

Biogeographic Breaks in Vanuatu, a Nascent Oceanic Archipelago¹

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Abstract: The study of distinct biogeographic demarcations has played a pivotal role in our understanding processes responsible for patterns of species distributions and, importantly, the role of geologic processes in promoting biotic diversification. Biogeographic barriers such as Wallace's line have been shown to be the result of old geologic processes shaping ancient faunal or floral diversification events. Based on distributions of birds, bats, reptiles, plants, and invertebrates we identify a distinct biogeographic disjunction in Vanuatu, a geologically nascent oceanic archipelago. We discuss mechanisms contributing to this concordant pattern across these disparate taxonomic groups in light of geologic history, ocean currents, vegetation, soil, and bioclimatic data, and propose the name Cheesman's line to indicate the faunal and floral discontinuity between the northern and southern islands of Vanuatu.

THE DISTRIBUTION of plants and animals among the isolated, oceanic islands of the tropical Pacific has been of interest to evolutionary biologists for more than 150 yr

(Sclater 1858, Wallace 1860, 1876). Discontinuity between distinct Asian and Australian biotas has motivated a large body of research, resulting in designations of the western (Huxley's line or Wallace's line) and eastern (Lydekker's line) limits of a region of biotic overlap between Asian and Australian faunas, a region generally referred to as Wallacea (Wallace 1860, Huxley 1868, Lydekker 1896, Weber 1902, Mayr 1944, Holloway and Jardine 1968, Simpson 1977). Efforts to identify the line of faunal balance within Wallacea, west of which greater than 50% of the biota is derived from Asia and east of which greater than 50% of the biota is Australian (Wallace 1876, Scrivenor et al. 1943, Mayr 1944, Lincoln 1975), led to detailed analysis of the biogeography of the region, enabling an appreciation of the roles of geology, ecology, and evolution in shaping these biotas.

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Within the Pacific Basin itself, the flora and fauna of the islands of the western Pacific are distinct from the biota of the islands occurring farther east and those in the northern or southern Pacific (Hedley 1899). Stoddart (1992:291) suggested that the most remarkable biotic discontinuity within the Pacific Basin occurs at the Tonga Trench (Hedley's line) and argued that this discontinuity was biologically significant because islands on either side of Hedley's line differed with respect to "altitude, climate, and other envi-

ronmental constraints,” rather than simply geographic coordinates.

In addition to the broad distributional patterns in the Pacific Basin, it is important to understand biogeographic patterns on a smaller scale, because the evolutionary history of the lineages within the Pacific can be accurately evaluated only when distributional patterns—and disjunctions within them—are recognized. The Outer Melanesian Arc (OMA), stretching from New Guinea through the Solomon Islands, Vanuatu Archipelago, Fijian Islands, the islands of Samoa, and southeast to Tonga (Kroenke and Rodda 1984), is a major geological feature of the Pacific Basin west of the Tonga Trench. Components of the OMA are the result of tectonic activity over the last 11.2 to 2 myr (Kroenke and Rodda 1984), and the biota of this region results from speciation within the OMA (Filardi and Moyle 2005, Hamilton 2008) as well as dispersal from Southeast Asia, New Guinea, Australia, and New Caledonia (Mayr 1965, Diamond and Mayr 1976, Bauer 1988, Brown 1991, Zug 1991, Flannery 1995, 2000, Allison 1996, Austin 2000, Mayr and Diamond 2001, Carvajal and Adler 2005, Helgen 2007, Hamilton et al. 2009).

Historically, sharp biogeographic demarcations that we recognize and name as lines have been shown to be the result of old geologic processes shaped by ancient faunal and floral diversification events. Wallace’s line, for example, identifies the suture between the ancient Austral Papuan fauna of Gondwanan origin with the ancient northern Asian fauna derived from Laurasia. Similarly, Huxley’s line is concordant with the edge of the continental Sunda and Sahul shelves and the deep Makassa and Lombok trenches (Hahn and Sytsma 1999), and Lydeker’s line occurs along the edge of the continental shelf to the west of West Irian and Australia (Simpson 1977). In contrast, our work in the geologically young Vanuatu Archipelago suggests that biogeographic breaks can be found in geologically young (likely less than 2 myr old) faunas.

