The butterflies of Vanuatu, with notes on their biogeography (Lepidoptera: Hesperioidea, Papilionoidea)

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Abstract: Following fieldwork in 2000 and 2002, and examination of museum collections in the UK, Australia and the USA, a tabulated list (Tab. 3) of the butterfly fauna of the Pacific island State of Vanuatu is presented. The number of taxa recorded from the country is increased from previous assessments, and several dozen "new" island records made. The fauna comprises 85 subspecies of 69 species (including an estimated 5 species of the group of *Jamides bochus* (Stoll, [1782])) in 42 genera. These are fundamentally widespread taxa, many of which have dispersed widely throughout the Pacific. There are no endemic butterfly genera in Vanuatu, and only two endemic species: *Deudorix mathewi* Druce, 1892, and *Polyura sacco* Smart, 1977. Some 26 described subspecies (31%) are endemic to Vanuatu. Further taxa (*Prosotas russelli* Tennent, 2003, *Ionolyce lachlani* Tennent, 2001, species of the group of *Jamides bochus*) are endemic to the New Hebrides Archipelago (i.e. found also on the Santa Cruz group, politically part of the Solomon Islands). Lines of faunal discontinuity are identified and comments made on regional biogeography.

Die Tagfalter von Vanuatu, mit Anmerkungen zu ihrer Biogeografie (Lepidoptera: Hesperioidea, Papilionoidea)

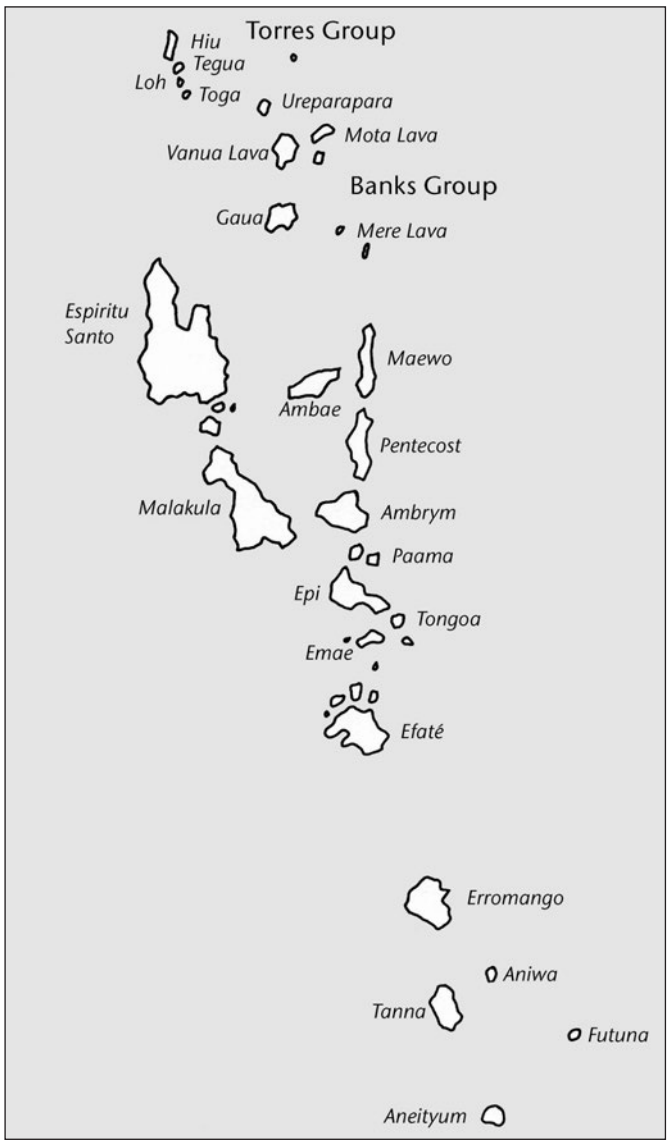
Zusammenfassung: Basierend auf eigenen Freilandarbeiten vor Ort in den Jahren 2000 und 2002 sowie Sammlungsstudien in England, Australien und den USA, wird eine Tabelle (Tab. 3) der Tagfalterfauna des pazifischen Inselstaates Republik Vanuatu vorgestellt. Die Anzahl der von diesen Inseln insgesamt bekannten Arten erhöht sich dadurch, und mehrere Dutzend neue Inselnachweise werden gemacht. Die Fauna umfaßt 69 Arten (in zusammen 85 Unterarten, einschließlich etwa 5 Arten aus der Gruppe von *Jamides bochus* (Stoll, [1782])) aus 42 Gattungen. Es handelt sich dabei in der Regel um weitverbreitete Taxa, von denen viele auf den pazifischen Inseln generell ein großes Areal besiedeln. Es gibt keine endemischen Gattungen auf Vanuatu, und nur zwei Arten sind endemisch: *Deudorix mathewi* Druce, 1892 und *Polyura sacco* Smart, 1977. Ungefähr 26 beschriebene Subspezies (31%) sind endemisch auf Vanuatu. Einige weitere Taxa (*Prosotas russelli* Tennent, 2003, *Ionolyce lachlani* Tennent, 2001 sowie die Arten der Gruppe von *Jamides bochus*) sind Endemiten des Archipels der Neuen Hebriden (sie finden sich also auch auf der Santa-Cruz-Inselgruppe, die politisch zu den Solomonen gehört). Die Grenzlinien der Faunenregionen werden aufgezeigt und Kommentare zur regionalen Biogeografie vorgetragen.

Introduction

The 100 or so islands, islets and atolls of the Republic of Vanuatu (Map 1) lie south of the Equator, between 13° and 23° South, in the south Pacific Ocean, extending in an approximately "Y"-shaped chain for some 1200 km from the Torres Island group in the north, to the tiny uninhabited islands of Mathew and Hunter in the south. Together with the Santa Cruz Islands (Solomon Islands) north of the Torres group, the islands form the New Hebrides archipelago, lying almost 2000 km northeast of Brisbane, 400 km southeast of San Cristobal in the Solomons Archipelago, 400 km northeast of New Caledonia and the Loyalties, and 800 km west of Fiji. Whilst many islands are small in area and low in elevation, others are substantial. Espiritu Santo (4000 km²), Malakula (2070 km²), Efaté (980 km²) and Erromango (900 km²) are the largest in area and Espiritu Santo also has the highest peak (Mount Tabwemasana is 1879 m), whilst Ambae, Ambrym and Tanna each have peaks higher than 1000 m. The total land area of Vanuatu is in the region of 12 000 km². Clothed with evergreen rainforest vegetation, the islands are fundamentally volcanic, with many volcanoes currently active. These include the Yasur volcano on Tanna, surely one of the most accessible active volcanoes in the world (and dramatically more active following an earthquake in 1994), which is a major tourist attraction. Most islands are extremely rugged and mountainous with, outside Efaté, Malakula, Espiritu Santo and Tanna, little or nothing in the way of roads and other infrastructure.

The archipelago is part of a continuous island arc system extending from the Bismarck and Solomons archipelagos, to Fiji and Tonga. An integral part of the Pacific "Ring of Fire", and situated on the leading (western) edge of the Pacific plate, Vanuatu remains tectonically highly active, with many islands undergoing substantial changes in geologically recent times. There have been major volcanic eruptions on islands other than Tanna. For example, Mere Lava was said to have been erupting in 1906 (Mallick 1971: 12), and local people are reluctant to visit Lopevi (between Paama and Epi) due to ongoing eruptions which caused local schools on Epi to close in 2001 because of drifting smoke and ash. Earthquakes also affect the islands. The Port Resolution area in southeastern Tanna was uplifted some 20 m as a result of severe earthquakes in 1878 and 1888 (Mawson 1905), and the largest earthquake ever reported in Vanuatu, when several buildings in Port Vila and roads on Efaté were damaged, occurred in January 2002, a few days before the author arrived to carry out fieldwork which provides the basis for this paper.

