu, *E. caeruleocauda* occurs throughout the entire archipelago: Banks and Torres groups, Santo, Malo, Aore, Pentecost (formerly sometimes called Raga), Malakula, Ambrym, Tongoa, Efate, Erromango, Aniwa, Tanna, Futuna, and Anatom. The occurrence of that species on Santo was reported by Baker in 1947, Medway and Marshall in 1975 and Brown in 1991. Specimens of that species from Santo are conserved in AMNH, AMS, BMNH, and MNHN.

Snout-vent length of adults range from 39-52 mm. Tail length varies from 147-178 % of SVL but is generally about 160 %. Prefrontals are well separated in all specimens. About 40 % (n = 47) of our Santo sample had skin parasites (mites). The frequency of the brown morph compared to the emerald green tailed morph on Santo is about 50 % (n = 47); both morphs include males and females as well as adults and juveniles. Midbody scale rows vary from 31 to 38 and fourth toe lamellae from 31 to 41.

SQUAMATA, SCINCIDAE
Emoia cyanogaster

The skink *Emoia cyanogaster* belongs to the *Emoia cyanogaster* group containing five species distributed across the Moluccas, New Guinea, Bismarck Archipelago, Solomon and Vanuatu. *E. cyanogaster* occurs in the Bismarck Archipelago, Solomon (including Santa Cruz and Reefs Islands) and Vanuatu. The species is absent from Fiji, like *E. atrocostata* and both absences certainly have an important zoogeographical significance.

In 1975, Medway and Marshall reported the species from seral and climax forest to elevations of about 500 m; it is absent from forest at 1 100 m elevation in Vanuatu. The species also occurs in gardens and other degraded areas with introduced vegetation. It is an arboreal species mostly restricted to small trees and bushes. It searches for its food at ground level as well as in trees but does not occur in deep forest. It seems to need more open and sunny areas.

I carefully examined two specimens from Malakula deposited in the MNHN and report below their respective morphological and scalation characters: snout-vent length 65 and 64 mm; tail length 131 and 156 mm; midbody scale rows 24 and 24; scale lines on mid back 55 and 56; fourth toe lamellae 79 and 78. Both show separated supranasals, separated prefrontals, parietal and nucal plates with a contact oriented left, single interparietal (epiphysal spot visible) and single frontoparietal. They have eight supralabials with the 6th enlarged and under eye, infralabials 5-6.

In the same way I observed MNHN 1934.0088: snout-vent length 70 mm, tail length 166 mm, midbody scale rows 24, scale lines on middle back 56, fourth toe lamellae 78, supralabials right/left 8(6)/8(6), infralabials 6/6, small interparietal with a small epiphyseal spot, parietal and nucal suture oriented left, supranasal well separated, prefrontals in left contact, supralabial under eye very large and clearly different in size compared to that of *E. sanfordi* and *E. nigra*, toe lamellae numerous and bladelike, mediodorsal scales enlarged (mostly the four median rows), irregular rows of dorso-lateral white spots, dark brown band from nostrils to midbody which disaperared progressively posteriorly.

Females lay two eggs that are deposited in loose soil, litter or rotting vegetation.

E. cyanogaster was reported from Vanuatu by McCoy in 1980 and Brown in 1991. The species is present on the following islands or island groups: Torres and Banks, Espiritu Santo, Malo, Aore, Aoba, Pentecost, Ambrym, Malakula, Epi, Efate, Erromango, Tanna. The occurrence of the species on Santo was reported by Medway and Marshall in 1975, and by Brown in 1991. Specimens from Santo are conserved in the following museums: AMS, BMNH, FMNH, and MNHN.

SQUAMATA, SCINCIDAE

Emoia cyanura or *Emoia impar* without precision

Most species of the *E. cyanura* species complex are difficult to distinguish and all together were until recently considered under the unique binomen *E. cyanura*. This is also true for all species records from Vanuatu prior to 1990. Some species of the complex still remain to be described and several of the available older names need to be revalidated. Three morphotypes can be clearly recognized in the complex, blue tailed and brown-greenish tailed striped specimens, but also melanistic specimens that are almost completely dark brown. All of those morphotypes comprise several distinct species. The names that should be applied to those different species

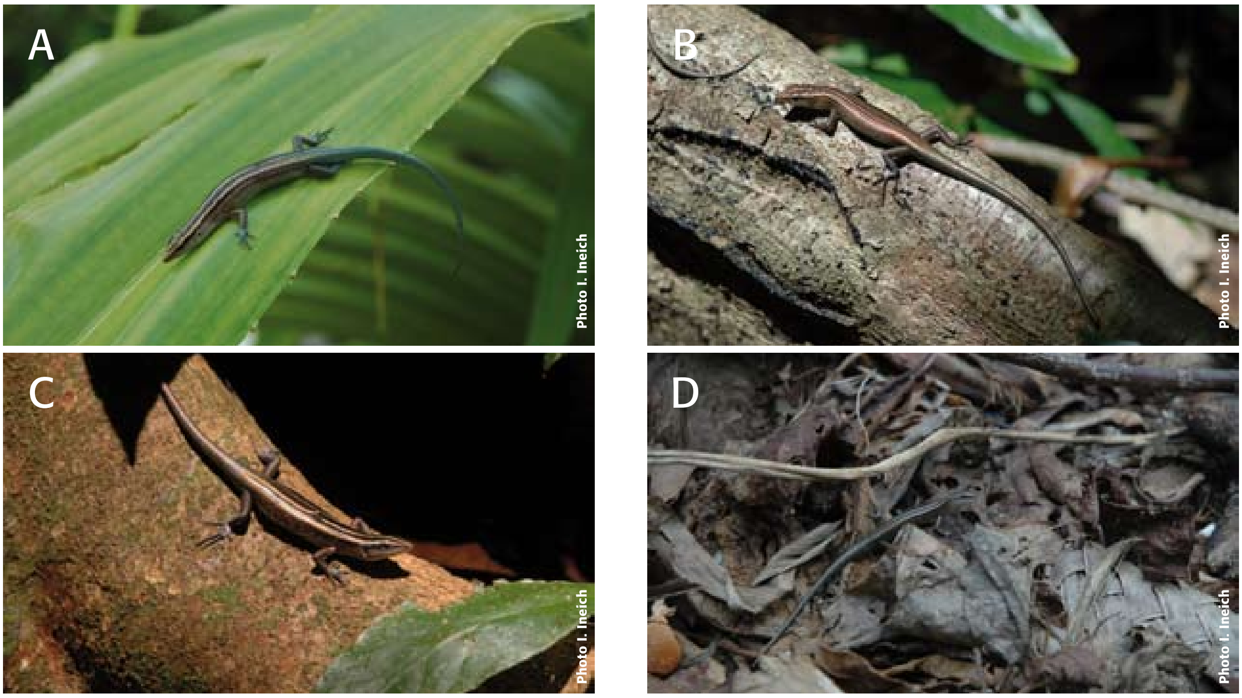

Figure 249: *E. cyanura* (all four pictures) has a variable tail colour but never shiny blue like that of *E. impar*. Both species share a similar size and habitat, but numerous other characters allow them to be distinguished.

are not clearly defined and numerous doubts still exist. The current attribution of names to most populations is not acceptable. Eastern brown tailed populations were generally referred to *Emoia cyanura* or *E. pheonura* and blue tailed specimens from the same area to *Emoia impar* or *E. cyanura*. The name *E. impar* should certainly be applied and restricted to western populations of the Bismarck Archipelago area, but this has still to be demonstrated through molecular studies. In the same way the name *E. cyanura* should be restricted to eastern Polynesian blue tailed populations (nowadays erroneously called *E. impar*), in accordance with the original description of that taxon by R.P. Lesson in 1826. The main problem is how to name the Polynesian brown tailed populations. Their valid name is either *E. arundeli*, *E. arundeli pheonura* or *E. pheonura*, but in no way *E. cyanura* as currently used. Valid names will be defined according to the fact that:

- Clipperton Atoll populations will be considered as belonging to a monotypic species identical to eastern Polynesian populations (thus *E. arundeli* will be valid for all eastern Pacific populations);
- Clipperton Atoll populations will be considered different at specific level from eastern Polynesian species (*E. arundeli* and *E. pheonura* will both be valid and distinct at specific level);
- Clipperton Atoll populations will be considered as belonging to a polytypic species (*E. arundeli arundeli* for Clipperton populations and *E. arundeli pheonura* for eastern Polynesian populations).

Beside these nomenclature problems, several other populations still have to be named, probably as new taxa: e.g. the southern Bougainville blue tailed populations, and some Vanuatu blue tailed populations. Anyway I here still consider only two distinct morphotypes from Vanuatu from what was previously called *E. cyanura*, the brown tailed morph that I will (provisionally) call *E. cyanura* and the blue tailed morph that I will (provisionally) call *E. impar*.

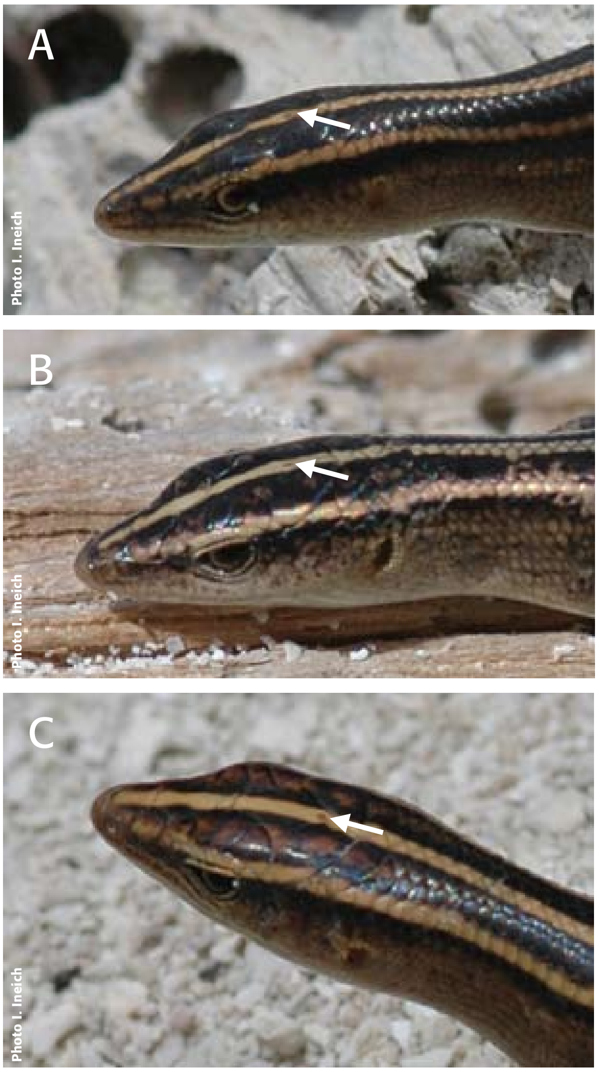

Figure 250: *E. cyanura* can easily be distinguished from *E. impar* and *E. caeruleocauda* by its dark simple or double parietal spot (black or bluish grey) which is always present.

E. cyanura and *E. impar* belong to the *Emoia cyanura* group and the *E. cyanura* subgroup as defined by Brown in 1991. This author considered *E. cyanura* as a superspecies but was wrong in not accepting the recognition of both morphs (blue tailed and brown-greenish tailed morphs) as distinct species. In 1986, Brygoo designated MNHN 7069A as the lectotype of *E. cyanura* but that decision cannot be accepted since the type series, having originated from Tahiti (French Polynesia), does not include blue tailed morph specimens such as the one illustrated on Lesson's original iconotype plate published in 1826, but only brown tailed morph specimens and some specimens of *E. caeruleocauda*, a species not occurring in French Polynesia (see above). Thus in 1987 Ineich recommended considering that type series as invalid and the syntypes of *E. cyanura* as having been lost (or mixed with other specimens in MNHN collections). That position was not followed by Ineich and Zug in 1991 but should be recommended now. In 1947, Baker did not distinguish *E. cyanura sensu stricto* from *E. impar* but however noted about *E. cyanura sensu lato*: "*The tail is dull olive green during life. In preserved specimens its colour sometimes changes to a blue resembling that of* E. werneri *[actually E. caeruleocauda]. It is unfortunate that the name cyanura (sic) should refer to a species in which the tail is in life so far from*

Table 25: Frequency variation of gravid adult females for both *Emoia* species of French Polynesia.