The Vanuatu Archipelago comprises 82 islands. The oldest Vanuatu rocks are dated to 14 mya; however, the entire archipelago went

through periods of emergence and submergence, with the last period of emergence only in the last 2 myr (Carney et al. 1985, Greene et al. 1988a, Macfarlane et al. 1988). In addition to being biologically and geologically nascent, the islands of Vanuatu are relatively isolated from other components of the OMA, surrounded by the Vanuatu Trench, the Vitiaz Trench, and the Johnson Trough (Coleman 1970). The current position of Vanuatu is a result of counterclockwise rotational movement since the Miocene (Gibbons 1985, Greene et al. 1988a); before that rotation the islands of Vanuatu were located to the north of Fiji and Tonga, adjacent to the Vitiaz Arc (Chase and Seekins 1988) and more isolated than now.

The geologically recent emergence of the Vanuatu Archipelago (2 mya) explains some of the reptile and amphibian faunal discontinuities previously identified in Vanuatu such as the absence of frogs (*Platymantis*) and elapid (*Ogmodon*) snakes (Schmidt 1930, Zweifel and Tyler 1982). In addition, the absence of *Ogmodon* and *Platymantis* from Vanuatu—as well as the presence of *Perochirus* lizards in Vanuatu—has been suggested to result from the north to south counterclockwise rotational geologic movement of this archipelago (Gibbons 1985). The historic position of Vanuatu was to the north of the current location (Chase 1971); a location that would explain how groups such as *Ogmodon* and *Platymantis* could have colonized Fiji from the Solomon Islands yet not be present in Vanuatu. The distribution of *Perochirus* is restricted to Micronesia, with a single species (*P. guentheri*) occurring in Vanuatu (Bauer 1988). An older Vanuatu located north of the current position of the archipelago would have permitted *Perochirus* to colonize Vanuatu from Micronesia (Gibbons 1985). The absence of groups of vertebrates such as frogs and elapid snakes led to the suggestion that the fauna of Vanuatu may be depauperate (Baker 1928, 1929, Darlington 1948, Bauer 1988). Recent examination of the terrestrial reptile diversity in Vanuatu in light of island area, isolation, and emergence history indicated that, in general, Vanuatu meets the expectations of diversity generated by predic-

tions of island biogeography theory (Hamilton et al. 2009).

The origin and distribution of the biota of Vanuatu have not received much attention but when discussed have generally been considered to result primarily from dispersal out of the Solomon Islands (Medway and Marshall 1975, Gibbons 1985, Bauer 1988, Ota et al. 1998). In addition, a distinct faunal and floral break between Vanuatu and neighboring New Caledonia has been noted (Bauer 1988, Bauer and Vindum 1990, Bauer and Sadlier 1993, 2000, Hamilton et al. 2009). Here, we present data from our ongoing research on the reptile fauna of the Vanuatu Archipelago on biogeographic patterns for squamate reptile species within this island group and note a distinct biogeographic barrier within the Vanuatu Archipelago. We focus on the scincid lizard species *Caledoniscincus atropunctatus* (Roux 1913) as an example, report new distributional records for *C. atropunctatus*, and use this species to illustrate and discuss general biogeographic patterns within the 82 islands of Vanuatu. The biogeographic patterns highlighted by *C. atropunctatus*, particularly a biotic break between the islands of southern Vanuatu (Erromango, Tanna, Futuna, Aniwa, and Aneityum) and the islands of central and northern Vanuatu, are congruent with patterns recovered from a review of the literature for a broad range of diverse taxonomic groups including vertebrates, invertebrates, and plants.