Spanning 10 degrees of latitude, the north of Vanuatu is predictably both warmer and wetter than the southern islands. In general terms, the climate is tropical in the north with little change in mean monthly temperature throughout the year, becoming gradually cooler and sub-



Map 1: The islands of Vanuatu.

tropical in the south, where there are more pronounced "seasons". The southern islands are cool and dry from April to October, and both warmer and more humid between November and March. On some islands, prevailing southeasterly winds cause the windward aspects of large islands to be significantly wetter than northern or western slopes. Climatic conditions on any island may vary from coast to coast, or with altitude, and the substantial mountain ranges of most of the larger islands are sufficiently high to affect weather conditions locally. The trade winds produce orographic cloud and rainfall over all except Aniwa (Carney & Macfarlane 1979), and striking climatic change from the northern to the southern New Hebrides probably accounts for significant floristic differences (Solem 1958). The characteristic vegetation of Vanuatu is evergreen rainforest that covers some 75% of the country (Chambers 1992: 29).

Cyclones, common between November and April, are frequently devastating and account for considerable habitat destruction. It is not known what impact the combined effects of volcanic activity and climate has had on island faunas, but it can be assumed that, at least in the case of some major eruptions, invertebrate (and other) faunas have occasionally been dramatically affected at intervals in the past, either locally or across a whole island.

The effects of "global warming" may, with predicted mid- to long-term rises in sea level, affect some of the islands of Vanuatu (e.g., the Reef islands in the Banks group are only 12 m above sea level), but at present only anecdotal evidence exists of recent changes. Interestingly, a village chief on the island of Loh in the Torres group, who had spent all of his long life on that island, related to the author how higher tides seen in recent years had resulted in swift erosion of a spit of land on the northeast of the island, with an associated loss of coconut trees through frequent immersion in salt water.

For some years, the Environment Unit of the Government of Vanuatu has been engaged in biodiversity studies of a number of botanical and vertebrate groups in Vanuatu. Independently, the author carried out a study of Vanuatu's butterflies in 2000 and 2002, the results of which were reported with a limited distribution (Tennent 2003b [unpubl.]). Since then, additional records were collated following visits to a number of Institutions with Pacific collections (see acknowledgements) in the UK, Australia and the USA. The butterflies of the Santa Cruz islands have already been dealt with (Tennent 2002a); this paper presents current knowledge of Vanuatu's butterflies, and provides brief notes on the biogeography of the New Hebrides Archipelago.

The butterflies

Between the 18th and early 20th centuries, butterflies (and other animals) were collected in Vanuatu by a number of "naturalists/explorers", who visited the islands briefly on global voyages of exploration. These included Gervase Mathew, Staff Paymaster Royal Navy, and Charles Morris Woodford (Tennent 1999a), who was to become the first Resident Commissioner of the Solomon Islands. Around the turn of the 20th century, Commander J. J. Walker also collected briefly on the islands of Efaté, Malakula, Tanna and Espiritu Santo (Walker 1902), finding (Gabriel 1936) the only specimen of *Papilio fuscus nomus* Gabriel, 1936 known for many years (Tennent 2001b). The intrepid lady entomologist Evelyn Cheesman, whose adventurous exploits were described in detail by her in a number of popular books, stayed on several Vanuatu islands for some months in 1929–1930. The collections of The Natural History Museum (BMNH) in London contain a small number of butterfly specimens collected by each of these people. More recently, the late Father Albert Sacco (Tennent 2003a), who lived for many years on Tanna, Pentecost, and Aneityum, made a collection of butterflies, some of which were presented to the Cultural Centre in Port Vila, where they have sadly suffered the ravages of insect pests (Tennent 2003d). No doubt others have pursued butterflies whilst visiting Vanuatu; the only significant private collection known to the author is that

of Rob Lachlan (Queensland, Australia), who kindly allowed incorporation of his data in this paper.

The first systematic attempt to list the butterflies of Vanuatu in any detail followed the joint Royal Society/ Percy Sladen New Hebrides Expedition (RSE), which visited Espiritu Santo, Malakula, Efaté, Erromango, Tanna and Aneityum between July and October 1971. Studies undertaken on the expedition were wide ranging, and the butterflies (and other selected invertebrate groups) were subsequently dealt with by Gross (1975), who reported 38 butterfly genera (1 endemic), and 63 species (4 endemic) from Vanuatu (Gross 1975: 393). There is some confusion here; a tabulated list of butterflies (Gross 1975: 417) also lists 38 genera (including *Pelopidas* Walker, 1870, *Delias* Hübner, [1819], *Arhopala* Boisduval, 1832, *Syntarucus* Butler, [1901] [*Leptotes* Scudder, 1876] and *Zizeeria* Chapman, 1910 [*Famegana* Eliot, 1973], none of which was actually reported as occurring in Vanuatu), but did not indicate which genus was considered to be endemic. The list also included *Graphium* Scopoli, 1777, believed to have been seen, but not collected. In fact, all the genera recorded by Gross are widespread throughout the region. Robinson (1976: 47) recorded 6 butterfly species seen or collected by the RSE as new records for Vanuatu: *Graphium sarpedon* (Linnaeus, 1758), *Ionolyce* sp. [= *lachlani* Tennent, 2001], *Zizula hylax* (Fabricius, 1775), *Hypolimnas misippus* (Linnaeus, 1764), *H. pithoeka* Kirsch, 1877, and *Parthenos sylvia* (Cramer, 1775). Of these, *H. pithoeka* (see Tennent 2003d) and *G. sarpedon* require confirmation.

Of the 63 species (4 endemic) recorded by Gross (1975: 393), only *Nacaduba novaehebridensis* Druce, 1892, and *Jamides morphoides* Butler, 1884, were listed by him as endemic species although, once again, neither was tabulated as occurring on any Vanuatu island (Gross 1975: 418). In addition to being widespread throughout Vanuatu, *N. novaehebridensis* occurs in the Santa Cruz group (Solomon Islands) and the Solomons Archipelago (Tennent 2002b), whilst *J. morphoides* is also known from the Santa Cruz group (Tennent 2001d, 2002b). Two butterfly species are currently believed to be endemic to Vanuatu: *Polyura sacco* Smart, 1977, described 6 years after the RSE, and *Deudorix mathewi* Druce, 1892, regarded by Gross (and others) as a race of *D. epijarbas* Moore, 1857 (Tennent 2003g). Material from the RSE was deposited in the BMNH, London, and the South Australian Museum, Adelaide. Tab. 1 (below) incorporates only those butterfly species actually reported from Vanuatu by the expedition. Nomenclature has been standardised in this and subsequent tables, to avoid confusion.