	October-December	January-March	June-August
Emoia cyanura s.s.	60.87 % (n = 92)	38.74 % (n = 111)	21.54 % (n = 130)
Emoia impar	56.72 % (n = 134)	64.44 % (n = 135)	31.25 % (n = 80)

Figure 251: *E. impar* is characterized by a shiny sky blue tail. Contrary to most eastern Polynesian populations, melanistic specimens are not present in Vanuatu.

Figure 252: Both *E. impar* (right) and *E. caeruleocauda* (left) have shiny blue tails. *E. impar* does not display the middorsal fusion of dorsolateral dark stripes into a Y shape on the middle of tail base seen in *E. caeruleocauda* (left).

Figure 253: Both *E. caeruleocauda* and *E. impar* (this picture) lack a dark parietal spot typical of *E. cyanura*.

glossy blue". His remark clearly applied to the species that I here erroneously call *E. cyanura* (brown tailed morph) since actual *E. impar* has a distinct shiny blue tail in accordance with the specific epithet *cyanura*.

E. cyanura sensu lato occupies the whole of the tropical Pacific from the Admiralty Islands, Bismarck Archipelago, Solomon and Vanuatu, Micronesia to the whole of Polynesia, including Hawaii and Clipperton Atoll in the eastern Pacific. *E. cyanura sensu lato* was reported from the Santa Cruz Islands (southern Solomon): Vanikolo, Lomlom, Tikopia and Matema by Roux in 1913, by Burt and Burt in 1932, and by Brown in 1991. This species group was also reported from Vanuatu by Brown in 1991. *E. cyanura sensu lato* was reported from the Torres and Banks groups, Santo, Malo, Aore, Aoba, Pentecost, Malakula, Ambrym, Tongoa, Efate, Emao (off Efate), Erromango, Aniwa, Tanna, Futuna, and Anatom. The occurrence of *E. cyanura s.l.* on Santo was reported by Roux in 1913 (as "Spiritu Santo"), Medway and Marshall in 1975, Burt and Burt in 1932, and Brown in 1991. Specimens of *E. cyanura s.l.* (registered as "*E. cyanura*") from Santo are located in the following museums: AMNH, AMS, BMNH, FMNH, MCZ, and NMBA.

Figure 254: *E. impar* is also distinguished by middorsal scale fusions. Scale fusions can involve one scale but more often several scales and can be repeated on the back separated by double scale rows. Such fusions are often present in *E. impar* but never in *E. cyanura*.

Species from that group are terrestrial and always found in relatively high densities. Syntopy between species is common and on Santo all three species, *E. cyanura sensu stricto*, *E. impar* and *E. caeruleocauda*, can be found together. However, their ecology is clearly distinct concerning microhabitat requirements. Baker in 1947 studied the reproduction of *E. cyanura sensu lato* on Santo (collections made during 1933-34) but does not distinguish *E. cyanura sensu stricto* from *E. impar*. He noted the occurrence of one unique egg in each oviduct. Despite the relative constancy of climate in the study area, he noted a reproduction peak in November-December (60% of adult females were gravid) and a clear decrease in May-June (only 15%). Unfortunately his data are not reliable since they mix both of the actually recognized species, *E. cyanura sensu stricto* and *E. impar*. Seasonal variations in the proportion of gravid females seems however constant throughout the distribution range of both species. In French Polynesia, I also observed a clear reproduction peak in November-December and a clear decrease during the austral winter with clear differences between both species. *E. impar* demonstrates a maximum during the full rainy season whereas *E. cyanura s.s.* shows a maximum just before (Table 25).

SQUAMATA, SCINCIDAE
Emoia cyanura [*sensu stricto*]

Specimens referred with confidence to *E. cyanura* from Vanuatu without more precise location are conserved in several museums (AMS, FMNH, MNHN). *E. cyanura s.s.* occurs at the following localities in Vanuatu: Torres and Banks groups, Santo, Malo, Aoba, Pentecost, Malakula, Ambrym, Epi, Tongoa, Efate, Emao (off Efate), Erromango, Tanna, Futuna, and Anatom. Specimens from Santo were deposited at AMS, AIM, BMNH, FMNH, MNHN, and UMMZ.

Adult specimens from Santo have a snout-vent (SVL) length of 45 to 54 mm with a tail of about 150% to 170% of SVL. The number of scale rows at midbody varies from 27 to 30 but is most often 28.

SQUAMATA, SCINCIDAE
Emoia erronan

The skink *Emoia erronan* belongs to the *Emoia concolor* subgroup of the *Emoia samoensis* group. It is often mixed with the latter binomen in collections. It is only known from Futuna Island, southern Vanuatu, an island formerly called Erronan. It can be readily distinguished from the other species of the *E. concolor* subgroup (except with *E. aneityumensis*) by its number of middorsal scale lines from the frontoparietal to the base of the tail (77 to 84). It can then be distinguished from *E. aneityumensis* by its number of fourth toe subdigital lamellae (36 to 42 in *E. aneityumensis* vs 47 to 53 in *E. erronan*). The species is endemic to the southern Vanuatu island of Futuna and has never been reported from other islands. No information is available on the habitat and reproduction of this species. Specimens are present in the following museums: AMNH and FMNH.

SQUAMATA, SCINCIDAE
Emoia impar

Bruna and co-authors in 1996 considered the blue tailed *E. impar* as originating in Vanuatu or a neighbouring area. I rather suggest the blue tailed *E. impar* clade to have originated in the Bismarck Archipelago area (Papua New Guinea). A recent molecular study by the aforementioned authors has shown that Vanuatu *E. impar* populations present a 13% genetic divergence in their mitochondrial DNA haplotype compared to those from Cook, Tahiti, Fiji, Arno and Kosrae in Micronesia. *E. cyanura* populations from Vanuatu only present less than 0.25% genetic divergence with regard to Hawaiian, Takapoto (Tuamotu, French Polynesia), Cook, Fiji and Clipperton Atoll (melanistic form) populations. Thus blue tailed populations from Vanuatu (at least some, i.e. the ones studied by them) should belong to an undescribed blue tailed taxon distinct from the eastern Polynesian one.

Figure 255: *E. nigra* is a semi-arboreal species that most often forages at ground level. Torres Islands.

Figure 256: Most adult Vanuatuan *E. nigra* are dark black with reddish eyes. Torres Islands.

E. impar was reported from the following islands of Vanuatu: Aore, Tatuba, Malo, Santo, Aoba, Pentecost, Wala (off Malakula), Malakula, Ambrym, Epi, Tongoa, Efate, and Tanna but I collected it recently in northern Vanuatu (Torres Islands) where it is sometimes common. Specimens of *E. impar* from Santo are present in the following museums: AMS, AIM (Auckland), FMNH, and MNHN.

Adult specimens of *E. impar* from Santo have a snout-vent length (SVL) of 41 to 50 mm with a tail of about 145% to 169% of SVL; they are on average smaller than *E. cyanura*. The number of scale rows at midbody varies from 27 to 31 and is usually above 28. Specimens without at least one fused medio dorsal scale row are very scarce (about 5%; n = 137) on Santo whereas the absence of such fusion concerns about 12% (n = 1266) of specimens in French Polynesia.

SQUAMATA, SCINCIDAE
Emoia nigra

E. nigra belongs to the *E. samoensis* group whose distribution extends from the Bismarck Archipelago to Solomon, Vanuatu, Loyalty, Fiji, Samoa, Tonga and Cook. That skink group comprises numerous species, almost all endemic to single islands or small island groups.

Emoia nigra has a small interparietal plate located just below the posterior edge of the frontoparietal. That interparietal shows a clear tendency to disappear and its anterior border is often linear and not V shaped as in most *Emoia* species. The parietal spot is distinct. The tail is transversally flattened. Adult males and females often present a dark to black throat whose function is unknown. Anterior and posterior loreals are generally of same size and shape. The tympanum is enlarged. Supranasals are sometimes nearly in contact but generally largely separated. Prefrontals are narrowly to moderately separate. Subdigital lamellae are broad and rounded. Snout-vent length of adult males and females (no observed dimorphism) varies from 103-116 mm and the tail is about 164-196% of SVL. Fourth toe lamellae vary from 33-36 and midbody scale rows from 35-44.

E. nigra is distributed on southern Pacific islands from Samoa to Tonga and west to Fiji, Vanuatu, Solomon and the Bismarck Archipelago (uncommon). *E. nigra* was reported from the Santa Cruz group, southern Solomon by Roux in 1913 and by Brown in 1991 from several localities. *E. nigra* was reported from Vanuatu by Burt and Burt in 1932, McCoy in 1980, and Cranbrook and Pickering in 1981. It was reported from the following islands of Vanuatu: Torres and Banks groups, Santo, Malo, Aore, Aoba, Maewo, Pentecost, Efate. Specimens from Santo were reported by Burt and Burt in 1932, Medway and Marshall in 1975, and Brown in 1991. Specimens from Santo are conserved in the following museums: AMNH, AMS, BMNH, FMNH, and MNHN.

On Santo this species clearly occupies open habitats, even if forested, but does not occur in deep dark forest like e.g. *Emoia nigromarginata*. It sleeps under stones and trunks at night, not on tree branches like some other similar large sized *Emoia* (*E. concolor*, *E. trossula*, *E. sanfordi*…). Such sleeping behaviour can explain the disappearance of *E. nigra* when mongoose or pigs are introduced. Competition between *E. nigra* and other large species of the *E. samoensis* group during daytime could have given rise to habitat separation: with *E. nigra* on the ground vs other *E. samoensis* species inhabiting tree trunks and branches. A similar kind of competition could occur during the night for shelter: branch forks for other *E. samoensis* group species vs soil level under logs and stones for *E. nigra*. Some *Emoia sanfordi* specimens are nearly totally black or at least greyish black and thus can be mistaken for E. nigra. They can however be easily distinguished since *E. sanfordi* prefrontals are in narrow to broad contact vs being separated in *E. nigra*, the last supralabial is dorso-ventrally entire and unique in *E. sanfordi* vs separated in *E. nigra*, finger and toe lamellae are broad and rounded in *E. nigra* vs thin and bladelike in *E. sanfordi*, and finally the interparietal plate is small in *E. nigra* vs larger in *E. sanfordi*. Juvenile *E. nigra* are also characteristic, as their ventral tail is whitish with a typical fine median black line. Juvenile *E. nigra* have generally strong keels, a dark brown back and black flanks. Medio dorsal scales are larger than those on the flanks (about twice the size) on 8-10 rows.

Figure 257: *E. nigromarginata* is an endemic species from Central and Southern Vanuatu. Tasmate, Santo.

Figure 258: *E. nigromarginata* is a semi-arboreal forest species living on small tree trunks and lower vegetation. It searches for shifting sunny patches where it can thermoregulate. Butmas, Santo.

Eggs of *E. nigra* were found on Santo under stones and under logs, including six eggs under the same stone, which certainly corresponds to two clutches, thus attesting to communal egg laying in that species. Mean egg size for 10 eggs was 15.1 +/- 0.6 mm x 10.3 +/- 0.2 mm (range 14.6-16.3 x 9.9-10.6). However egg size varies considerably for skinks according to the development state of the embryo: one additional egg measured 18.5 x 13.0 and it certainly corresponds to an egg ready to hatch. One of our collected females was gravid with three eggs

Figure 259: *E. sanfordi* is a beautiful Vanuatu endemic arboreal skink.


Figure 260: Complete green morph of *E. sanfordi*.


Figure 261: Black headed green morph of *E. sanfordi*. Torres Islands.


Figure 262: Black headed green morph of *E. sanfordi*. Santo.


Figure 263: Grey headed morph of *E. sanfordi*. Santo.


Figure 264: Marbled morph of *E. sanfordi*. Santo.


Figure 265: Marbled morph of *E. sanfordi*. Santo.


Figure 266: Uniform grey morph of *E. sanfordi*. Santo.


Figure 267: Uniform grey morph of *E. sanfordi* with greenish dots.

in the genital tract (20.5 x 11.1, 18.9 x 12.1, and 21.2 x 11.5 mm). One egg hatched in Paris yelding a juvenile with a snout-vent length of 29 mm and a tail of 53 mm. I have observed an adult *Candoia bibroni* eating a large adult of that lizard in the field after both were placed in the same bag.