MATERIALS AND METHODS

Between 2001 and 2005 we conducted four comprehensive field expeditions that surveyed 53 sites on 19 islands throughout the Vanuatu Archipelago and encompassed all major islands (Figure 1). At each site the lizard fauna was surveyed using a variety of techniques (Hamilton et al. 2007, 2008, Hamilton 2008). Voucher specimens were collected and deposited in the herpetology collection at the Louisiana State University Museum of Natural Science (LSUMZ).

We obtained data for seven bioclimatic variables from WorldClim (Hijmans et al. 2005), gridded to a 1 km resolution: annual

mean temperature, mean diurnal range, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month, and precipitation of the driest month. These variables were chosen to capture major variation among islands in annual means and seasonality of precipitation and temperature because these environmental conditions are likely to influence the distribution of a small, ectothermic reptile. To determine whether environments were differentiated across the species range limit of *C. atropunctatus*, we performed a principal components analysis (PCA) on environmental variables collected for the approximate center of each island.

RESULTS AND DISCUSSION

Relationship between Vanuatu and New Caledonian Squamate Faunas

Despite the geographic proximity of the New Caledonian Loyalty Islands and the southernmost Vanuatu island of Aneityum (only 150 km between these island groups), the reptilian faunas of New Caledonia and the Vanuatu Archipelago are dissimilar (Bauer 1988, Hamilton et al. 2009). New Caledonia has a highly endemic reptile fauna, with 86% of the terrestrial reptile species of New Caledonia restricted to those islands (Bauer and Sadlier 2000). Only nine of the 71 New Caledonian squamate species are shared with Vanuatu (Hamilton et al. 2009), and three of those nine species (*Ramphotyphlops braminus*, *Lepidodactylus lugubris*, and *Hemidactylus frenatus*) are the result of human-mediated introductions into both island groups (Bauer and Sadlier 2000, Hamilton et al. 2009). Previous authors have provided evidence for a distinct faunal break between New Caledonia and the Vanuatu Archipelago (Baker 1928, 1929, Solem 1976, Bauer 1988), and noted that the two regions are separated by the deep (6,400 m) Vanuatu Trench (Greene et al. 1988b). In contrast to the dissimilarity with Vanuatu fauna, the New Caledonian squamate fauna has affinities with Australia and New Zealand (Bauer and Sadlier 1993, 2000), reflecting the