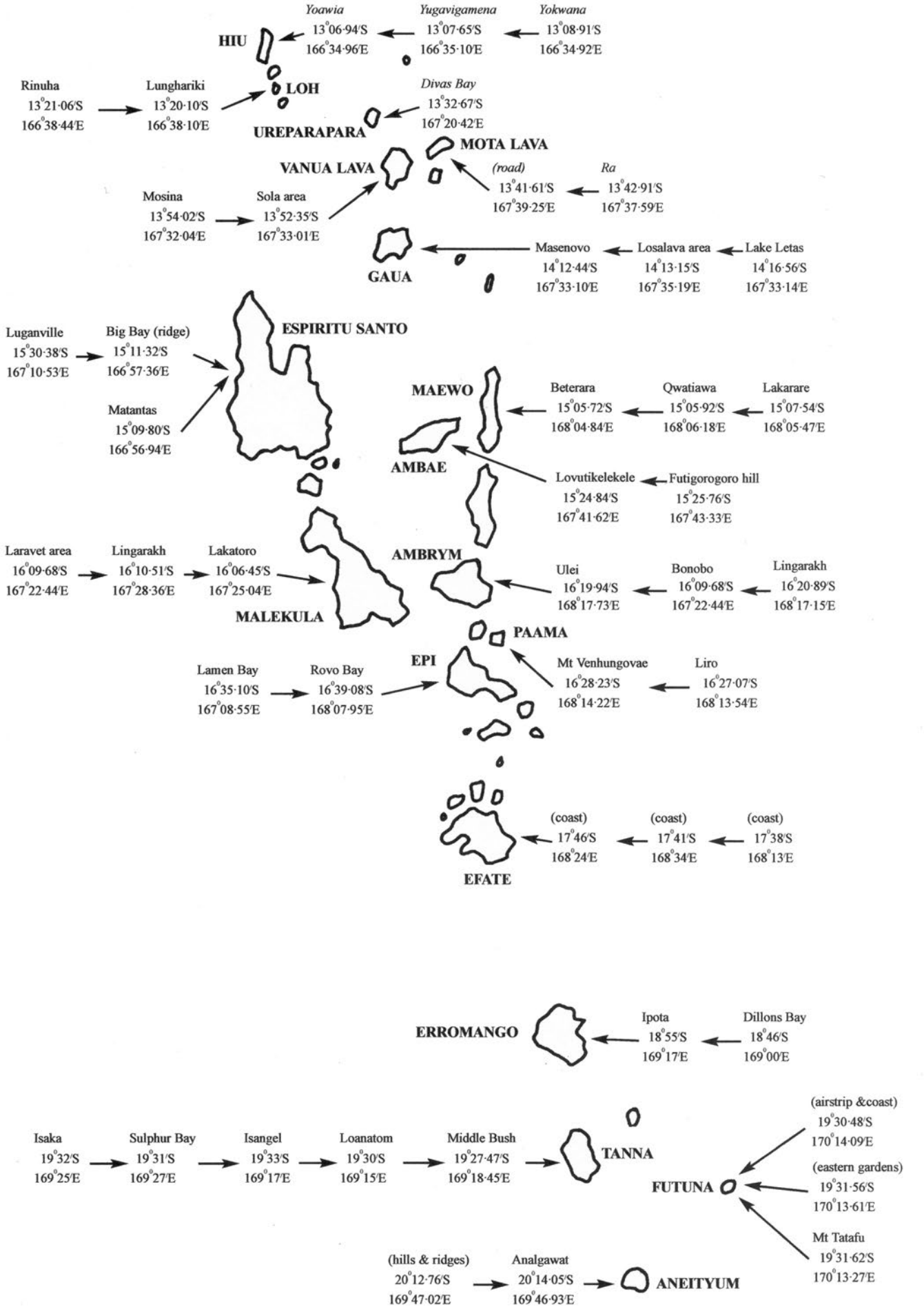
Several taxa of the group of *Jamides bochus* (Stoll, [1782]) of lycaenid species, a complex group presenting some fundamental identification difficulties, have been recorded from Vanuatu and it has not yet been possible to resolve their systematics and nomenclature. *Jamides* Hübner, [1819] remains one of the most complicated groups in the Polyommatini and has never been revised systematically (Hirowatari 1992). Structure of the male genitalia, of fundamental value in identification of many lycaenid butterflies, appears to be of only limited use in the *Jamides bochus*-group. In particular, the shape of the valva, diagnostic in many other polyommatine butterflies, is variable in *bochus* and its allies, consisting of a broad structure with an open, rounded posterior indentation somewhat variable in size. Valvae may be similar in species which are quite different in phenotype. In Vanuatu and the Pacific islands (Rarotonga, Cook Islands, Fiji) almost 20 names have been bestowed on *bochus*-group taxa: *J. goodenovii* Butler, 1876, *J. pulcherrima* Butler, 1884, *J. morphoides* Butler, 1884, *J. carissima* Butler, 1875, and *J. kava* Druce, 1892, have all been reported from Vanuatu. It is planned to address this subject in due course but, because difficulties in identification make assessment of island distribution unreliable at present, species are referred to here and tabulated as "*Jamides bochus*-group".

Further valuable research in Vanuatu was carried out by Chris Samson, who collected and photographed butterflies during a visit to Efaté from January to March 1983. The bulk of this material was deposited in the self-styled "National Butterfly Museum", known also as the Saruman Museum, Sussex, England (Samson, pers. comm.), and was dispersed when the historically important premises and its contents were auctioned by Sothebys in October 1983. The results of Samson's Efaté fieldwork were published in the form of the first list devoted to the Vanuatu butterflies (Samson 1983) and publications dealing with systematics of certain groups (Samson 1982, 1984, 1986). A number of genera and species reported by Samson (1983) are treated here as requiring confirmation (see below). These include *Eurema candida* (Stoll, 1782), *Appias albina* (Boisduval, 1836), *Arhopala*, *Curetis* Hübner, [1819], *Tartesa* Hirowatari, 1992, *Nacaduba deplorans* (Butler, 1875), *Pithecops dionisius* (Boisduval, 1832), *Morphopsis* Oberthür, 1880, *Vindula* Hemming, 1934 and *Yoma algina* (Boisduval, 1832).

Fieldwork in preparation for the present paper was a natural extension of the author's research into Solomon Islands butterflies (Tennent 2002b). Following fieldwork in the Santa Cruz group (Tennent 2002a), the Torres group of islands were visited in August and September 2000, in order to investigate faunal affinities between the butterflies of these two island groups. This preliminary visit highlighted unexpected faunal differences between the groups and, with the agreement of Mr Ernest Bani, Head of the National Environment Unit, Government of Vanuatu, it was agreed that a more comprehensive study might prove productive. Further fieldwork was therefore carried out from January to May 2002. During these two combined periods of fieldwork, the following islands were visited: Hiu, Tegua (very briefly, en route from Loh to Hiu), Linua, Loh (2 visits), Ureparapara, Mota Lava, Vanua Lava (3), Gaua, Espiritu Santo (3), Ambae, Maewo, Malakula (2), Ambrym, Paama, Epi, Efaté (sev-

Table 1: Species collected or seen by the Royal Society Expedition 1971, adapted from Gross (1975).