SQUAMATA, SCINCIDAE
Emoia nigromarginata

After comparison of the holotypes of *E. nigromarginata* and *E. speiseri* and an examination of a complementary series of 30 specimens, Brown in 1991 showed that the midbody scale count and coloration differences on which Roux had based the separation of both species in 1913 correspond to the extremes of a continuous variation within the same species. He placed *E. speiseri* in the synonymy of *E. nigromarginata* since the description of the later species is situated on page 154 whereas that of *E. speiseri* is on page 155 in the same publication. It has been proposed that *E. parkeri* (endemic to Fiji) could be a sister species of *E. nigromarginata*, thus implying faunal exchanges between Vanuatu and Fiji. This hypothesis has of course to be demonstrated with modern molecular technics before it can be given any credit. I have observed important colour differences between west coast (Tasmate) and central Santo (Butmas) populations (see pictures).

E. nigromarginata is a medium-sized species (adult snout-vent length varies from about 50-80 mm). It is a forest species that never frequents open habitats. It is endemic to Vanuatu. Cranbrook in 1985 noted that the species was not found again during the important collections made in Vanuatu in 1971. It was reported from Vanuatu from the following islands: Santo, Pentecost, Malakula, Ambrym, Epi, Efate, and Anatom. In 1975, Medway and Marshall considered that the species could be present on Erromango and Tanna; this has not been assessed since that time but seems realistic to us. Only few specimens from Santo (reported by Brown in 1991) are deposited in museums: FMNH, and additional specimens from the Santo 2006 expedition in MNHN.

SQUAMATA, SCINCIDAE
Emoia sanfordi

Before its description, specimens of *Emoia sanfordi* from Vanuatu were refered to *Emoia samoense* by Roux in 1913, Baker in 1928, and Angel in 1935. *E. sanfordi* was described based on specimens from Vanuatu (including Banks Islands) and two specimens from the Solomon Islands (Fauro Island) of doubtful origin.

In 1974, Medway noted: "E. samoensis*, on the other hand, has been found in the New Hebrides only on Erromanga [Erromango], some 180 km north-northwest of Aneityum [Anatom] and the next large island but one. The specimens (BM 1860.3.18.8 & 1860.3.18.11) were collected more than a century ago by Mr Cuming (Boulenger, 1887). In 1971 we did not find the species, but our stay on Erromanga was brief and collecting not intensive; there are no grounds to doubt the record. The third of Cuming's specimens allocated to this species by Boulenger (BM 1860.3.18.12) is in fact* E. sanfordi*, an identification which confirms at least that the collection derived from the New Hebrides. … All New Hebrides specimens identified by Roux (1913: 155) as* Lygosoma *(*Emoa*)* samoense*, a synonym of* E. samoensis*, prove to be* E. sanfordi *and thus provide a fallacious basis for comparison. …* E. samoensis *and* E. aneityumensis *may replace each other ecologically on their respective islands in the New Hebrides, but there are no grounds for treating the two taxa as geographical races of one species*". In 1975 Medway and Marshall stated that *E. sanfordi* was not distinguished from *E. samoensis* in the previous publications of Boulenger (1887), Roux (1913) and Angel (1935). Specimens attributed to *E. samoensis* by those authors were re-examined by Medway and Marshall in 1975 and with only two exceptions all correspond to *E. sanfordi*. The two specimens they refer to as *E. samoensis*, among which one is from the same locality as *E. sanfordi*, are of uncertain location (Erromango). The species was not found again by Medway on Erromango in 1971, but his sojourn was short and collections done in low elevation areas only. In 1981, Cranbrook and Pickering noted about *E. sanfordi*: "*Doubfully recorded from the island of Fauro in the western Solomons*". They also mention both specimens of *Emoia samoensis* collected on Erromango in 1860.

Figure 268: *E. sanfordi* often shows a typical lighter eye border.

Figure 269: Dark museum specimens of *E. sanfordi* can be distinguished from *E. nigra* by their typical blade like toe and finger lamellae (vs rounded in *E. nigra*).

The specimen BMNH 1860.3.18.12 was later determined as *E. concolor* by W.C. Brown in 1983 in the British Museum catalogues, and its collecting locality questioned. Both of the other problematic Cuming specimens from Erromango were regarded as *E. samoensis* by Lord Medway in 1972, and later as *Emoia trossula* by Brown and Gibbons during their description of that species. The collection locality of both lizards is highly uncertain, thus excluding them from the type series of *E. trossula* during its description. The University of Hamburg (Germany) specimen R01974 from Ovalau (Fiji) was identified as *E. sanfordi* by W.C. Brown in 1983 regarding *E. sanfordi* from Vanuatu. That specimen was different from other Fijian species and Brown supposed its location to be a mistake.

In his 1991 revision of the genus *Emoia*, Brown restricted the distribution of *E. samoensis* to Samoa and that of *E. sanfordi* to Vanuatu (including Banks in the north), with a doubtful record for Solomon, but he did not examine the important specimens mentioned above. The Genova Museum in Italy (Museo Civico di Storia Naturale) possesses one or more paratypes of *E. sanfordi* according to their catalogues.

E. sanfordi is large with a maximal snout-vent length of about 115 mm and a tail about two times snout-vent

Figure 270: *L. noctua* is a small terrestrial skink that often lives in leaf litter and dead fallen tree trunks. It can climb on tree trunks but seldom above one or two meters above ground. Santo.

Figure 271: *L. noctua* is the only viviparous lizard of Vanuatu. Its black and white barred lips are unique among Vanuatuan skinks. Santo.

Figure 272: Like some other skinks, *L. noctua* can change its ground colour from light to dark. It is also found in the detritus in the axila of *Pandanus* leaves. Torres Islands.

Figure 273: Another unique trait of *L. noctua* is the yellow to white head spot borded by black located at the anterior end of the light middorsal stripe. Santo.

length; midbody scale rows 30-32, fourth toe lamellae 62-72; always five supralabials in front of the subocular; interparietal always present; parietal suture and nuchal suture oriented left. All examined specimens show a high uniformity for scalation characteristics but not for coloration going from uniform green to almost completely and nearly uniform greyish. When few black marks are present they are restricted to the head area and to some parts of the back and flanks, with black punctuations only concerning some scales. Prefrontals are always in wide contact. Anterior and posterior loreals are identical, flat and elongate but the anterior is higher; supranasals are largely separated and prefrontals fused. Juveniles are sometimes uniform green or uniform dark brown to almost black. The throat is sometimes more or less marbled. Differences between *E. nigra* and *E. sanfordi* can be seen above (see *E. nigra*). I can add that the tail is rather circular or subcircular in section in *E. sanfordi* whereas it is rather laterally flattened in *E. nigra*. During my trip to Santo I observed that uniform grey specimens were usually associated with deeper and dense forest.

In 1975, Medway and Marshall noted that: "*Of large* Emoia, E. sanfordi *is recorded from every island visited except Tanna; the species* E. samoensis, E. aneityumensis *and* E. nigra *occur with* sanfordi, *but never with each other on any island. It is notable that among each pair, one species has a high count of subdigital lamellae and the other low. This feature is possibly a scansorial adaptation. Certainly* E. sanfordi *is highly arboreal in habit*." On Santo *E. sanfordi* occurs as several clearly distinct colour morphs that are certainly related to habitat characteristics: a complete green morph, a green body with black top of head morph, a marbled body morph, a complete grey headed green morph and a totally uniform grey body morph.

This species, a Vanuatuan endemic, was reported from Banks (Vanua Lava, Santa Maria), Santo, Aore, Malo, Aoba, Pentecost, Malakula, Ambrym, Epi, Tongoa, Efate, Erromango, and Anatom. In 1975, Medway and Marshall recognized that *E. sanfordi* could occur on Tanna where they only briefly sampled. I collected it recently on the Torres Islands. Collections from Santo were reported by Medway and Marshall in 1975, and by Brown in 1991. Specimens from Santo are deposited at AMS, BMNH, FMNH, and MNHN. Note that recent molecular investigations showed that the true *E. sanfordi* does not exist south of Efate, an area occupied by other cryptic species.

E. sanfordi is the most widespread endemic species in Vanuatu. Such a distribution probably relates to the age of this skink species. The diversified colour polymorphism observed on Santo was not seen on the Torres Islands.


Photo B. Fontaine

Figure 274: *Ramphotyphlops braminus* is often called the flower pot snake. It was easily accidentally introduced, probably with soil, on most tropical and subtropical Pacific islands. It is also called the two headed snake since tail and head are similar in shape. The tail, however, ends in a spine that does not inject venom. This snake is completely harmless. Santo.


Photo B. Fontaine

Figure 275: *R. braminus* feeds on ants and termite eggs and larvae. Populations are composed only of females since the species reproduces by producing clones through parthenogenesis. Santo.

SQUAMATA, SCINCIDAE
Lipinia noctua

The genus *Lipinia* belongs to the *Sphenomorphus* group of lygosomine skinks and comprises 21 species. It has two main radiation centers, the Philippines (eight species) and New Guinea (seven species). In 1975, Medway and Marshall noted that the species is rare and secretive in Vanuatu. I can add that this is the case throughout its distribution range and in Vanuatu it is as abundant as in other places. *L. noctua* occupies most of the area where the genus is distributed; it can be found from the Papuasian area to Oceania, including Hawaii and Pitcairn, but the species is not present on Easter Island. It is also absent from Clipperton Atoll, thus showing clearly reduced colonisation abilities compared to other similar sized skinks (e.g. *Emoia cyanura* and *E. impar*); such characteristics certainly have to be associated with its partly fossorial habits. Its type locality is located on Kosrae Island, State of Kosrae, Federated States of Micronesia. Classically the genus was considered as having a Papuasian origin but molecular studies conducted by Austin and published in 1998 have shown that its origin is instead located on the Asian mainland or on the Philippines.

L. noctua was reported in Vanuatu from Santo, Malo, Aore, Pentecost, Malakula, Ambrym, Epi, Efate, Tanna, and Anatom. *L. noctua* also occurs north of the archipelago since I collected it recently on most of the Torres islands, so it is widespread on the whole archipelago. The species was reported from Santo by Medway and Marshall in 1975. Specimens from Santo are conserved in the following museums: AMS, BMNH, MNHN, and UMMZ.

••• Reptiles from Vanuatu – SNAKES (Typhlopidae)

SQUAMATA, TYPHLOPIDAE
Ramphotyphlops braminus

Fossil remains recovered from presumably prehuman levels in the Marianas (Micronesia) suggest that this species occurs naturally there. *R. braminus* was first reported from Vanuatu on Efate by Medway and Marshall in 1975 and later by Cranbrook and Pickering in 1981. The first specimens were collected in the gardens of White House, British Paddock, Independance Park, Port Vila and in plantations in the Agricultural College of Tagabe on Efate. According to Medway and Marshall, on Efate the species seems only to occupy cultivated areas highly modified by man. The Australian Museum collections also possess a specimen from Efate collected by I.W.B. Thornton in 1976.

The species was until now reported from Vanuatu only from both main islands, Santo and Efate, and more recently from Ambrym. I collected it recently (November 2007) in the very far north of the archipelago, on Toga Island (Torres Group), thus clearly indicating that the snake has largely expanded its distribution range in Vanuatu. On that island I also collected *Gehyra mutilata*, another recently introduced gecko (see above). The species arrived in Vanuatu probably shortly after 1970 but it seemed to be absent in 1971 during the Percy Sladen Expedition. Specimens from Santo are conserved in several natural history museums: AMS, MHNG and MNHN. The oldest record known for Santo was collected at Luganville by A. de Chambrier between 9 and 26 June 1979.

Figure 276: *C. bibroni* is the most arboreal species of its genus. Its prehensile tail allows it to climb high in trees and to hang by only its tail, when necessary, e.g. to explore bird nests. Torres Islands.

Figure 277: The typical snout shape (flattened rostrum) of *C. bibroni* explains its common name of the shovel nosed snake. Santo.