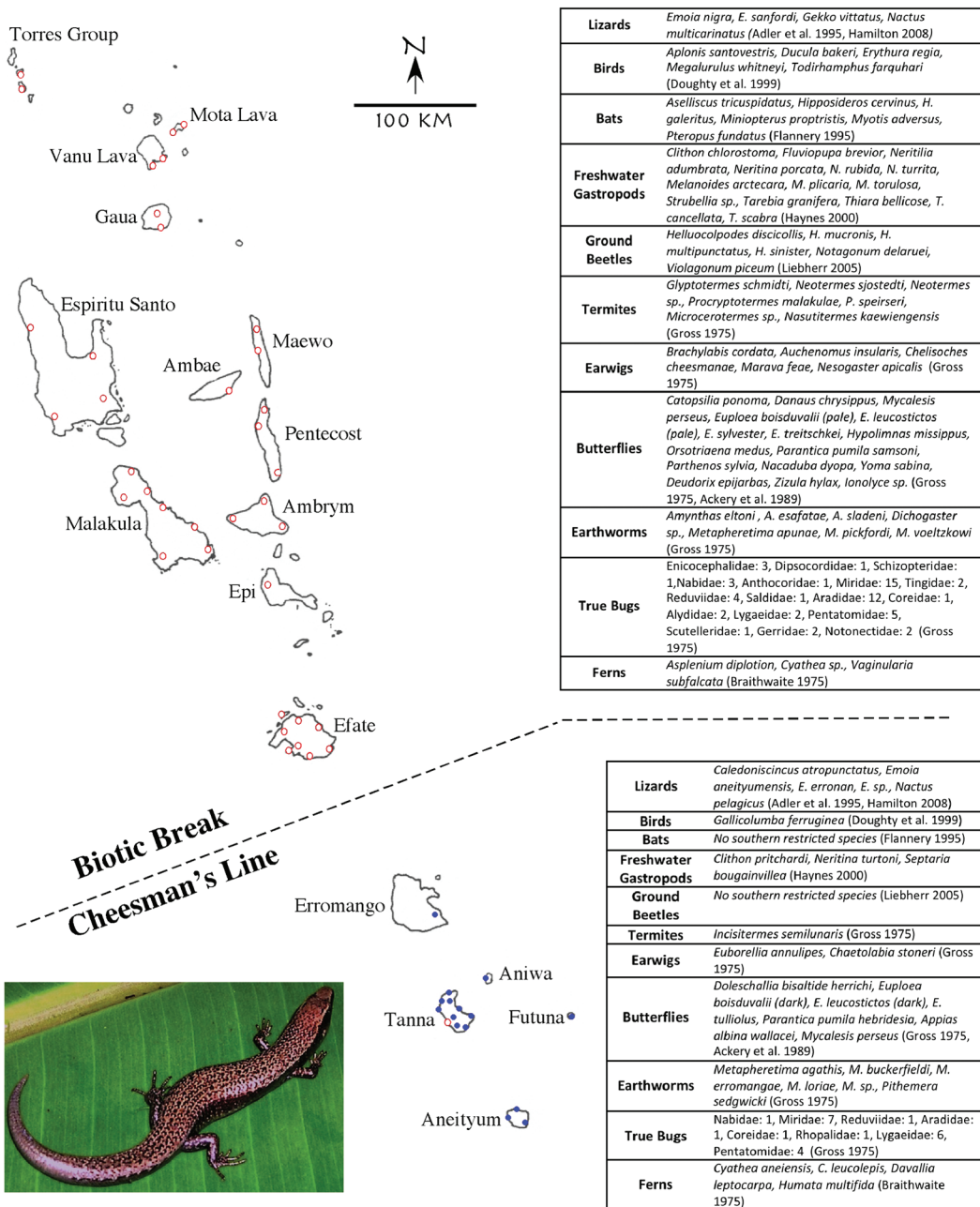


FIGURE 1. Distribution of *Caledoniscincus atropunctatus* in the Vanuatu Archipelago based on fieldwork conducted at 53 sites on 19 islands over a 5 yr period is indicated by circles: survey sites at which *C. atropunctatus* was not observed are indicated with open circles and sites at which *C. atropunctatus* was collected are indicated by closed circles. The location of Cheesman's line, a biotic break within the Vanuatu Archipelago congruent with data from several taxonomic groups including invertebrates, vertebrates, and plants is shown along with the summarized data and sources supporting this barrier. Distribution of *C. atropunctatus* in Vanuatu is congruent with this suggested biotic break because the species is restricted to the islands south of Cheesman's line.

Gondwanan origin of New Caledonia. In addition, the long history of island emergence and isolation is likely responsible for the high rate of endemism in New Caledonia.

The oceanic islands of the Vanuatu Archipelago are considerably younger than New Caledonia (Greene et al. 1988b, Macfarlane et al. 1988, Bauer and Sadlier 2000), and, in general, the squamate fauna is derived from overwater dispersal from New Guinea via the Solomon Islands (Bauer 1988, Allison 1996). Due to its Papuan origin, the Vanuatu squamate fauna is generally more similar to those of other components of the Outer Melanesian Arc, such as the Fiji Archipelago and the Solomon Islands (Hamilton et al. 2009). Of the six reptile species that are components of the native reptile fauna and have distributions that encompass both New Caledonia and the Vanuatu Archipelago, five are Papuan in origin, with *Caledoniscincus atropunctatus* representing the sole species originating in New Caledonia. This disparity may be due to the ocean current between Vanuatu and the New Caledonian Loyalty Islands, because the southerly direction of this flow system has been suggested to promote colonization of New Caledonia from Vanuatu or Fiji (Gibbons 1985, Treml et al. 2008).