Taxon	Espiritu Santo	Malekula	Efate	Erromango	Tanna	Aneityum
Hesperiidae						
Badamia exclamationis (Fabricius, 1775)			×			×
Badamia atrox (Butler, 1877)			×			
Borbo cinnara (Wallace & Moore, 1866)	×	×		×		×
Papilionidae						
Papilio fuscus Goeze, 1779	×	×	×	×	×	×
Pieridae						
Catopsilia pomona (Fabricius, 1775)	×		×			
Catopsilia pyranthe (Linnaeus, 1758)	×	×			×	
Eurema hecabe (Linnaeus, 1758)	×	×	×	×	×	×
?*Appias athama* (Blanchard, 1848)						×
Cepora perimale (Donovan, 1805)		×	×		×	
Belenois java (Sparrmann, 1768)	×	×	×		×	
Lycaenidae						
Deudorix mathewi Druce, 1892			×			
Nacaduba dyopa (Herrich-Schäffer, 1869)	×		×			
Nacaduba biocellata (C. & R. Felder, 1865)			×		×	
Nacaduba mallicollo Druce, 1892		×	×		×	
Catopyrops nebulosa Druce, 1892			×	×		
Ionolyce lachlani Tennent, 2001	×					
group of *Jamides bochus* (Stoll, [1782])		×	×	×		
Catochrysops taitensis (Boisduval, 1832)	×		×	×		×
Euchrysops cnejus (Fabricius, 1798)	×	×	×	×		×
Lampides boeticus (Linnaeus, 1767)	×	×				
Zizula hylax (Fabricius, 1775)	×					
Zizina labradus (Godart, 1824)	×	×	×	×		
Luthrodes cleotas (Guérin-Méneville, 1838)	×		×		×	
Nymphalidae: Danainae						
Parantica pumila (Boisduval, 1859)	×	×	×	×	×	×
Tirumala hamata (Macleay, 1827)	×	×	×	×	×	
Danaus plexippus (Linnaeus, 1758)	×	×	×	×	×	×
Danaus affinis (Fabricius, 1775)			×	×	×	
Danaus chrysippus (Linnaeus, 1758)	×	×				
Euploea leucostictos (Gmelin, 1790)	×		×	×		×
Euploea tulliolus (Fabricius, 1793)				×	×	
Euploea boisduvalii Lucas, 1853	×		×	×	×	×
Euploea treitschkei Boisduval, 1832			×	×		
Euploea lewinii C. & R. Felder, [1865]	×		×	×	×	×
Nymphalidae: Satyrinae						
Orsotriaena medus (Fabricius, 1775)	×					
Melanitis leda (Linnaeus, 1758)	×	×	×	×	×	×
Nymphalidae: other subfamilies						
Parthenos sylvia (Cramer, 1775)	×					
Doleschallia browni Salvin & Godman, 1877	×	×	×			
Hypolimnas antilope (Cramer, 1777)	×		×			×
Hypolimnas octocula (Butler, 1869)	×	×	×	×	×	×
Hypolimnas bolina (Linnaeus, 1758)	×		×	×	×	×
Hypolimnus misippus (Linnaeus, 1764)	×					
Yoma sabina (Cramer, [1780])		×				
Junonia villida (Fabricius, 1787)	×	×	×	×		×
Vagrans egista (Cramer, [1779])	×		×	×		×
Acraea andromacha (Fabricius, 1775)		×		×		×



Map 2: Collecting localities: 2001 and 2002 fieldwork.

Table 2: Species/island data following fieldwork in 2000 and 2002. — Explanation: **1** = only one individual seen; **2** = two or more individuals seen (infrequent); **3** = seen on all/most days in all/most habitats, or in moderate to large numbers in one or more habitats — this is the "default" and covers a wide range of abundance, from uncommon (infrequent) to abundant — may only be common locally; **4** = present in unusually large numbers in all or some habitats (the dominant species).

Taxon	Torres			Banks				Espiritu Santo	Ambae	Maewo	Malakula	Ambrym	Paama	Epi	Efate	Erromango	Tanna	Futuna	Aneityum
	Hiu	Tegua	Loh	Ureparapara	Mota Lava	Vanua Lava	Gaua												
HESPERIIDAE																			
Badamia exclamationis (FABRICIUS, 1775)	2		3	2	2	2	2	2			2	2	2	1	3		2	2	2
Badamia atrox (BUTLER, 1877)																2	1		1
Hasora chromus (CRAMER, [1780])				3	3	3	3	2	2	2	3	2	3	3				2	
Borbo cinnara (WALLACE & MOORE, 1866)	3		3				3	3	2	2	3	3	3	3	2	3	3	3	3
Pelopidas lyelli (ROTHSCHILD, 1915)					2	2					2								
PAPILIONIDAE																			
Papilio fuscus GOEZE, 1779	3		3	3	3	3		3	3	3	3	3	3	3	3	3	3	3	2
PIERIDAE																			
Catopsilia pomona (FABRICIUS, 1775)					3	2	2	3	3	2	3	3	3	3	3	3	2		1
Catopsilia scylla (LINNAEUS, 1764)																3	2	3	
Catopsilia pyranthe (LINNAEUS, 1758)	3	2	3	2	2		3	2	3		2	2	3	2					
Eurema hecabe (LINNAEUS, 1758)	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Appias athama (BLANCHARD, 1848)					2		2	3	2		3		1	3		2		2	
Appias paulina (CRAMER, [1777])																		3	
Cepora perimale (DONOVAN, 1805)								3			3			3	3	3	3	3	
Belenois java (SPARRMANN, 1768)			3				3	3	3		3		3	3	3	3	3	3	2
LYCAENIDAE																			
Deudorix mathewi DRUCE, 1892			3					1	1	1				2		2	3		
Petrelaea tombugensis (RÖBER, 1886)								2		2	2						1		
Nacaduba dyopa (HERRICH-SCHÄFFER, 1869)	2		3			2	2		1		2	1	1	2	2	2	2	2	
Nacaduba biocellata (C. & R. FELDER, 1865)			2								3	2	2	2		3	1	2	3
Nacaduba kurava (MOORE, 1858)				3		3	2		2		2			2		2	2	3	
Nacaduba novaehebridensis DRUCE, 1892			3		2	2	3	3	3	3	3	3	3	3	3	3	3	3	2
Nacaduba mallicollo DRUCE, 1892				2		2	3	3	3	2	2	2	3	3		2	3	4	
Prosotas russelli TENNENT, 2003								1		2	2								
Prosotas patricae TENNENT, 2003																		3	
Catopyrops nebulosa DRUCE, 1892			3		2	3	3	3	3	3	3	3	3	3	3	3	3	3	2
Ionolyce lachlani TENNENT, 2001			3				1	1	1	2	2	2	3	3	1	1	2	3	1
group of *Jamides bochus* (STOLL, [1782])	3		3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Jamides celeno (CRAMER, [1775])	4		3	3	3	3	3	3	3	3	3	3	3	3	3		3		
Catochrysops panormus (C. FELDER, 1860)																3	3	3	3
Catochrysops taitensis (BOISDUVAL, 1832)			3			2				3	3		3	2		3	3	3	3
Euchrysops cnejus (FABRICIUS, 1798)	3		3	2	3	3	4	3	3	3	3	3	3	2	3	3	3	3	3
Everes lacturnus (GODART, 1824)									1		3								
Lampides boeticus (LINNAEUS, 1767)	3		2	3	3	3	3	3		3	3	3	3	3	3	2	3	3	3
Famegana alsulus (HERRICH-SCHÄFFER, 1869)																			2
Zizula hylax (FABRICIUS, 1775)	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Zizina labradus (GODART, 1824)	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Leptotes plinius (FABRICIUS, 1793)															3				
Luthrodes cleotas (GUÉRIN-MÉNÉVILLE, 1838)						3	2	2	2	2	4	2	2	3			2	3	2