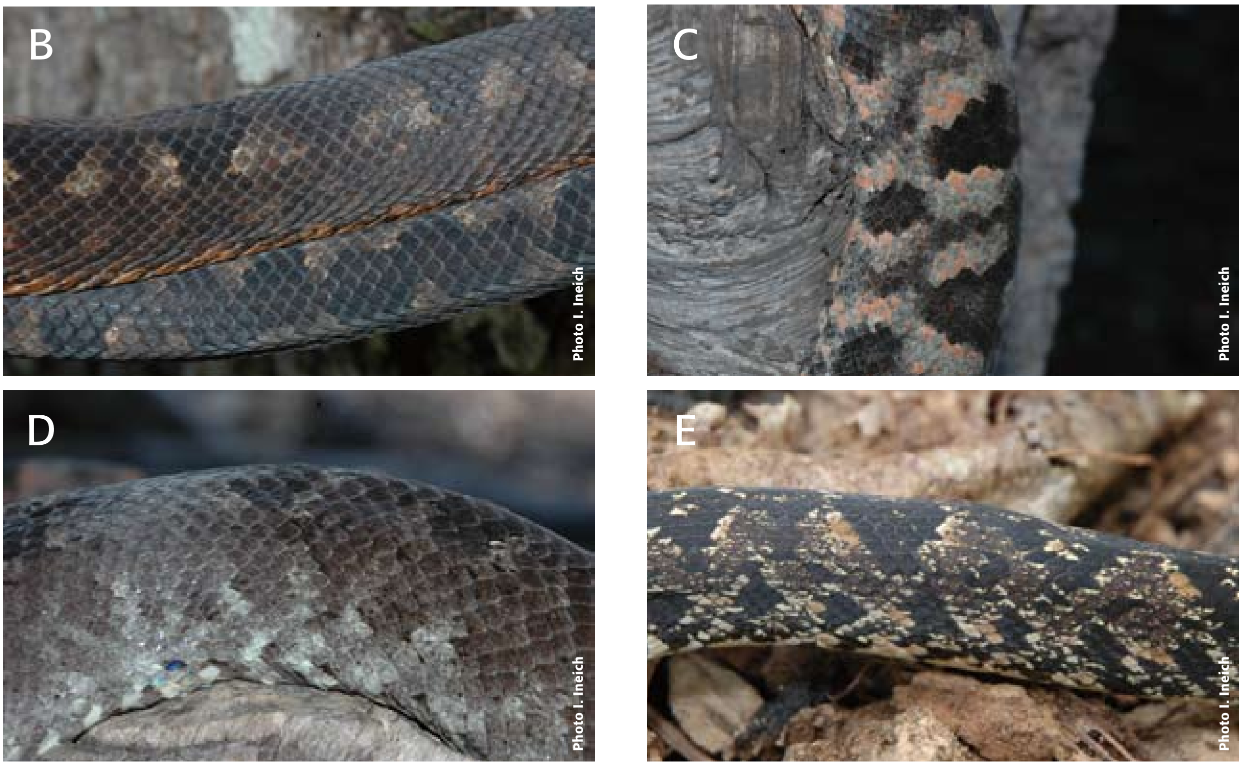

Figure 278: Dorsal colour polymorphism is considerable in *C. bibroni*, varying from red to grey or even nearly black. Santo and Torres Islands.

Some specimens can have a light electric grey blue colouration and they can thus be confused and considered as belonging to another species. In fact such coloured specimens correspond to the same species when shedding its skin. All the specimens I observed in Vanuatu were from human disturbed habitats, but they can be found far from human habitation (e.g. roadsides and cattle parks). They can locally reach high densities and several snakes can be seen under the same small stone. Local people often consider them as worms rather than snakes.

••• Reptiles from Vanuatu – SNAKES (Boidae)

SQUAMATA, BOIDAE
Genus *Candoia*

The position of the genus *Candoia* inside boine snakes has always been controversial. Three distinct hypotheses can be considered:

- A basal position;
- A sister group of the Neotropical forms (e.g. *Boa constrictor*);
- A sister group of the Madagascan forms (*Sanzinia* and *Acrantophis*).

These hypotheses are either related to dispersion or to the biogeographical mechanisms of vicariance. An additional difficulty to resolve is that the genus only occurs on former Gondwana fragments. Three species are classically recognized. *C. bibroni* occupies the largest distribution from eastern Solomon and the Loyalty Islands east to American Samoa. *C. carinata* occupies the whole of Solomon, including Santa Cruz, western New Guinea, Sulawesi and north of Palau. *C. aspera* is a New Guinea species, living below 1 500 m elevation, also present in the Bismarck Archipelago and Manus Island. Despite important morphological differences, those three species show a similar diet mostly based on rodents. A recent molecular analysis, albeit based on limited material, demonstrates the basal position of *C. bibroni* in the genus and close links between *C. aspera* and *C. carinata*. It also shows that a clade (*Sanzinia*/*Candoia*) diverged from Neotropical boas at least 40 million years ago. The basal position of *C. bibroni* is controversial but in 2000, Austin formulated the hypothesis that it is in competition with species of the genus *Python*, while also sympatric with both other species of *Candoia* but absent from the distribution of *C. bibroni*. Other interpretation problems also arise from absence of calibration through fossils; it is in fact not possible today to distinguish vertebrae of Boinae from those of Pythoninae inside boid snakes. Complementary works are necessary to obtain a clear view of the evolutionary history of the genus *Candoia* in the Pacific.

Figure 279: Juvenile *C. bibroni* usually are yellowish orange and mistaken for a different species by non familiar observers. Torres Islands.

SQUAMATA, BOIDAE
Candoia bibroni

According to osteological characters, McDowell in 1979 distinguished two forms in *Candoia bibroni* that he considered as valid subspecies, one eastern (*C. bibroni bibroni*: Loyalty, Fiji, Samoa and extending to the east as far as Tokelau in Polynesia) and one western form (*C. bibroni australis*: Vanuatu, southeast Solomon). The specimens used in Austin's study (see above) unfortunately only comprised the eastern form. In 1985, Gibbons noted: "*Based on distribution the genus [*Candoia*] is Papuan in origin, and resembles that of* Emoia *skinks and* Gehyra *geckos, both of which are present in the Loyalty Islands, but absent from New Caledonia.*"

C. bibroni is a highly polymorphic species concerning its colouration in Vanuatu, with blackish, reddish, brownish, orange and grey blue morphs. It seems that orange-yellowish specimens are largely predominant in northern Vanuatu (Torres) where its size seems smaller. Juveniles are often without patterning and uniformly orange, thus giving them the look of a different species for people who are not aware of this. Specimens of about 1.5-2 m in length were observed around Port Vila. I also have seen a specimen well over 2 m (unfortunately not measured) at Penaoru (Santo).

That snake is arboreal in habit but can sometimes be observed resting at ground level. It seems to be more terrestrial in the north of Vanuatu (Torres). It shows a clear sexual dimorphism for size (females larger than males) and cloacal spurs (absent in about 50 % of females). Maximum published snout-vent is 1 460 mm for females and 1 190 mm for males but larger specimens clearly exist and are not uncommon, except perhaps in museum collections. Each gravid female gives birth to 15 to 18 live youngs but reproduction is not annual since about only 1/3 of the females in collections are gravid. Juveniles eat lizards (skinks) and adults mammals (rats and mice). In 1935, Angel noted that one skink (erroneously called *Emoia samoensis* but in fact *E. sanfordi*) was found in the digestive tract of one *Candoia* from Vanuatu. Burt and Burt also noted the occurrence of the skink *Emoia cyanogaster* regurgitated by such a snake from Tapua Island (Santa Cruz Group, Solomon). I also have observed predation by that snake on adult *Emoia nigra* on Santo.

C. bibroni was reported from the Santa Cruz group (southern Solomon) by Roux in 1913, and Burt and Burt in 1932. In Vanuatu, the species is reported from Torres and Banks groups, Santo, Malo, Aore, Aoba, Maewo, Pentecost, Malakula, Ambrym, Efate, Emao (off Efate), Erromango, Tanna, and Futuna. The species was reported from Santo by Roux in 1913 (on "*Spiritu Santo*"), by Burt and Burt in 1932, Medway and Marshall in 1975 and Horrocks in 1989. Specimens from Santo are present in numerous world museums (AMNH, AMS, BMNH, MNHN, NMBA, and UMMZ).

SQUAMATA, BOIDAE
Candoia carinata

In 1932, Burt and Burt proposed the eastern distributional limit for the boa *Candoia carinata* as the Banks and Santa Cruz groups. They report a specimen from Santa Cruz. In 1989, Horrocks reported a curious observation: "*As I look at the colour picture of* C. carinata *in the magazine [*Solomon Airlines inflight magazine *1988 or 1989] I instantly see the Boa which we kept for several weeks in an observation tank at Malapoa. Our Malapoa specimen came from the Vila [Port Vila, Efate] rubbish tip.* C. carinata *is described as a very adaptable and variable species. It seems highly likely that we have both* C. bibroni *and* C. carinata *Boas in Vanuatu.*" Recently A. H. Whitaker kept a captive boa collected on Efate and which he identified as *C. carinata*. That specimen could have been a recent accidental introduction, but its genetic analysis by C. Austin revealed a unique pattern among other studied Pacific populations. On the web, it is easy to find *Candoia carinata paulsoni* from Vanuatu in the international pet trade (September 2006; e.g. Society "*World Wild Fauna*"). It seemed highly probable that this snake was also deliberately introduced to Vanuatu (at least on Efate) through the German reptile dealer Bregulla, as he certainly did for *Brachylophus* iguanas.

In 1979, McDowell demonstrated the existence of two morphotypes inside that species, one "short tailed" and one "long tailed". Austin's molecular studies showed clear differences between populations of southern and northern New Guinea, the central mountain chain being an important biogeographical barrier. This suggests that the colonisation of the Solomon Islands occurred through a southern route via the d'Entrecasteaux Archipelago rather than via a northernly route through the Bismarck Archipelago.

C. carinata has supralabials in contact with the eye whereas they are separated from the eye by suboculars in *C. bibroni*. The snake is nocturnal and terrestrial. It can be observed during daytime in tree trunk holes and, like *C. bibroni*, is common in and around caves. It feeds on lizards and rodents, but sometimes also on frogs and bats. Austin (2000) considered the species to be semi-arboreal and an ecological intermediary species between *C. bibroni* and *C. aspera*.

••• Reptiles from Vanuatu – SEA KRAITS or AMPHIBIOUS SEASNAKES
(Elapidae, Hydrophiinae)

SQUAMATA, ELAPIDAE, HYDROPHIINAE
Laticauda colubrina

In 1913, Roux reported a juvenile specimen from Malo (Vanuatu) (deposited in NMBA) and noted that: "*Les taches noires ne forment pas des anneaux complets comme chez les exemplaires trouvés en Calédonie*". He thus made an interesting observation recently taken into account by Heatwole and co-authors when revalidating *L. frontalis* from Vanuatu (see below). The specimen examined by Roux certainly refers to *L. frontalis*. Old records of *L. colubrina* from Vanuatu could refer either to the true *L. colubrina* (*sensu stricto*) or to *L. frontalis*, since both Vanuatu species were previously mixed under the binomen *L. colubrina*. Thus old records are not really relevant without a re-examination of the concerned specimen.

In 2005, Heatwole and coauthors examined a large sample and proposed the following distribution of *L. colubrina sensu stricto* in Vanuatu: Santo, Elephant Island (= Ais Island) near Santo, Ngoriki Islet near Kakula Island, Malakula, Efate, Tanna, and Anatom. Numerous specimens of *L. colubrina* were reported from Santo by Heatwole and coauthors in 2005; they are conserved in AMS, FMNH, MNHN, UMMZ, USNM.

Table 26: Morphometric and meristic comparison of *L. frontalis* and *L. colubrina*. **MBS M/F**: Midbody scale rows for males (M)/ females (F). **V M/F**: Number of ventrals for males (M)/females (F). **SVL max M/F**: maximum snout-vent length for males (M)/ females (F).

	MBS M/F	**V M/F**	**SVL max M/F**
Laticauda frontalis	19-21/21-23	192-208/199-211	654/783
Laticauda colubrina	23-24/23-27	216-234/202-239	893/1450

Pickering in 1984 supposed that this seasnake could feed on littoral skinks of the species *Cryptoblepharus novohebridicus*, a hypothesis that is completely wrong since these seasnakes only feed on marine fish. Even though skinks are common on many small islands where sea kraits are abundant, they don't feed on lizards; no explanation is available for this.