Results of Herpetofaunal Surveys in Vanuatu

Fieldwork documented that *Caledoniscincus atropunctatus* was common and widely distributed on Erromango Island, Aneityum Island, and Tanna Island (Figure 1). Collections made during our fieldwork expanded the known range of the species in Vanuatu to include the southern islands of Aniwa and Futuna (Figure 1). On all islands from which it was collected, *C. atropunctatus* was numerically common in both natural and semi-disturbed habitats. This species was found in the leaf litter and was observed basking in patches of sunlight on the forest floor. Although this species was collected from patches of the forest edge adjacent to gardens, villages, and overgrown coconut plantations, it was more abundant in larger patches of coastal forest or interior mixed hardwood forests.

Burt and Burt (1932) also recorded *C. atro-*

punctatus from the central island of Efate. A.M.H. examined that specimen (AMNH 42002) and determined that it is not *C. atropunctatus* but a species of *Emoia* based on the presence of supranasals and fused frontoparietals (Brown 1991). We surveyed eight different localities on and around Efate Island (Figure 1), and *C. atropunctatus* was never observed or collected despite extensive searches of habitats typically occupied by this species elsewhere in Vanuatu. Based on our extensive field surveys and the erroneous single specimen record from Efate we conclude that *C. atropunctatus* does not occur on Efate Island or any of the northern or central islands.

Biogeographic Patterns within the Vanuatu Archipelago

Caledoniscincus atropunctatus is distributed throughout the southern islands of the Vanuatu Archipelago but does not occur in the central and northern islands of this group. This distribution within Vanuatu mirrors the distribution of other lizard species. The gecko *Nactus pelagicus* occurs on the same five southern islands, with its congener, *Nactus multicaarinatus*, being found on the northern and central islands. The distributions of some scincid lizards in the genus *Emoia* also provide support for the presence of a faunal break between northern and central islands (the islands of the Torres Group south to Efate Island) and southern islands (Erromango Island south to Aneityum Island) (Figure 1). *Emoia sanfordi* is distributed throughout the northern and central islands of the Vanuatu Archipelago but does not occur south of Efate Island (Hamilton 2008, Hamilton et al. 2008). Other species of *Emoia* (including *E. aneityumensis* and *E. erronan*) that are similar in body size, habitat use, and ecology to *E. sanfordi* are endemic to southern Vanuatu (Hamilton 2008) and further corroborate the presence of a distinct lizard fauna in the southern islands of the archipelago. In addition, other lizard species such as *Gekko vittatus* (Gekkonidae) and *Emoia nigra* (Scincidae) have a distribution that encompasses the Solomon Islands and the islands of northern Vanuatu but no farther south (Medway and Marshall 1975, Cranbrook

1981, 1985*a,b*, Whitaker and Whitaker 1994, Hamilton Jennings and Austin 2002).

This biogeographic pattern is not restricted to squamate reptiles. Distinctly similar distributional breaks have been documented in plants (Braithwaite 1975, Chew 1975, Gillison 1975), bats (Medway and Marshall 1975, Flannery 1995), birds (Doughty et al. 1999), freshwater gastropods (Haynes 2000), ground beetles (Liebherr 2005), butterflies (Gross 1975, Ackery et al. 1989), and a number of other invertebrates (Gross 1975). Two general distributional patterns can be seen across a broad range of unrelated taxa: (1) a genus is distributed throughout the Vanuatu Archipelago, with the biota of northern and central islands represented by a different assemblage of species than the southern Vanuatu islands; (2) each biotic region in Vanuatu (northern and central versus southern) is represented by a suite of genera, none of which bridges the biotic break between Efate and Erromango islands.