Nymphalidae: Danainae																			
Parantica pumila (Boisduval, 1859)								2	3	3	3		3	2	2	3	3	3	3
Tirumala hamata (Macleay, 1827)								3	2	2	2		2	2	3	3	2		
Danaus plexippus (Linnaeus, 1758)			2					2	3		2		2	2	2	3	2		
Danaus affinis (Fabricius, 1775)	2		3												1			2	
Danaus chrysippus (Linnaeus, 1758)															2	2			
Euploea sylvester (Fabricius, 1793)	3	3	3						2										
Euploea leucostictos (Gmelin, 1790)	3	3	3	3	3		3	3	3	3	3	3	3	3	3	3	3	3	3
Euploea tulliolus (Fabricius, 1793)								2	2	1	2			2		3	3	2	
Euploea boisduvalii Lucas, 1853	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Euploea treitschkei Boisduval, 1832	3		3	2	2						3				2	2			
Euploea lewinii C. & R. Felder, [1865]								3			3	3	3	3	3	3	3		2
Nymphalidae: Satyrinae																			
Mycalesis perseus (Fabricius, 1775)						3		2	3	3	3	3	3	2					
Melanitis leda (Linnaeus, 1758)						2		2	2	2	2	2	2	2	2	2	2	2	3
Nymphalidae: other subfamilies																			
Polyura sacco Smart, 1977								1								2	2		
Parthenos sylvia (Cramer, 1775)	2		3	2		2		3		3									
Doleschallia browni Salvin & Godman, 1877	3	1	3	3		3	3	3	3	3	3	3	3	3	3	3	3	3	3
Hypolimnas antilope (Cramer, 1777)	2		2		1		2	2	2	2	2	3			2	2			2
Hypolimnas pithoeka Kirsch, 1877	2		3											1					
Hypolimnas octocula (Butler, 1869)							2	3	3	3	3	3	3	3	3	2	3	3	2
Hypolimnas bolina (Linnaeus, 1758)	3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2
Hypolimnus misippus (Linnaeus, 1764)														1					
Yoma sabina (Cramer, [1780])	3		3		3	3	3		3	3	3	3	3	3	3	3	3	3	1
Junonia villida (Fabricius, 1787)	3		3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
Vagrans egista (Cramer, [1779])	3		3	3	3	3	3	3	3	3	3		3			3	2	4	4
Acraea andromacha (Fabricius, 1775)											3			4		3	2		

eral), Erromango (2), Tanna (3), Futuna and Aneityum. Major collecting localities are plotted on Map 2.

A combination of unseasonally heavy rainfall at the start of the 2002 fieldwork, dangerous sea conditions, and the vagaries of domestic airline schedules, necessitated some changes in travel plans, and it was not possible to visit all the islands intended. In particular, two attempts to reach remote Mere Lava (where there is no airstrip) were foiled by rough seas, and the airstrip on Emae was closed due to the presence of crab holes. Additionally, poor weather in the southern islands caused last minute changes to Vanair schedules, and left insufficient time to visit Pentecost. A decision was made not to visit Aniwa, a low and heavily-populated island, since flights to and from the island are weekly and it was decided time could be more productively spent on other islands.

Eleven new taxa (3 species and 8 subspecies) were described as a result of the project, and three lycaenid genera (*Everes* Hübner, [1819] [Malakula, Ambae], *Petrelaea* Toxopeus, 1929 [Maewo, Malakula, Tanna], and *Prosotas* Druce, 1891 [Espiritu Santo, Maewo, Malakula, Futuna]) were recorded from Vanuatu for the first time. Additionally, numerous "new" island records were made.

Species recorded by the author during this project are tabulated below, together with indication of relative abundance. It should be pointed out that these data pertain only to the author's observations during fieldwork, and may not represent more general, or long-term, relative abundance.

As part of a related project to prepare a species checklist of Pacific islands butterflies (in prep.), the author visited a number of museums in the UK, Australia and the USA, when further data additional to those already reported (Tennent 2003b [unpubl.]) were collated. A consolidated systematic list of Vanuatu butterfly species and distribution, taking account of all data sources, is provided in Tab. 3.

Unconfirmed species

In addition to species tabulated in Tab. 3, reported occurrence of an additional 8 genera and 17 species are questioned or remain unconfirmed. This group includes those species (e.g. *Graphium sarpedon*, *Pieris rapae* (Linnaeus, 1758)), which might reasonably be considered "accidental" visitors or introductions.

Table 3: Butterflies of Vanuatu: Consolidated species/island data from published sources, museum and private collections.

Taxon	Torres				Banks							Espiritu Santo	Ambae	Maewo	Pentecost	Malakula	Ambrym	Paama	Epi	Tongoa	Efate	Erromango	Aniwa	Tanna	Futuna	Aneityum
	Hiu	Tegua	Loh	Toga	Ureparapara	Reef Islands	Mota Lava	Vanua Lava	Mota	Gaua	Mere Lava															
Hesperiidae																										
Badamia exclamationis exclamationis (Fabricius, 1775)	×		×	×	×		×	×	×	×		×			×	×	×	×	×		×			×	×	×
Badamia atrox flava Evans, 1934												×				×			×		×	×		×		×
Hasora chromus bilunata (Butler, 1883)					×		×	×		×		×	×	×		×	×	×	×		×	×			×	×
Borbo cinnara (Wallace & Moore, 1866)	×		×						×	×		×	×	×		×	×	×	×		×	×		×	×	×
Pelopidas lyelli mathewi (Evans, 1937)							×	×				×			×	×		×								
Papilionidae																										
Papilio fuscus nomus Gabriel, 1936	×		×																							
Papilio fuscus hypsicles (Hewitson, 1868)					×		×	×	×	×		×	×	×	×	×	×	×	×		×					
Papilio fuscus burgessi (Samson, 1982)																						×		×	×	×
Pieridae																										
Catopsilia pomona pomona (Fabricius, 1775)		×					×	×		×		×	×	×	×	×	×	×	×		×	×		×	×	×
Catopsilia scylla gorgophone (Boisduval, 1836)												×										×		×	×	
Catopsilia pyranthe lactea (Butler, 1870)	×	×	×	×	×		×		×	×		×	×		×	×	×	×	×		×	×		×	×	×
Eurema hecabe sulphurata (Butler, 1875)	×	×	×	×	×		×	×	×	×	×	×	×	×	×	×	×	×	×		×	×		×	×	×
Appias athama athama (Blanchard, 1848)							×			×		×	×			×		×	×		×	×	×		×	×
Appias paulina ega (Boisduval, 1836)												×									×			×	×	
Cepora perimale jeanneli Viette, 1950												×		×		×			×		×	×		×	×	
Belenois java peristhene (Boisduval, 1859)			×						×	×		×	×		×	×	×	×	×		x	×	×	×	×	×
Delias nysa santo Talbot, 1937												×														
Lycaenidae																										
Deudorix mathewi mathewi Druce, 1892			×						×			×	×	×		×	×		×		×					
Deudorix mathewi narua Tennent, 2003																						×		×		×
*Petrelaea tombugensis (*Röber, 1886)												×		×		×								×		
Nacaduba dyopa lepidus (Tennent, 2000)	×		×					×		×		×	×			×	×	×	×		×	×		×	×	×
Nacaduba biocellata armillata (Butler, 1875)												×		×	×	×	×	×	×		×	×		×	×	×
Nacaduba kurava euretes (Druce, 1891)					×			×	×	×	×	×	×			×	×		×		×	×		×	×	
Nacaduba novaehebridensis nubilus Tennent, 2003			×																							
Nacaduba novaehebridensis novaehebridensis Druce, 1892							×	×		×		×	×	×		×	×	×	×		×	×		×	×	×
Nacaduba mallicollo mallicollo Druce, 1892					×			×		×		×	×	×	×	×	×	×	×		×	×		×	×	
Prosotas russelli Tennent, 2003												×		×		×										
Prosotas patricae Tennent, 2003																									×	
Catopyrops nebulosa opacus Tennent, 2003			×																							
Catopyrops nebulosa nebulosa (Druce, 1892)							×	×		×		×	×	×		×	×	×	×		×	×		×	×	×
Ionolyce lachlani Tennent, 2001			×	×						×		×	×	×		×	×	×	×		×	×		×	×	×
group *of Jamides bochus* (Stoll, [1782])	×		×		×		×	×	×	×		×	×	×	×	×	×	×	×		×	×		×	×	×
Jamides celeno niger Tennent, 2003	×		×																							
Jamides celeno evanescens (Butler, 1875)					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×			×		
Catochrysops panormus caerulea Tite, 1959																					×	×		×	×	×
Catochrysops taitensis (Boisduval, 1832)			×					×			×	×		×		×		×	×		×	×		×	×	×
Euchrysops cnejus cnidus Waterhouse & Lyell, 1914	×		×		×		×	×	×	×		×	×	×	×	×	×	×	×		×	×		×	×	×