SQUAMATA, ELAPIDAE, HYDROPHIINAE
Laticauda frontalis

L. frontalis can be distinguished from *L. colubrina* by the following combination of characters: midbody scale rows, number of ventral plates, smaller size (Table 26), and in sympatry by the absence of a lower lateral connexion between the black cephalic band and the first nucal black band, and the absence of black bands contacting at least the anterior ones at mid-belly. *L. frontalis* occurs in Loyalty and Vanuatu (from Santo south to Anatom) but is reported from New Caledonia by a single specimen without a precise collection locality (also Loyalty Islands?). Food is based on moray eels, mostly Muraenidae and Congridae as in other species of the genus. That species is less common than *L. colubrina* in Vanuatu.

In 2005, Heatwole and coauthors reported *L. frontalis* from several Vanuatu localities. It was cited from Santo, Elephant Island (east coast of Santo), Efate, Ngoriki Islet near Kakula Island (northern coast of Efate), and Anatom. Specimens of *L. frontalis* from Santo are conserved in AMS, FMNH, LACM, MCZ, and UMMZ.

SQUAMATA, ELAPIDAE, HYDROPHIINAE
Laticauda laticaudata

In 1913, Roux reported the occurrence of *Laticauda laticaudata* from southern Solomon (Santa Cruz group). The MNHN François collection comprises one specimen from Vanuatu without a precise locality. The species is known from the following islands of Vanuatu: Ambrym, Efate, and Anatom. The species was not previously reported from Santo but I collected a specimen from Tasmate (west Cape Cumberland coast) during the Santo 2006 expedition.

••• Reptiles from Vanuatu – TRUE SEASNAKES (Elapidae, Hydrophiinae)

SQUAMATA, ELAPIDAE, HYDROPHIINAE
Hydrophis coggeri

The seasnake *Hydrophis coggeri* is present from northern Australia to Fiji, through the Philippines, the north coasts of Sulawesi (Indonesia), the Coral and Timor seas, New Guinea, New Caledonia and Vanuatu. In 2005, Kharin reported the occurrence of the species from Vanuatu and placed it in the genus *Leioselasma*, a position not always followed. In 1986, David reported the shed skin of a seasnake found near a mangrove on Malakula and identified as a *Hydrophis*. It could correspond to *H. coggeri*. No specimen of *H. coggeri* from Vanuatu is present in BMNH or MNHN collections.

SQUAMATA, ELAPIDAE, HYDROPHIINAE
Pelamis platura

The pelagic seasnake *Pelamis platura* is represented from Vanuatu by only a few museum specimens. It was only reported from Malakula and Efate, but the species certainly occurs in waters around Santo and even throughout the whole archipelago. No specimen of that species from Vanuatu is present in either the BMNH or in the MNHN collections.

• • • Potential and doubtful species

Several lizard and snake species are reported from the southern Solomons (Santa Cruz group) and thus are potentially present in northern Vanuatu (Torres and Banks). The Santa Cruz Islands are the closest of the Solomon Islands to Vanuatu. However, fresh water is absent on the Torres Islands, which are composed of coral limestone and rarely exceed 300 m elevation.

••• Skinks

Potential Santa Cruz lizards that could occur in Vanuatu include several skink species. In 1913, Roux reported the occurrence of *Lamprolepis smaragdina* as *Dasia smaragdina* on the Santa Cruz group and noted: "*Cette espèce n'avait pas encore été signalée aussi loin à l'est en Mélanaisie (sic)*". In 1932, Burt and Burt also reported that species from Duff and Santa Cruz islands of the Santa Cruz group. In 1980, McCoy also reported *Lamprolepis smaragdina* from Santa Cruz and Reefs Islands (Solomon) where it is common. That arboreal species is present in forest but also in coconut plantations, mostly on tree trunks but rarely on branches. *Emoia trossula* was formerly considered as a regional endemic (Fiji, Tonga, and Cook) and its situation is still incompletely resolved (species complex). Two specimens at the BMNH are registered from Vanuatu, under the binomen *E. samoensis* [note however that one is reported as a syntype of *Perochirus guentheri*?]. That mention is considered as a locality mistake because those specimens are actually *E. trossula*, a species not present in Vanuatu. In 1986, Brown and Gibbons stated: "*(these specimens), which were purchased from Mr. Cuming, are stated to be from Eumonga and Vanuatu. However, since they agree in most characters with examples from populations of* E. trossula *from the Fijis and not with samples from any of the species known from Vanuatu, we assume that the locality data are probably in error and have referred these two specimens to* E. trossula, *but have not included them in the paratypes*". Another skink species of the genus *Emoia*, *E. rufilabialis*, is an endemic skink from Santa Cruz Island, southeastern Solomon. That *E. cyanura* group and *E. cyanura* subgroup species could be present in northern Vanuatu but our recent searches on the Torres Islands proved that this was not the case.

Another large skink, *Eugongylus albofasciolatum*, was reported by Roux in 1913 from the Santa Cruz Islands, by Burt and Burt in 1932 on Tikopia Island, Santa Cruz Group, and by McCoy in 1980 from the same island group. *E. albofasciolatum* is particularly shy and difficult to observe. It could be potentially present in northern Vanuatu (Torres and Banks). Our recent searches on Torres Island showed however that one is unlikely to encounter this skink in Vanuatu. One smaller skink, *Prasinohaema virens*, is reported from Santa Cruz and Reefs Islands by McCoy in 1980. One specimen from Vanikolo (Santa Cruz Group), labelled as "*Lygosoma anolis*, *Leiolopisma* or *Lipinia anolis* Boulenger" corresponds to the subspecies *Prasinohaema virens anolis*. That subspecies was described from Treasury and Santa Ana Islands. Its status is uncertain and the taxon was not recently compared with the nominotypical subspecies. This arboreal species can be observed as high as 2-20 m in forested areas. It is easily recognisable since the head and body stay close to the tree trunk when the lizard moves. The species can be observed at night when sleeping on accessible branches. Its blood pigment is typically green, as are its mouth and tongue, and also the egg shell. This skink has toe lamellae like geckos and can easily climb glass walls.

Snakes

Finally one snake species, *Dendrelaphis salomonis* [sometimes referred to as *Dendrelaphis calligaster*, or *D. calligastra*] was reported by Roux in 1913, based on several specimens from the Santa Cruz Islands. He noted: "*Cette espèce n'avait pas encore été signalée à l'est des îles Salomon*". In 1932, Burt and Burt collected that species on Nendö (Santa Cruz) and Utupua (Tapua) Islands, Santa Cruz Group; in 1980, McCoy reported the species (as *D. salomonis*) from this island group. This snake could be present in northern Vanuatu but it is unlikely. It is a diurnal and active snake present in forests and cultivated areas. It feeds on amphibians and lizards.

Discussion

Pacific herpetofauna origin

Pacific island herpetofaunas have Oriental, Gondwanian and Neotropical origins. Natural recent arrivals originated from the Papuan area (animal flotation for short distances or drifting rafts) and by more recent man mediated introductions during pre-historical and historical events originating from the Papuan area or through exotic alien species introductions from different origins (Asia, Australia). Short distance flotation implies air pockets and impermeable skin permitting the animal to remain on the surface without sinking. Sea currents can be totally reversed during climatic anomalies like hurricanes, thus explaining the scarcity of Neotropical elements even in eastern Polynesia, despite trade winds going from east to west. Neotropical elements are however clearly present in southern Pacific herpetofaunas with two endemic genera containing several species each, the iguanid lizard genus *Brachylophus* and the boid snake genus *Candoia*.

Biogeographical analyses are still tentative since numerous species have yet to be described or even discovered, some of them being cryptic species. Also the phylogenetic relationships between species are still unresolved for the most important speciose genera like the geckos *Lepidodactylus* and *Gehyra* or the skinks *Emoia*. Furthermore, several important areas have only been weakly explored. Nonetheless, three factors can explain the biogeographical patterns observed for South Pacific herpetofaunas:

- Vicariance [separation of populations previously in contact through plate tectonics and/or orogenesis];
- Dispersion [natural through rafts for reptiles];
- Accidental or voluntary human transportation.

In human transportation we have to distinguish between ancient human transportation through early Pacific settlers (mostly Polynesians and the first European explorers) that I call **historic introductions** and more **recent introductions**, some of them clearly being intentional like the frog *Litoria aurea* or the iguanid *Brachylophus bulabula* on Efate. *Gehyra oceanica* and *G. vorax* are generally considered as having been mostly transported by man but I disagree with that hypothesis proposed by Beckon. In his 1992 work, this author concluded that his morphological data on *Gehyra oceanica* and *G. vorax* are in accordance with human transportation but with different time scales between *G. oceanica* and *G. vorax*, the later being a forest species with a limited distribution. Brown in 1956 and Gibbons in 1985 also considered geckos and skinks as recent arrivals constituting the main element of the current herpetofauna; no endemic genera are present east of Solomon. Most of these species have a distribution to the west, adjoining their center of origin, the Papuan area. Specific endemism stops at a line joining American Samoa/Niue and only few endemics are present to the east. I think that this scarcity of endemism, even at the specific level, is rather explained by a strong selection for island efficient colonists east of Fiji, thus not allowing populations to become isolated on any island. Pacific lizards east of Fiji are all ecological generalists that are biogeographically specialized to efficient island colonization.

A recent genetic study of Pacific Islanders has shown the same for *Homo sapiens*: "*At some point, prehistoric Oceanic mariners apparently became so accomplished that the inter-island water crossings in the central Pacific were often no more of an impediment to travel than the (already occupied) rugged terrain of the larger island interiors in the western Pacific. In many areas the ocean was transformed from a formidable barrier into a highway*". They also have shown that shore-dwelling Oceanic-speaking human groups are more intermixed since dispersal along the shorelines was easier. The sailing capabilities of the ancestors of the Polynesians transformed the nature of their diaspora and kept them relatively homogenous through constant gene mixing and flow. Thus the situation seen for widespread lizard species on Pacific Islands is exactly the same as the one observed for earlier island human settlers: they all are homogenous since they had specialized to favourise frequent inter-island travels long before the human colonization of those islands, not because they arrived recently.

Pacific island reptile distribution was and still is controlled by: geology (including plate tectonics and volcanism), sea level variations, hurricanes, natural dispersion (rafts) and the role of man. It is classically accepted by most herpetologists that Pacific island species with large distributions have benefited from recent man mediated transportation, but if one endemic species has strong affinities to another geographically separated species then their separation is due to natural colonisation. Such an interpretation seems to not be really logical! In the same way the biology of some alien reptile species like the gecko *Hemidactylus frenatus* or the parthenogenetic snake *Ramphotyphlops braminus*, which recently colonised almost all tropical or subtropical areas of the world, cannot explain why they were not present earlier on Pacific tropical islands through human transportation. Also, how could some shy species like the skink *Lipinia noctua* have been transported by man on such a large scale as the whole tropical Pacific while both the former recently introduced species were not?

Since 1957 and the studies of Darlington, the following dichotomous paradigm has been accepted:

- Natural dispersion with breaks giving birth to micro-differentiations and geographical variations eventually producing endemism;
- Recent human introduction, which has been rapid and thus gives rise to uniform populations.

The reality is of course not so dichotomous. One important faunal break between the Oriental region and the Pacific islands is the lack of several genera such as the skinks *Carlia*, *Sphenomorphus* and *Tribolonotus*, as well as the monitor *Varanus* on most islands. Another second break can be observed more to the east with the lack of *Candoia* boid snakes and all larger *Emoia* species east of a line through Niue/Samoa (but reaching the Cook Islands). Interestingly, terrestrial elapids have arrived not far from Vanuatu at Santa Cruz and Reefs Islands. Fijian endemism of old faunistical elements (*Platymantis* frogs, *Brachylophus* endemic iguanid lizards and the endemic genera *Ogmodon*, an elapid snake) could be related to a mixture of island size and former position through plate movements, island age, colonization hazards but perhaps also former volcanic events.