The concordance between the Vanuatu distribution of *C. atropunctatus* and other biota that dispersed from New Caledonia suggests that the occurrence of this species in Vanuatu results from a natural dispersal event from New Caledonia. The widespread distribution throughout the range and the high abundance and frequent occurrence of this species in native, forested habitats provide further support for the inclusion of *C. atropunctatus* as a component of the native reptile fauna of Vanuatu.

The distributional disjunction between the islands of southern Vanuatu and the northern and central islands of Vanuatu was previously noted by Cheesman (1957), who suggested that this break represented a zoogeographic line analogous to Wallace's line but not as sharply defined. Cheesman (1957), in a pre-plate tectonics era, suggested a vicariance model for the pattern she observed. She argued that the floral and faunal similarity of the southern islands of Erromango, Tanna, and Aneityum is due to a land-bridge connection between these islands and presumed that Erromango, Tanna, and Aneityum were previously a single landmass with a connection to New Caledonia. Subsequent hypothesized

connection between this southern landmass and the northern islands of Vanuatu during the Miocene-Pliocene allowed the invasion from the north of the Papuan (Melanesian) biota that is present in southern Vanuatu (Cheesman 1957). The contemporary geological literature, however, has provided a better understanding of the tectonic and geologic history of the Vanuatu Archipelago and indicates that the islands of Vanuatu are young and of oceanic origin (Lee 1975). Further, there is no evidence for a previous connection between the islands of Erromango, Tanna, and Aneityum, nor for a connection between these islands and the Gondwanan landmass of New Caledonia (Lee 1975, Greene et al. 1988*b*). The distributional pattern of the flora and fauna of Vanuatu therefore has been the result of dispersal rather than vicariance.

The biotic disjunction between the islands of northern and central Vanuatu and those of southern Vanuatu may be influenced by climate as well as soil and vegetation type (Figure 2). A PCA of seven climate variables likely to influence the distribution of organisms (such as ectotherms and plants) sensitive to environmental conditions shows clear differences between the two biotic regions (Table 1, Figure 2). The climate data suggest that the environmental conditions of the islands of northern and central Vanuatu are wetter and less thermally variable than on southern Vanuatu islands, as indicated by the increases in mean annual precipitation and minimum temperature of the coldest month in the northern islands, and the greater diurnal temperature variation in the southern islands (Figure 2). Although the environments of the islands clearly vary with latitude, the PCA of the WorldClim bioclimatic data illustrates the environmental differences among islands within the Vanuatu Archipelago.

In addition to the latitudinal cline in environmental conditions, soil type varies among these islands. The islands of Erromango and Tanna have different soils, and fewer soil types, than the central islands of Efate, Epi, Espiritu Santo, Maewo, Malakula, Pentecost, and the Shepherd Islands (Quantin 1975). Habitats and habitat diversity also vary be-