*Everes lacturnus palliensis (*Ribbe, 1899)												×			×										
Lampides boeticus (Linnaeus, 1767)	×		×		×		×	×	×	×		×	×	×	×	×	×	×	×		×	×		×	×	×
*Famegana alsulus (*Herrich-Schäffer, 1869)																					×					×
Zizula hylax dampierensis (Rothschild, 1915)	×		×		×		×	×	×	×		×	×	×	×	×	×	×	×		×	×		×	×	×
Zizina labradus caduca (Butler, 1875)	×		×		×		×	×		×	×	×	×	×		×	×	×	×		×	×		×	×	×
Leptotes plinius pseudocassius (Murray, 1873)							×					×			×	×		×			×	×		×		
Luthrodes cleotas excellens (Butler, 1875)								×		×		×	×	×	×	×	×	×	×		×			×	×	×
Nymphalidae: Danainae																										
Parantica pumila samsoni Ackery, Taylor & Renevier, 1989												×	×	×	×	×	×	×	×		×					
Parantica pumila hebridesia (Butler, 1875)																						×		×	×	×
Tirumala hamata moderata (Butler, 1875)												×	×	×	×	×	×	×	×		×	×		×	×	
Danaus plexippus (Linnaeus, 1758)			×				×	×	×			×	×		×	×	×	×	×		×	×	×	×	×	×
Danaus affinis atchinii Tennent, 2003	×		×																							
Danaus affinis albistriga Talbot, 1943									×			×				×			×		×	×		×	×	×
Danaus chrysippus petilia (Stoll, 1790)									×			×				×		×			×	×		×	×	×
Euploea sylvester tristis (Butler, 1866)	×	×	×	×				×		×		×	×		×	×			×							
Euploea leucostictos iphianassa (Butler, 1866)	×	×	×																			×	×	×	×	×
Euploea leucostictos novarumebudum (Carpenter, 1942)					×		×	×	×	×		×	×	×	×	×	×	×	×	×	×					
Euploea tulliolus forsteri (C. & R. Felder, 1867)												×	×	×	×	×			×		×	×	×	×	×	
Euploea boisduvalii torvina (Butler, 1875)	×	×	×																			×		×	×	×
Euploea boisduvalii bakeri (Poulton, 1927)					×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×				
Euploea treitschkei jessica (Butler, 1869)	×	×	×		×		×	×	×	×		×	×	×	×	×	×		×		×	×			×	
Euploea lewinii lilybaea Fruhstorfer, 1911		×							×			×	×		×	×	×	×	×		×	×		×	×	×
Nymphalidae: Satyrinae																										
Mycalesis perseus lugens (Butler, 1875)								×				×	×	×	×	×	×	×	×		×	×				
Orsotriaena medus mutata (Butler, 1875)									×			×			×	×	×		×		×					
Melanitis leda solandra (Fabricius, 1775)								×			×	×	×	×	×	×	×	×	×		×	×		×	×	×
Melanitis amabilis amabilis (Boisduval, 1832)																×										
Nymphalidae: other subfamilies																										
Polyura sacco santoensis Lachlan, 1993												×				×										
Polyura sacco sacco Smart, 1977																						×		×		
Parthenos sylvia thesaurinus Grose-Smith, 1897	×		×		×			×	×			×	×	×	×		×		×		×					
Doleschallia browni herrichi (Butler, 1875)	×	×	×		×			×	×	×		×	×	×	×	×	×	×	×		×	×		×	×	×
*Hypolimnas antilope shortlandica (*Ribbe, 1898)	×		×				×		×	×		×	×	×		×	×				×	×		×		×
Hypolimnas pithoeka impostor Tennent, 2002	×		×																							
Hypolimnas octocula octocula (Butler , 1869)							×	×	×	×		×	×	×	×	×	×	×	×		×					
Hypolimnas octocula perryi (Butler, 1875)																						×				
Hypolimnas octocula tanna Samson, 1986																								×		
Hypolimnas octocula futunaensis Samson, 1986																									×	
Hypolimnas octocula bellus Tennent, 2003																										×
Hypolimnas bolina nerina (Fabricius, 1775)	×	×	×		×		×	×	×	×		×	×	×	×	×	×	×	×		×	×		×	×	×
Hypolimnas misippus (Linnaeus, 1764)									×			×			×		×		×		×		×	×		
Yoma sabina sabina (Cramer, [1780])	×		×				×	×		×		×	×	×	×	×	×	×	×		×	×		×	×	×
Junonia villida villida (Fabricius, 1787)	×	×	×		×		×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×		×	×	×
Vagrans egista hebridina (Waterhouse, 1920)	×	×	×		×		×	×	×	×		×	×	×	×	×	×	×	×		×					
Vagrans egista samsoni Tennent, 2003																						×		×	×	×
Acraea andromacha andromacha (Fabricius, 1775)												×				×	×		×		×	×	×	×	×	×

Hesperioidea

Hesperiidae

Hasora khoda Mabille, 1876

Reported from the "eastern arc" (a term which refers to the islands of Maewo, Ambae, Pentecost, Ambrym, Paama, Epi etc.; Robinson, pers. comm.) of Vanuatu by Gross (1975: 417), and by Samson (1983: 3) from Paama, Erromango, Futuna and Aneityum. This widespread species occurs in a number of races from India to New Guinea, the Bismarck and Solomons archipelagos, Australia and New Caledonia. Evans (1949) did not include Vanuatu in the distribution of this species. Nominotypical *khoda* occurs on New Caledonia and the Loyalties. Evans (1949: 71) restricted distribution of *H. khoda* to New Caledonia and the Loyalty Islands (1 ♂ and 2 ♀♀ reported from "Sandwich Is." [an early name for Efaté] are from New Caledonia). A series seen/collected during this project from Ureparapara, Mota Lava, Vanua Lava, Gaua, Espiritu Santo, Ambae, Maewo, Malakula, Ambrym, Paama, Epi and Futuna, were all *H. chromus* (Cramer, [1780]). The two species are very similar in appearance.