Other species biological characteristics like parthenogenesis (*Hemidactylus garnotii*, *Hemiphyllodactylus typus*, *Lepidodactylus lugubris* complex, and *Nactus pelagicus*, the introduced snake *Ramphotyphlops braminus*), saltwater tolerance, delayed incubation time, continuous reproduction, sperm storage, communal egg laying, adhesive eggs… have clearly favourised older natural or man mediated more recent island colonisations. Those characteristics can be in accordance with both hypotheses (old natural colonisations or recent man mediated colonisation) and thus cannot help choose one theory against the other.

••• The role of plate tectonic movements around Vanuatu

Plate tectonics provide an explanation for part of the current distribution, at least for the most ancient elements. Eustatic movements resulting from plate tectonics and sea level variations are also important biogeographical factors. The border between the Pacific and Australo-Asiatic plates is unstable and irregular with several important subduction areas according to age and in different directions. Micronesia, Samoa, and the whole of Eastern Polynesia (east of Tonga) are located on the Pacific plate whereas New Caledonia and New Zealand are located on the Indo-Australian plate. Fiji, Vanuatu, Solomon and Tonga are located at a dynamically unstable area called the Outer Melanesian Arc (OMA). That Arc stretches from New Guinea, through the Solomon Islands, Vanuatu Archipelago, Fijian Islands, the islands of Samoa, and southeast to Tonga. It is a major geological feature of the Pacific basin, west of the Tongan Trench. Components of the OMA are the result of tectonic activity over the last 11.2 to 2 MY, and the biota of this region results from speciation within the OMA as well as dispersal from Southeast Asia, New Guinea, Australia, and New Caledonia.

Strong interactions between both plates (Indo-Australian and Pacific) occur at OMA. Vanuatu was located on that arc between the Solomon Islands (north) and Fiji (south) in mid Oligocene (30 MY) times. The Bismarck Archipelago is located on a different arc. Fiji and Tonga are ancient and estimated to about 40 MY. The Pacific plate is moving under the Indo-Australian plate and the Tongan Trench is located on one end of that subduction area, with the Vanuatu Trench on the other end. On the Melanesian border of that subduction area several movements have taken place, including partial rotations explaining the variable relative positions of some of those archipelagos during time. The Australo-Oriental collision is dated from the mid-Miocene, about 17 MY. Note also that between New Guinea and Australia there existed a now disappeared insular chain that was absorbed to the north of New Guinea during the Australo-Oriental collision at mid-Miocene. That chain permitted the connexion of the southwestern Pacific islands with Southeast Asia.

••• **Geologic movements of Vanuatu through time**

Differences in the herpetofaunal composition between the Loyalty Islands and the New Caledonia mainland are considerable and constitute a clear biogeographical indication of a more important geographical separation in the past. Loyalty possesses mostly Papuan elements (skinks of the genera *Emoia* and *Lipinia*; gecko genus *Gehyra*; snake genera *Ramphotyphlops* and *Candoia*). The presence of *Cryptoblepharus* in New Caledonia can certainly be explained by its strictly littoral life. In the same way *Emoia impar* is absent from Loyalty whereas *E. cyanura* (*sensu stricto*) is present, a situation uncommon on Pacific islands were both species most often occur together. One explanation of such considerable faunal differences should be related to a different past position of Loyalty and the only recent arrival at its present position. Thus Loyalty could have been closer to Vanuatu, explaining its long separation from New Caledonia but also the strong observed faunal affinities between Loyalty and Vanuatu (*Caledoniscincus*, *Emoia loyaltiensis* which is related to Vanuatu endemics of that genus, *Gehyra vorax* [absent from Solomon but present on Loyalty and Vanuatu], *Nactus pelagicus*, *Candoia bibroni* [probably arrived in Vanuatu from the south through Loyalty], and *Laticauda frontalis* [a regional endemic from Vanuatu and Loyalty, sister species of the New Caledonian endemic *Laticauda saintgironsi*]); it would thus not be surprising that an endemic forest gecko species of group II of the genus *Lepidodactylus* will one day be discovered on the Loyalty Islands.

The current position of Vanuatu was only reached recently. In 1996, Allison noted that the emergence of Vanuatu is associated with that of the Vitiaz Arc (= OMA), an intense subduction area formed by the convergence of Indo-Australian and Pacific plates south of the Ontong Java Plateau and the dilation of the north Fiji basin. At the beginning of the Oligocene, the Vitiaz Arc represented an eastern extension of the North Solomon Arc to west of actual Fiji. Relictual islands formed by that arc comprise Santa Cruz and Duff archipelagos (politically the most eastern Solomon Islands) and Banks Islands located north of Vanautu. During the late Miocene (10-8 MY), the New Hebrides arc began to form itself as an eastern extension of the southern Solomon Arc in conjunction with the reverse subduction reported above in relation to the Solomons. Later during the Miocene (about 6 MY), the area between both arc systems began to inflate, thus forming north of Fiji basin and giving rise to a rotation of the New Hebrides Arc of about 30° clockwise. Volcanism began during that time and later moved during the Pliocene to the west to form the central chain currently active in Vanuatu and the active part of Santa Cruz. Following previous tectonic movements, 6-8 MY ago, Vanuatu was still close to north or northwest of Fiji. Colonisation of Fiji and Vanuatu by *Gehyra vorax* from New Guinea is old and predates their separation. Later Vanuatu drifted counter clockwise to progressively reach its current position. Such movements can explain the current distribution of Micronesian elements such as *Perochirus*, if such an origin is confirmed. The Vanuatu herpetofauna is of Papuan origin with a low level of local endemism. Bats are the only native mammals and about half of Vanuatu bird species are shared with New Guinea. The Vanuatu herpetofauna has no old endemic elements compared with Solomon, Fiji or New Caledonia. In 1957, Cheesman admitted that the flora of Vanuatu's southernmost islands (Anatom, Erromango and Tanna) probably originated from a land connexion between Vanuatu and New Caledonia during the Cretaceous before the breaking away of both elements from northern Queensland. However, current data shows rather that Vanuatu has never been in contact with New Caledonia. An important ceratobatrachid frog speciation exists on Solomon (comprising several endemic genera) and Fiji (two endemic species), as well as an ancient snake group, elapid genus *Ogmodon*, an endemic Fijian genus.

Vanuatuan faunas are in all likelihood less than 2 MY old. The oldest Vanuatu rocks are dated to 14 MY but the whole archipelago only emerged out of the sea about 2 MY. The present position of Vanuatu is a result of counterclockwise rotational movement since the Miocene; prior to this rotation the islands of Vanuatu were located to the north of Fiji and Tonga, and were more isolated than at present. Its recent emergence and position could explain the lack of *Platymantis* frogs and *Ogmodon* elapid snakes and the presence of *Perochirus* geckos. The biogeographic patterns highlighted by *C. atropunctatus* show in particular a biotic break betwen the islands of southern Vanuatu (Erromango, Tanna, Futuna, Aniwa and Anatom) and the islands of central and northern Vanuatu. That break is congruent with patterns recovered from a literature review made by Hamilton and co-authors in 2009 for a broad range of diverse taxonomic groups including vertebrates, invertebrates, and plants. That biogeographical line is defined as Cheesman's line by these authors.

Can fossil help us to understand the biogeographical history of Vanuatu's reptiles?

With the exception of one mekosuchine dwarf crocodile, no native vertebrate species seem to have been eliminated by human activity in Vanuatu. According to fossil records, the past distributions of most Pacific island birds were clearly larger than at present. Numerous bird species considered as island or archipelago endemics today correspond in fact to relictual distributions of previously more widely distributed species. Lizard fossil remains are not very common but it seems unlikely that situation was similar. Bird extinctions are classically attributed to man's arrival but sea level movements during glaciation times also produced important habitat variations on islands (increasing salinity, plant mortality, expansion and contractions of littoral plains). During the sea level changes related to glaciations, evolution for survival and colonisation of new habitats mainly took place on smaller islands. On those smaller islands, larger endemic lizard species are rare or absent but this can also be explained because they are more dependent on favourable physical conditions and food than smaller skinks or geckos such as the eastern Polynesian species. In a 1986 paper, Gibbons and Clunie suggested that the major human migrations in the west Pacific could be correlated to migrations for food during such sea level variations resulting from glaciations and dated -700 000 to -2 MY. The situation could be the same for reptiles. Those sea level variations also had a considerable impact on coral reef faunas producing mass extinctions and recolonisation events from refuges as shown for bivalve molluscs by Paulay in 1990. Gibbons and Clunie propose that the current sea level was reached 4 000 years ago and that the lowest sea level was reached 18 000 years ago and increased progressively thereafter. For example, the exposed area of the Seychelles during the glacial maximum was about 600 times greater than the current area. Concerning Vanuatu, almost all islands were separated from each other, even during the glacial maxima, except Santo and Malakula, which were attached together. Endemism on Anatom and Futuna, which is difficult to explain regarding the small size and relative isolation of both islands, could perhaps be explained by their increased size during glacial maxima and perhaps their more diversified habitats.

There is a possibility that fossil bird remains aged more than 3 000-3 500 years could have been present on the islands, but that the areas where these might have been found have been inundated by the sea level rises that started 18 000 years ago. That active period of sea movements could have favourised speciation events through the considerable modification of island ecosystems. Speciation could have taken place through different ways: adaptation to new habitats arising from the increasing salinity of littoral habitats after 18 000 years ago when the sea slowly rose again, increasing numbers of dead trees allowing egg deposition and producing favourable microhabitats, possible recontact between separated species, subspecies, or populations giving rise to parthenogenesis or speciation through hybridisation. In the same way, sea level rises might also have separated populations giving rise to an important subsequent vicariant speciation on Pacific islands.

During glacial periods, sea levels were low, exposing large dry calcareous areas around the edges of islands that were impossible to colonise by elapid snakes and amphibians originating from the wet forests of Fiji and Solomon, whereas smaller lizards could better support such xeric conditions, even for *Lipinia* which needs humidity but can survive in open areas if small wet patches can be found under stones or in trunks, in dead trees or in *Pandanus* sp. crowns. The study of fossil remains from Vanuatu, with the exception of the recent discovery of an extinct mekosuchine dwarf crocodile, have unfortunately not provided significant biogeographical information on the herpetofaunal history of the archipelago.

Biodiversity of the herpetofauna of Vanuatu and Santo

The number of reptile species listed for Vanuatu is regularly being increased. Baker (1947) reported 14 lizard species from Vanuatu and stated that the two most common were *E. cyanura* (*sensu lato*) and *E. caeruleocauda* (named *E. werneri*). In 1975, after having surveyed six islands of the archipelago, Medway and Marshall listed 20 species of terrestrial reptiles (five gekkonids: *Gehyra oceanica*, *G. mutilata*, *Perochirus guentheri*, *Lepidodactylus lugubris*, *Nactus pelagicus* [as *Cyrtodactylus pelagicus*]; 13 scincids: *Emoia cyanura*, *E. caeruleocauda* [as *Emoia werneri*], *E. nigronarginata*, *E. speiseri* [later considered a synonym of *E. nigromarginata*], *E. atrocostata*, *E. cyanogaster*, *E. sanfordi*, *E. samoensis* [mostly *E. sanfordi*], *E. aneityumensis*, *E. nigra*, *Lipinia noctua*, *Caledoniscincus atropunctatus* [as *Lampropholis austrocaledonica*], *Cryptoblepharus novohebridicus* [as *Cryptoblepharus boutonii*], and two snakes: *Ramphotyphlops braminus* [as *Typhlops braminus*] and *Candoia bibroni*). They considered four species to be endemic and four as introduced, and one introduced amphibian from Vanuatu. Thus a total of 18 native species were reported from Vanuatu in 1975. They noted that the origin of the terrestrial vertebrate fauna of Vanuatu has clear Indo-Australian affinities with some species having an exclusively insular distribution and others that are endemic. They also noted that 95 of the 98 terrestrial vertebrate species known at that time from Vanuatu were present on the six islands they

Table 27: Current knowledge on amphibians and reptiles of Vanuatu reported from Islands excluding Santo (Vanuatu excl. Santo), previously reported from Santo and collected during the Santo 2006 expedition. *Crocodylus porosus* has not been recently observed on Santo (?); *Hemidactylus garnotii* was previously only reported from Anatom from a BMNH specimen that I have not checked; during the Santo 2006 expedition I have not explored sea margin and mostly collected inland in forested areas, thus common sea margin species like *Emoia atrocostata* and sea kraits (except *Laticauda laticaudata*) were not observed. I do not consider *Gehyra mutilata* as an introduced species except the recently arrived population of the Torres Islands. Species that I consider as introduced by man (historic or recent) are indicated with an *.