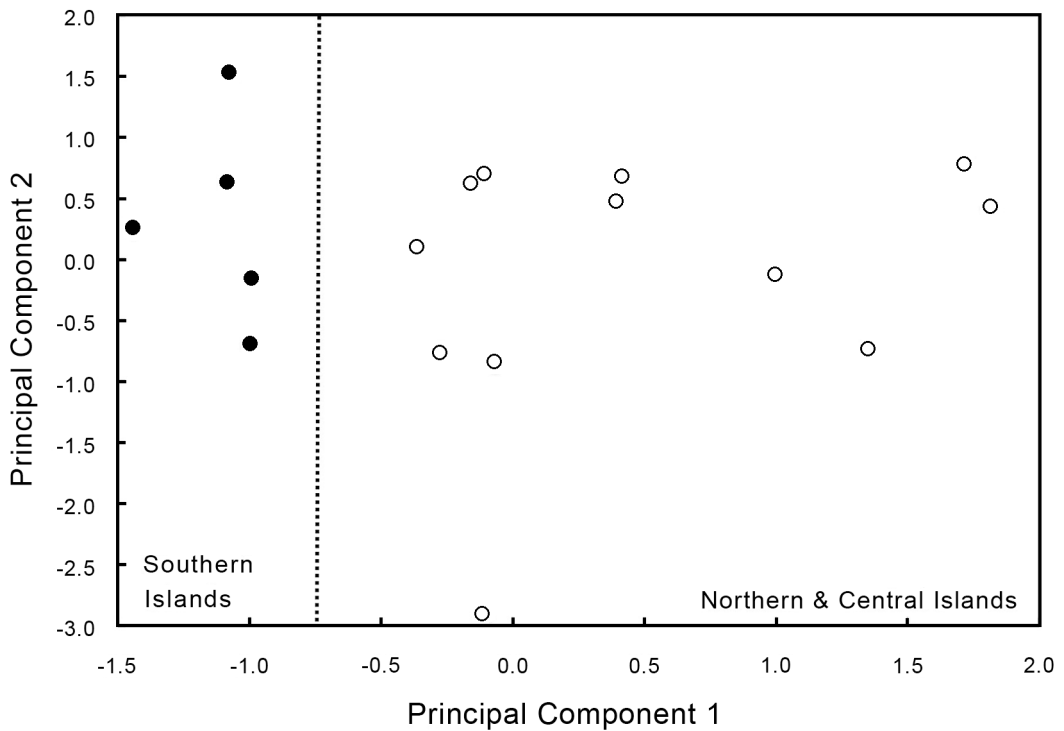


FIGURE 2. Results of a principal components analysis of seven bioclimatic variables influencing the distribution of plants, ectotherms, and invertebrates. Bioclimatic variables included in this analysis and the factor loadings for each principal component are provided in Table 1. Data for the five southern islands (south of Cheesman’s line) are indicated with black circles, and the data for the northern and central Vanuatu Islands (north of Cheesman’s line) are indicated with open circles. Northern and central islands are characterized by greater precipitation, higher minimum temperatures, and lower mean variation in daily temperature than are the islands of southern Vanuatu.

TABLE 1
Climate Variables for Islands in the Vanuatu Archipelago and Loading for Each Variable on the First Two Principal Components

Climate Variable	PC1	PC2
Annual precipitation	0.931	-0.355
Mean diurnal range	-0.929	0.218
Precipitation of the driest month	0.918	-0.305
Precipitation of the wettest month	0.887	-0.430
Minimum temperature of coldest month	0.841	0.525
Annual mean temperature	0.629	0.777
Maximum temperature of warmest month	0.278	0.949

Note: PC1 explains 64.85% of the variation, and PC2 explains an additional 31.89%. Climate variables used in this analysis were obtained from the WorldClim database.

tween the islands of northern and central Vanuatu and the southern Vanuatu islands, likely driven by clinal variation in climatic factors and variation in island soils. Based on vegetation data collected from 54 sites in the Vanuatu Archipelago, Gillison (1975) recognized 12 major structural vegetation types in this island group. Ten of these 12 vegetation types occur only in the northern and central islands: fern forest, fern thicket, and eight types of vine forest; the two others (both types of evergreen vine forest) occur only in the southern islands (Gillison 1975).

Differences in environmental conditions and vegetation structure within the Vanuatu Archipelago in turn influence ecological factors such as resource availability and habitat

suitability (such as the thermal preferences of ectothermic species) and contribute to the observed biotic disjunction. We conclude that dispersal of the flora and fauna from the disparate Papuan and New Caledonian regions combined with intra-archipelago differences in climate, soil, and vegetation have produced one of the most distinct biogeographic disjunctions in the Pacific. We suggest that this discontinuity between the northern (and central islands) of Vanuatu and the southern islands of the archipelago be referred to as Cheesman's line in honor of the contributions of Evelyn Cheesman to the study of Pacific herpetology and biogeography.

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