Papilionoidea

Papilionidae

Graphium sarpedon (Linnaeus, 1758)

Unconfirmed sightings of a butterfly resembling *G. sarpedon* were reported from Espiritu Santo and Erromango as a result of the RSE (Gross 1975: 417, Robinson 1976: 47). Although *G. sarpedon* is not known from adjacent island groups and is infrequent in the Solomons Archipelago (Tennent 2002b), *G. hicetaon* (Mathew, 1886) and *G. gelon* (Boisduval, 1859) occur on the Santa Cruz group and New Caledonia, respectively, and there is no reason why a species of *Graphium* should not be resident in Vanuatu, or occur irregularly as a vagrant.

Pieridae

Pieris rapae (Linnaeus, 1758)

The occurrence of *Pieris rapae* on Tanna is based on the apparently genuine record of a solitary ♀ in the Bishop Museum, Honolulu, collected by N. L. H Krauss on Tanna in December 1985. The species occurs on New Caledonia, but is clearly not established on Tanna since it appears not to have been reported before or since.

Eurema candida (Stoll, 1782)

Samson (1983: 3) reported this species from Espiritu Santo and Efaté. *E. candida* occurs from the Lesser Sunda Islands, the Moluccas, New Guinea, northeast Australia, the Bismarck and Solomons archipelagos (Tennent 2002b: 61), and New Caledonia, where its presence also requires confirmation (Holloway & Peters 1976: 286). No specimen of *E. candida* from Vanuatu has been seen. Its presence there is considered unlikely.

Appias albina (Boisduval, 1836)

This species is widely distributed over much of the Indo-Australian Region, but does not reach the Bismarck, Solomons or New Hebrides archipelagos, or New Caledonia. Reports from Vanuatu almost certainly represent misidentification or confusion in nomenclature.

Lycaenidae

Curetis ?insularis (Horsfield, [1829])

Samson (1983: 4) apparently observed a male *Curetis,* reported as "*Curetis ?insularis* subsp." on Efaté. *C. insularis* occurs in southern Burma, Thailand and Sundaland and has not been reported from east of Borneo (Eliot 1990: 223). Its congener, *C. barsine* (C. Felder, 1860), is not known from further east of the New Georgia group in the Solomons Archipelago (Tennent 2002b: 71). Occurrence of the genus in Vanuatu appears unlikely.

Arhopala Boisduval, 1832

A. eurisus Druce, 1891 (formerly often referred to as a race of *A. centaurus* (Fabricius, 1775)) was reported (as *A. araxes eurisus*) from Espiritu Santo and Pentecost by Samson, who also "observed" *A. sophrosyne* Grose-Smith, 1889, on Efaté (Samson 1983: 4). Parsons (1998: 386) reported a ♂ "*A. centaurus*", in the BMNH, London, "supposedly from the New Hebrides" and suggested this record required confirmation (there is some confusion over the name *centaurus* which has previously been applied [Corbet 1941, Parsons 1998, Braby 2000, etc.] to the taxon which occurs in New Guinea and northern Australia, which should properly be referred to as *A. eupolis* (Miskin, 1890) [Gaonkar & Vane-Wright, in prep.]). *A. eurisus* is restricted to the Bismarck and Solomons archipelagos and is not known from further east than San Cristobal and its satellites (Tennent 2002b: 75). Unlike many species of *Arhopala*, which are similar in appearance and difficult to identify, *A. sophrosyne* is distinctive in appearance, and is known to occur on several islands in the Solomons Archipelago, the most easterly of which is Ulawa (Tennent 2002b: 76). Aside from the "suspect" specimen of *A. centaurus* in the BMNH, no Vanuatu specimen of the genus is known to the author. Occurrence of the genus *Arhopala* in Vanuatu requires confirmation.

Tartesa Hirowatari, 1992

Samson (1983: 4) recorded "*Nacaduba astarte* (Butler, 1882) subsp. — Samson unpub., F[utuna]" and *Nacaduba ugiensis* Druce, 1891, from Efaté (the genus *Tartesa* was raised by Hirowatari to separate *astarte* and *ugiensis* from *Nacaduba* in 1992). Through the kindness of Chris Samson, colour transparencies of butterflies taken by him in 1983 on Efaté were examined. A transparency labelled "*ugiensis*" appears to be a small specimen of *Nacaduba novaehebridensis*, which differs from *T. ugie-*

nsis in lacking blue-green basal scales on the under surface. It is suspected that the report of *T. astarte* may also represent a misidentification. A distinctive population of what has been placed provisionally as *Nacaduba mallicollo* Druce, 1892, but which bears a superficial resemblance to *T. astarte*, was collected on Futuna. Difficulties in identification of *T. ugiensis*, reported also from the Santa Cruz group (Samson 1979: 8), stem from its close resemblance to *Nacaduba novaehebridensis* (and other lycaenid species), and the fact that the ♂ remains unknown. So far as is known, *T. ugiensis* is endemic to the island of San Cristobal and its satellites in the east of the Solomons Archipelago. The ♂ genitalia of *T. astarte* are very distinctive and could not be confused with the "difficult" group of allied *Nacaduba* species. Presumably the genitalia of male *ugiensis* will also prove diagnostic (the genus *Tartesa* was raised in recognition of distinctive genitalia of both sexes of *astarte* and male *ugiensis*). Neither Tite (1963: 76) nor Hirowatari (1992: 23) recorded *astarte* from any further east than the Bismarck and Solomons archipelagos. It does not occur on New Caledonia. The occurrence of either *Tartesa* species on islands of Vanuatu seems rather unlikely.

Nacaduba deplorans (Butler, 1875)

Reported by Samson, who apparently photographed a ♀ on Efaté (Samson 1983: 4). No transparency (Samson, pers. comm.) or specimen from Vanuatu is extant. Both Tite (1963: 87) and Hirowatari (1992: 22) recorded the species only from the Loyalty group. Holloway & Peters (1976: 310) added New Caledonia to the distribution. So far as is known, *N. deplorans* is endemic to the New Caledonia group. Whilst the occurrence of lycaenid taxa may often be under-reported, the presence of *N. deplorans* in Vanuatu requires confirmation.

Nacaduba berenice (Herrich-Schäffer, 1869)

Samson (1983: 4) reported photographing a ♂ "*N. berenice ?korene* (Druce, 1891)" on Efaté, but no picture of a butterfly which could be identified as *N. berenice* was found among transparencies kindly loaned to the author by Chris Samson. Tite (1963: 78) recognised 18 races of *Nacaduba berenice* from India eastwards to the Solomons archipelago, where *N. b. korene* flies. He did not report the species from any locality further east. Hirowatari (1992: 19–20) did not recognise the species from further east than the Solomons archipelago.

Pithecops dionisius (Boisduval, 1832)

Reported by Samson (1983: 5) (as *Eupsychellus dionisius*) from Aneityum, Vanuatu was also included in the range of this species by Hirowatari (1992: 57). It is not clear on what these records are based. The author has seen no specimens claiming to be from Vanuatu and there appear to be no records of this distinctive lycaenid species from the numerous islands between San Cristobal, in the east of the Solomons Archipelago, and Aneityum, in the south of the New Hebrides Archipelago.