	Vanuatu excl. Santo	Santo	Santo 2006 exped.
AMPHIBIA			
Hylidae			
**Litoria aurea*	+	+	+
REPTILIA, CROCODYLIA			
Crocodylidae			
Crocodylus porosus	+	(?)	-
REPTILIA, SQUAMATA			
Iguanidae			
**Brachylophus bulabula*	+	-	-
Gekkonidae			
Gehyra mutilata	+	-	-
Gehyra oceanica	+	+	+
Gehyra vorax	+	+	+
Gekko vittatus	+		-
**Hemidactylus frenatus*	+	+	+
Hemidactylus garnotii	+	-	+
Hemiphyllodactylus typus	-	-	-
Lepidodactylus buleli	-	-	+
Lepidodactylus guppyi	+	-	-
Lepidodactylus lugubris	+	+	+
Lepidodactylus vanuatuensis	+	+	+
Nactus multicarinatus	+	+	+
Nactus pelagicus	+	-	-
Perochirus guentheri	+	-	-
Scincidae, Lygosominae			
Caledoniscincus atropunctatus	+	-	-
Cryptoblepharus novohebridicus	+	+	+
Emoia aneityumensis	+	-	-
Emoia atrocostata freycineti	+	+	-
Emoia caeruleocauda	+	+	+
Emoia cyanogaster	+	+	+
Emoia cyanura	+	+	+
Emoia erronan	+	-	-
Emoia impar	+	+	+
Emoia nigra	+	+	+
Emoia nigromarginata	+	+	+
Emoia sanfordi	+	+	+
Lipinia noctua	+	+	+
REPTILIA, SQUAMATA, SERPENTES			
Typhlopidae			
**Ramphotyphlops braminus*	+	+	+

Boidae			
Candoia bibroni	+	+	+
Elapidae, Hydrophiinae			
Laticauda colubrina	+	+	-
Laticauda frontalis	+	+	-
Laticauda laticaudata	+	-	+
Hydrophis coggeri	+	-	-
Pelamis platura	+	-	-

visited. The most diverse vertebrate fauna was on Espiritu Santo but the most diverse herpetofauna was on Efate. They could not attribute the faunal decrease observed on the southern islands of Vanuatu to isolation or to supposed distance from potential sources, not even to diminution of island area or elevation. They also noted that all endemic species were found in mature seral or primary forest and that few species, all cosmopolitan or with large repartition, are restricted to open habitats. Forest faunas show a clear elevation zonation and a vertical stratification under the canopy. The distributions of the three larger skink species [*E. sanfordi*, *E. samoensis* and *E. nigra*] were considered to be mutually exclusive and complementary by Medway and Marshall in 1975, a situation not seen for birds or bats; recent distribution data however disagree with that old observation. Distributions of some bird species indicate that complete archipelago colonisation has not been achieved. Later, in 1994, Whitaker and Whitaker listed 26 reptile species from Vanuatu, including introduced species. Nonetheless the Vanuatu herpetofauna is generally considered to be poor, Allison in 1996 numbered a total of 27 native terrestrial and freshwater species, a number nearly identical to that of Fiji (29 species): *Crocodylus porosus*, 11 gekkonids in six genera, 13 skinks in four genera, one boid and one typhlopid probably introduced but for which he indicated that natural dispersion cannot be ruled out.

There is currently no synthesis of all the available information on the Vanuatu herpetofauna. Our field and literature survey allowed the recognition of 27 native reptile species from Vanuatu (Table 27), four recently introduced species, three sea kraits and two sea snakes (elapids), excluding sea turtles. Native species include one crocodile, 12 geckos, 13 skinks, and one boid snake; note however that the gecko *Hemiphyllodactylus typus* is certainly present in Vanuatu. Thus a total of 37 amphibian and reptile species (32 native species, one potential species [*H. typus*] and four introduced species) are confirmed for Vanuatu today. This diversity of course does not reflect a depauperate herpetofauna when compared with neighbouring archipelagos.

Concerning native species (excluding sea turtles and elapid snakes), Santo has 18 of 27 species, which is about 2/3 of the Vanuatu species. Differences (lacks) are mostly related to southern endemics of the skink genus *Emoia* and northern endemics with clear Solomon affinities (*Gekko vittatus*, *Lepidodactylus guppyi*), all lacking from Santo probably due to its intermediate geographic position.

The herpetofauna of Vanuatu is unique for its lack or scarcity of several widespread Pacific island gecko species (*Gehyra mutilata*, *Hemidactylus garnotii* and *Hemiphyllodactylus typus*). Other Vanuatu species include widespread Pacific species (*Gehyra oceanica*, *Emoia caeruleocauda*, *E. cyanura*, *E. impar*, *Lipinia noctua*, *Laticauda colubrina*, *L. laticaudata*, and *Pelamis platura*), southern species which are absent north of the archipelago (*L. buleli*), species with Solomon affinities (*Gekko vittatus*, *Lepidodactylus guppyi*, *Nactus multicarinatus*, *Emoia atrocostata freycineti*, *E. nigra*, and *E. cyanogaster*), species with Micronesian affinities (*Perochirus guentheri*), species with Loyalty affinities (*Gehyra vorax*, *Nactus pelagicus*, *Caledoniscincus atropunctatus*, *Candoia bibroni*, *Laticauda frontalis*) (note however that *G. vorax* was reported from Tonga and that fossil remains attributed to *Perochirus* sp. were also found on Tonga), and southern Vanuatu with possible Loyalty affinities (*Emoia aneityumensis*, and *E. erronan*) or strict or nearly strict Vanuatu endemics (*E. nigromarginata*, and *E. sanfordi*), all probably also with Loyalty affinities.

••• Originality of southern Vanuatu islands: Cheesman Line

Anatom Island is particularly important from a biogeographical perspective owing to its intermediate position between New Caledonia in the west and other oceanic islands in the east. Anatom experienced volcanism but possesses a rich biota thus suggesting less perturbation than Tanna and Erromango. Erromango, Tanna and Anatom, the three southernmost islands of Vanuatu, probably constituted a unique landmass in the past and their connexion to New Caledonia has been suggested regarding their Australasian flora and fauna. Anatom is located at the crossroads of two important migratory routes. The first coming from north Vanuatu, Solomon and New Guinea where Papuan affinities can be found, including the occurrence of some Australasian elements, the second coming from southern Vanuatu, New Caledonia and Australia where Australasian affinities can be found with again the occurrence of some Papuan elements. Botanists have established strong affinities between the flora of the southern group of islands and that of New Caledonia. Species considered as New Caledonian endemics are present in southern Vanuatu (*Caledoniscincus* for lizards but also e.g. *Araucaria columnaris*, nine other flowering plants and seven fern species). Entomological samples collected on Anatom by Cheesman allow for the recognition of 11 species with Australian affinities related to New Caledonian forms. In 1957, Cheesman proposed that the continental mass comprising Australia (Queensland) and New Caledonia should also comprise southern Vanuatu, a hypothesis no longer considered valid today. The Australia/New Caledonia separation is dated from the end of the Cretaceous. Cheesman however does not reject the second hypothesis of natural colonisation: "*But if the colonization of islands could be considered due mainly to adventitious means of introduction, there would not exist such distinct faunal areas*". I agree with that point of view since all Vanuatu endemic *Emoia* are clearly biogeographically related to southern Vanuatu. Even though Anatom is only 150 km from New Caledonia, it shows considerable faunal dissimilarities and a land connexion is refuted by modern data. Vanuatu is also separated from New Caledonia by the deep Vanuatu Trench (6400 m). Cheesman suggested a zoogeographical line in southern Vanuatu, analogue to the Wallace line but not as clearly defined. This biogeographic line was recently defined and named the Cheesman Line; all my data agree well with its validity.

• • • Endemism of Vanuatu herpetofauna

In 1996, Allison noted that only seven reptile species are endemic to Vanuatu but that number now has grown to eight species regarding the new *Lepidodactylus* species that was recently described. All genera, except two (*Perochirus* and *Caledoniscincus*), are present in New Guinea and the Solomon Islands. The absence of iguanids, elapids and native ceratobatrachid frogs from Vanuatu is generally explained through the young age of the archipelago and the plate rotation hypothesis indicating a different position of the archipelago over time. Solomon and Fiji had secondary radiations after the dispersal of ancient elements like elapids, iguanids or ceratobatrachids and ranid amphibians from continental landmasses. In 1985, Gibbons considered *Brachylophus* iguanid lizards to be an old Fijian element since they show important morphological and ecological differences compared to actual Neotropical forms considered as ancestral. Curiously, Vanuatu that is located between them (south of Solomon and north of Fiji on the Outer Melanesian Arc, but near Fiji) has no such elements. Ceratobatrachid frogs of the genus *Platymantis* certainly migrated from Solomon to Fiji when Vanuatu was located elsewhere, north of Fiji. In the same way the occurrence of the Micronesian genus *Perochirus* in Vanuatu, located near Micronesia during its migration to its current position, can be explained, as can the occurrence of some flowering plants or birds. Endemism is low in Vanuatu, particularly endemic genera. Gibbons considered that most species derived from Fijian forms and reverse is not true; however it would be interesting to know if southern Vanuatu endemic *Emoia* species are more closely related to the Loyalty endemic *Emoia* or to the Fijian endemic *Emoia*, implying an east-west migration in the second case. Gibbons noted that most Vanuatu fauna is recent since it is rich in geckos and skinks with at least two endemics; such an assumption has of course no biological reality. Dispersal to the east continued to operate after Vanuatu reached its current position between Solomon and Fiji. Absence of the ancient skink genera *Leiolopisma* [Fiji] and *Tachygyia* [Tonga] on Vanuatu and Samoa, which are young islands, suggest an older occurrence of those genera in Fiji and Tonga, both of which are old archipelagos.

Historically it was believed that the low Vanuatu biodiversity [compared to Solomon and Fiji] is related to the young age of the archipelago, the presence of volcanoes modifying habitats and the influence of hurricanes giving birth to major habitat perturbations. However, several Solomon Islands or island groups are in the same situation but possess a much more diverse fauna. Thus the varying geographical position of Vanuatu over time seems to have had a much more important impact on levels of endemism. Vanuatu was also a site for local speciation and diversification, not at generic but at species level. Among the 13 native gecko species four (including *N. multicarinatus*) are endemic (33%) and among the 13 native skink species five are endemic (38%), a situation similar to most other Pacific archipelagoes of that area.

Factors classically believed to influence insular fauna diversification are isolation (distance from the source area), island area, elevation range, number of plant species and number of insect species. There is a progressive increase of isolation from Santo to Anatom and a decrease in elevation range and island area. The vegetation shows a clear southern diversity decline; a break in that sense seems to appear at a latitude of around 18° south. All vertebrate classes show an impoverishment of their faunas from Santo to the south. Differences in the geological ages of the islands are also obviously correlated with variations in latitude. Southern islands are younger. During the period before the Pleistocene, exposed areas above sea level were limited and restricted to northern Vanuatu. One cannot exclude that the endemic southern species require an ecology that does not allow them to

Figure 280: Small village cultivated areas surrounded by deep forest are not unfavourable to lizards and herpetofaunal biodiversity is often high. It is easier in such places than in deep forest to observe forest species at the interface between forest/opened cultivation zones or even on trees that have been killed and lie on the soil. Dead trees have to be preserved as long as possible (not burned) in such cultivations to ensure lizard dynamics.

colonise the northernmost islands with different climatic or edaphic conditions.

The Efate fauna is exceptionally rich for all vertebrate classes. Such an anomaly seems to be simply related to survey intensity on that island which is the political center of Vanuatu hosting the capital Port Vila and the main trading centre thus explaining why recent introductions have begun on Efate. Some herpetologists are reluctant to prospect northern islands like Santo where malaria is present and thus focus on Efate. Vegetation is also more diverse on Efate. Inversely the fauna of Tanna, for all vertebrate classes, is abnormaly low (birds and plants) and that could be related to particular edaphic conditions. Most tropical islands, in both the Indian and Pacific Oceans, present a physiography based on the same model. They have primary rainforest on the east coast that is subjected to trade winds, a central mountain chain constituting a barrier to that rain, and a drier western side often covered with typical dry forest. Such habitat differences constitute the first speciation dynamic on most large islands like New Caledonia or New Guinea (north/south separation rather than east/west), or even larger islands like Madagascar. Such differences could certainly exist on Santo, particularly for species like *E. sanfordi*. However available data have not yet shown their occurrence.

Vertebrate fauna is richest in low elevation areas, a rule on all Indo-Australian islands. On Santo it is clear that a significant number of birds and reptiles of low elevation forest are excluded from higher elevations. A specialized montane fauna is only present for birds among which few species occurs only at higher elevations on Santo. The vertebrate fauna restricted to nonforested areas only comprise Indo-Pacific or cosmopolitan or widespread species. Two lizards show a distribution centered on coastal habitats (*E. atrocostata* and *C. novohebridicus*), thus explaining their wide distribution. Among introduced vertebrates only two species occur in primary forest (*Gallus gallus* and *Rattus exulans*), other introduced species do not occur there. If such a man modified habitat restriction is generated by a competitive exclusion phenomenon by native forest species, a limited ecological range or simply recent arrival through man-mediated transport is unknown. *E. caeruleocauda*, *E. impar* and *E. cyanura* are sympatric but not syntopic, with different ecologies and competition between species has not been demonstrated. On the other hand, Medway and Marshall noted competitive exclusion of *E. samoensis* [*E. sanfordi*], *E. nigra* and *E. aneityumensis*. They never found these species in sympatry on one island; the occurrence of one species seems to exclude the others. However, I observed what probably could be considered to be an ecological separation between *E. nigra* and *E. sanfordi* on Santo (see above). Medway and Marshall also argued that skinks are in dietary competition with insectivorous birds at ground and lower vegetation levels. Thus skink diversity on Anatom Island could be related to bird scarcity in these ecological strata of the vegetation. We however find such an explanation unlikely.

Gibbons considered snakes to be rare on Pacific islands since most micromammals on which they normally feed are lacking. *Candoia* is a large boid snake reaching over 2 m length. It is generally considered to feed on birds and bats, less frequently on lizards. Rodents are not native on tropical Pacific islands, thus those snakes could not always have preyed on them, even if they represent the most frequent prey found today in the stomachs of adults. Recent studies have shown that juveniles feed mostly on lizards whereas adults eat mainly rodents. There is certainly something to conclude about the absence of *Candoia* east of Samoa, in relation to the time of arrival of lizards on those islands or more relevantly in relation to the occurrence/absence of larger prey lizards like *Emoia* of the *E. samoensis* group prior to the arrival of rats. It is certain that adults of that species undertook a dietary shift from lizards to rats once those rodents were introduced to the Pacific islands; rats could be more abundant and easier to catch relative to large lizards. Other snakes, *Ogmodon* and *Ramphotyphlops* feed on invertebrates. Solomon endemic snakes also feed on invertebrates, except one species that preys mainly on amphibians and small lizards rather than invertebrates.

In 1995, Adler and coauthors made a biogeographical analysis of skink occurrence on southern Pacific islands. They distinguished three kinds of species:

- **Continental** [species present on a continent (Australia, New Guinea, Asia) or a set of large islands not far from a continent (Sunda Islands or Philippines)];
- **Pacific** [species endemic to the southern Pacific but occupying more than one archipelago];
- **Endemic** [species present on only one archipelago].

They performed a multivariate analysis with nine variables reflecting archipelago size, isolation and maximal elevation. Their results show that island size and isolation are the main factors explaining the nature of faunal composition whereas elevation is less important. No endemic skink is present beyond Samoa/Tonga in Polynesia (except one recently described species from Cook Islands) and the Carolines/Mariannas in Micronesia. Generally, skink endemism is similar to that observed for birds. That is curious since the reduced mobility of lizards compared to that of birds should give rise to an increased endemism by the former. Comparison with birds shows that the most important differences are seen in Hawaii and the

Marquesas Islands (French Polynesia) where birds are nearly all endemic whereas skinks are only represented by few widespread Pacific island lizards. That clearly shows a different colonization potential between them. However, they noted that Pacific island skinks shows a morphological conservatism formerly demonstrated for other groups of the same family where the existence of cryptic species was evident and demonstrated by genetic analysis. Several cryptic species could exist within the wide distribution of many species. The low diversification of Pacific skinks in the easternmost area of their distribution could also be related to undetermined ecological interactions. Adler and co-authors show a high endemism of south Pacific skinks (66 %) where 79 % of the species do not occupy defined continental areas and 87 % have a distribution limited to three archipelagos or less. Vanuatu possess 13 skink species among which four are continental [they considered the Vanuatu form of *Cryptoblepharus* as belonging to the continental species *C. boutonii* (sic) but that form is presently considered to be an endemic species, *C. novohebridicus*], five Pacific and four endemic, whereas the Santa Cruz Islands (nine species) comprised respectively four, three and two and Fiji (11 species) three, five and three. Island size is correlated with diversity in all those three categories, whereas geographical isolation is mostly correlated with total diversity and to the diversity of Pacific elements. I think that if man is responsible of such transportations then these species should occur randomly and there should be only weak correlations with source distance and also abnormal occurrences should be seen since the Polynesians were island settlers. Their travels were not always from one island to the nearest island but also from one archipelago to other more distant ones. Abnormalities should thus exist but they do not; the Pacific herpetofauna east of Samoa is uniform and widespread, without abnormalities due to stochastic colonisation. Adler and coauthors' analysis is interesting but omits some important factors to explain faunal composition with strongly biased conclusions, notably on species size and ecological requirements of each species. If man had intentionally transported lizards he certainly would have selected large species that he could eat (Monitor, *Gehyra vorax*, *Gekko vittatus* used for tattooing, *Brachylophus* from Tonga to Marquesas). Moreover species size decreases clearly in skink faunal compositions with increasing distance from source areas from the east and thus seems to me to be an important factor that cannot be overlooked. On another hand, species inhabiting sea margins are more easily transported accidentally than primary forest inland endemics, a habitat not present on all islands and probably scarce during sea level movements during glaciation events, a critical period for inter-island lizard movements. They consider the biogeographical origins for the 13 Vanuatu skink species to be continental (*Emoia atrocostata*, *Emoia caeruleocauda*, *Lipinia noctua*), Pacific (*Caledoniscincus atropunctatus*, *Emoia cyanogaster*, *Emoia cyanura*, *Emoia impar*, *Emoia nigra*) or endemic (*Cryptoblepharus novohebridicus* [they considered in fact *C. novocaledonicus* as endemic and *C. boutonii* (sic) as continental, thus implicitely *C. novohebridicus*, whose specific status is now accepted, as endemic], *Emoia aneityumensis*, *Emoia erronan*, *Emoia nigromarginata*, and *Emoia sanfordi*).

Some Santa Cruz Group islands, like Tikopia and Anuta, were clearly colonised by Polynesians as stated by Steadman and co-authors in 1990: "*The contemporary inhabitants of both islands are Polynesians, whose oral traditions indicate that their ancestors came from islands to the east, including 'Uvea, Futuna, Samoa, and Tonga. Culturally and linguistically, the people of Anuta and Tikopia are closely related and maintain regular inter-island contact through canoe-voyaging. Their languages are mutually intelligible, though distinct*". Those islands are geologically recent, 80 000 years old, but still possess endemic bird subspecies. They however have no reptile species that are not found on surrounding islands, suggesting that Polynesians are not at the origin of the introduction of lizards to these islands.

••• Dynamic of faunal changes

All tropical Pacific islands possess a common set of small lizards. Their common size (around 50 mm SVL) is not accidental and can certainly be related to their capacity to survive and to travel on floating rafts during trans-oceanic travel. Most herpetologists believe that these lizards were recent colonists on those islands and that their colonisation is mostly related to man mediated introduction. In fact, I believe that most of these reptiles (except of course the introduced *Hemidactylus frenatus* and *Ramphotyphlops braminus*) were present on the Pacific islands long before human colonisation. Their morphological and genetic uniformity has to be linked to their significant colonisation abilities rather than to recent arrival. Such colonisation abilities do exclude populations becoming isolated on any island (except partial isolation on the most remote eastern islands like Easter Island or Clipperton Atoll), thus explaining the scarcity of endemism east of Tonga. That "*reptile eastern rush*" could certainly have been favoured during important sea level movements related to glaciations, long before human arrival in the area. Small sized skinks and geckos could have benefited from such ecological modifications. Major salinity variations and modifications of the fresh water lens related to sea level variations certainly had considerable repercussions on littoral trees, perhaps even on rainfall in the area (through accelerated evaporation on increased littoral seawater covered areas during sea level rise), thus allowing easier colonisations (increased island size) or favouring lizard dispersal (unsatisfactory conditions found on an island). On the other hand, such vegetation dynamics, particularly in increasing the number of littoral dead trees, had a positive impact on lizard demography in producing a high number of favourable egg laying and shelter sites (dead trees). Volcanism and hurricanes certainly also played an important role in the faunal dynamics of Vanuatu.

In 1975, Medway and Marshall noted that 53% of Vanuatuan reptile species are forest species. All endemic species are present in closed habitats. On Santo at least two endemic bird species are exclusively montane species. Most species, however, also occupy modified habitats where not all trees have been destroyed. Natural regeneration following man made vegetation perturbations (mostly for agriculture) are probably comparable to those that happen after natural cataclysms like earthquakes, volcanic eruptions and hurricanes, all frequent events in the area and for which the fauna as well as flora seemed to be adapted. The ecological niche of most vertebrate species on Vanuatu includes the vegetation that covers those islands in the observed conditions without human interventions other than local agriculture at small village level, with small and well separated cultivated areas around each village, distributed like spots on the forest surface. Agriculture as practised in small villages and without modern techniques certainly has no negative impact on the Vanuatu herpetofauna. In contrary it should have a positive impact in creating egg laying sites, shelters (dead trees) and small forest openings useful for thermoregulation of forest species on the forest edge. The threat is from the changing scale of agriculture, e.g. large uniform pineapple fields, which completely eliminate the local herpetofauna.

The Vanuatu herpetofauna is fragile and sensitive to habitat change and plant and animal introductions. It is unique, with particular regard to numerous endemic species or others with a restricted distribution. That herpetofauna is unique among the whole Pacific and has to be preserved for the coming generations but also as a national heritage for the local Vanuatu Melanesian culture.

The Natural History of Santo

The islands of the Pacific are renowned for the high levels of endemism of, and threats to, their unique faunas and floras. Espiritu Santo, affectionately known simply as Santo, is an island of superlatives: the largest and highest in Vanuatu, Santo is an extraordinary geographical and cultural microcosm, combining reefs, caves, mountains, satellite islands, and a history of human habitation going back 3 000 years. In the spirit of famous voyages of discovery of the past, the Santo 2006 expedition brought together over 150 scientists, volunteers and students originating from 25 countries. With contributions by more than 100 authors, *The Natural History of Santo* is a lavishly illustrated homage to the biodiversity of this "planet-island". Bridging the gap between scientific knowledge and conservation and education, *The Natural History of Santo* was written with local stakeholders as well as armchair naturalists from all over the world in mind.

Les îles du Pacifique sont célèbres pour le très haut niveau d'endémisme et la grande vulnérabilité de leurs faunes et de leurs flores. L'île d'Espiritu Santo, ou Santo, cumule les superlatifs : la plus grande et la plus haute du Vanuatu, Santo est un extraordinaire microcosme géographique et culturel, avec récifs, grottes, montagnes, îles et îlots satellites, et une occupation humaine qui remonte à 3 000 ans. Renouant avec l'esprit des "Grandes Expéditions Naturalistes", l'expédition Santo 2006 avait mobilisé sur le terrain plus de 150 scientifiques, bénévoles et étudiants de 25 pays. Petit tour de force éditorial avec plus de 100 auteurs, ce *Natural History of Santo* est un éloge de la biodiversité de cette "île-planète". À la fois beau livre richement illustré et bilan des connaissances scientifiques, *The Natural History of Santo* se veut un outil de connaissance pour sa conservation durable. Il s'adresse autant aux acteurs locaux du développement et de l'éducation qu'aux naturalistes du monde entier.

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