Nymphalidae

Morphopsis Oberthür, 1880

Samson (1983: 4) reported observation of a "?*Morphopsis* species" on Efaté. The subfamily Morphinae is not otherwise reported from Vanuatu, and the genus *Morphopsis* is a small genus of only five described species of moderately large butterflies, apparently endemic to mainland New Guinea and its satellites (Parsons 1998: 523). The Satyrinae are also not well represented in terms of total species in the South Pacific, although there are some interesting endemic Pacific satyrine genera (e.g. *Argyronympha* Mathew, 1886 in the Solomons Archipelago, *Paratisiphone* Watkins, 1928 and *Austroypthima* Holloway, 1974 in New Caledonia, and *Xois* Hewitson, 1865 in Fiji). The possibility of some hitherto unrecognised satyrine genus/species occurring in Vanuatu is not discounted.

Vindula Hemming, 1934
Phalanta alcippe (Cramer, [1780])

Samson (1983: 4) reported seeing a "*Vindula* species" on Efaté. This related to ♂♂ apparently observed in a garden between Port Vila and Pango on the island of Efaté, one of which was seen sufficiently closely to note that it lacked white patches typical of some Solomons races of *V. arsinoe* Cramer, 1777 (Samson *in* Tennent 2001a: 9). Samson (1983: 4) also reported "*Phalanta alcippe* subsp. — Samson unpub." from Tegua, Mota and Espiritu Santo. Aware of these records, both genera were looked for especially during this project, but neither was seen. Male *Vindula* are fundamentally orange in colour with black markings, as are both sexes of *Phalanta alcippe*, and it is considered possible that the widespread *Vagrans egista* (Cramer, [1779]) could be mistaken for either. No material of either genus is apparently available from any island of the New Hebrides Archipelago. Although occurrence of a *Vindula* species in Vanuatu may be considered unlikely, the presence of endemic *Phalanta* species (*Ph. gaberti* Guérin-Méneville, 1828 in the Society islands and *Ph. exulans* Hopkins, 1927 in Samoa) may make the presence of a *Phalanta* species in Vanuatu more likely.

Yoma algina (Boisduval, 1832)

Gross (1975: 418) reported only *Y. sabina* (Cramer, [1780]) from Malakula, whilst Samson (1983: 4) reported *Y. sabina* from Espiritu Santo, Malakula, Efaté, Erromango and Tanna, and *Y. algina pavonia* Mathew, 1887, from Ambrym, Paama and Epi. Aware of these published records of *Y. algina*, *Yoma* specimens were examined on all islands visited, whenever the opportunity arose. Without exception, *Yoma* specimens seen, including on Ambrym, Paama and Epi (the species is common on each of these islands), were *Y. sabina*. *Y. algina* ranges from Waigeu, through New Guinea, to the Admiralities, Bismarck and Solomon archipelagos, as far east as Guadalcanal (Parsons 1998: 612, Tennent 2002b: 149), and the species may be sympatric with *Y. sabina* in part of

this range. The two species of *Yoma* are superficially similar. No specimen of *Y. algina* has been seen from Vanuatu and it can be declared with some confidence that the species does not occur there.

Notes on biogeography

Several groups of animals have been used to illustrate aspects of Vanuatu biogeography, including vertebrates generally (Lord Medway & Marshall 1975), birds (Diamond & Marshall 1976, Diamond 1984, Bregulla 1992, etc.), land snails (Solem 1958, 1981), lizards (Brown 1991) and cicadas (de Boer 1995, de Boer & Duffels 1996, etc.). So far as insects are concerned, the late J. Linsley Gressitt provided much of the discussion on which modern Pacific biogeographic assessments are based, although he admitted (Gressitt 1956: 11) some of the views he expressed were tentative and that insect faunas of various Pacific island groups were unequally known. In particular, the fauna of Vanuatu had hardly been investigated, and required further fieldwork for adequate studies on their biogeography (Gressitt 1956, 1961). However, subsequent research does support (in general) his assertion that "[the islands of Vanuatu] appear to be oceanic with a poor fauna as compared with that of the Solomons, and it has far fewer endemic genera than has either New Caledonia or Fiji" (Gressitt 1956: 14). Widespread attachment to theories of land-bridges (e.g. Meyrick 1926, Cheesman 1957, etc.) in order to explain faunal distributions are now rightly disregarded and, with a few exceptions, e.g. *Papilio aegeus* Donovan, 1805, on the Santa Cruz islands, probably accidentally introduced by missionaries with *Citrus* plants (Tennent 1999b, 2002b) and *Strymon bazochii* (Godart, 1824), introduced deliberately as a *Lantana* control on Fiji (Parham et al. 1956), dispersal and establishment of Pacific butterflies has been largely "natural". The isolated islands of the New Hebrides archipelago predictably support substantially fewer taxa than the Solomons Archipelago, which lies close to a major potential "source" area (i.e. New Guinea).

Gross (1975) and Robinson (1976) made tentative assessments of the biogeography of Vanuatu based on data obtained by the RSE in 1971, when a large number of moth species were recorded for the first time (species reported from the islands were increased from 70 to 300). Robinson (1976: 51) concluded that the lack of endemic radiation, lower endemicity at species level in comparison with Fiji and New Caledonia, and the presence of only one endemic moth genus, suggested comparatively recent development of the New Hebridean Macrolepidoptera fauna and found no evidence to support recognition of the Vanuatu fauna as impoverished (Robinson 1976: 52).

A previous basic lack of field data has hampered interpretation of Pacific butterfly biogeography. For example, in assessing butterfly distribution across the Pacific, Adler & Dudley (1994) reported 121 species from the Solomons Archipelago (including Bougainville), 26 from the Santa Cruz group, and 57 (including several requiring confirmation) from Vanuatu. A total of 196 species are currently known from the Solomons Archipelago (excluding Bougainville) (Tennent 2002b), 52 from the Santa Cruz group (Tennent 2002a), and 69 (excluding those requiring confirmation) from Vanuatu (this paper). Recent work has also resulted in the known distribution of several butterfly genera being extended eastwards by many hundreds of kilometres.

Several butterflies have distinct races on "central" islands of the archipelago, taken here to include all those islands from the Banks group in the north, to Efaté in the south. The "southern" islands comprise Erromango, Tanna, Aniwa, Futuna and Aneityum. The "northern" islands are taken to be the Torres group, north of the Banks group, and south of the Santa Cruz group, politically part of the Solomon Islands, at the northern extremity of the New Hebrides Archipelago.

Faunal discontinuity in the south

The larger southern islands in the New Hebrides Archipelago support a number of butterfly taxa with quite different phenotypes to those occurring on the "central" islands. It is noted that the butterfly fauna of Aniwa is little known (see Tab. 3), and it will be interesting to find in due course which races of taxa with "variable" phenotypes (e.g. *Parantica pumila* (Boisduval, 1859), *Hypolimnas octocula* (Butler, 1869), *Vagrans egista*) occur there. The other substantial islands of this southern group (Erromango, Tanna, Futuna and Aneityum) support butterfly populations which, in the case of several species, are not only "different" in phenotype to populations of the same species further north, but also vary between the southern islands themselves. The southern islands of the New Hebrides archipelago have interested biogeographers for some years (e.g. Cheesman 1957, Solem 1958) and a line of faunal discontinuity at approximately 18 degrees South, between the islands of Efaté and Erromango, has long been postulated and commented upon (e.g. Samson 1983, Ackery et al. 1989, etc.), although the situation on Erromango itself is less clear.

The best illustration of differences in "southern islands" butterflies is *Hypolimnas octocula,* which occurs in the same general form on all islands from Efaté north to the Banks group, where it appears to be uncommon. On the southern islands, phenotypes become dramatically less stable, with distinct subspecies described from each of the four islands. In addition to *H. octocula,* a further 7 species (*Papilio fuscus* Goeze, 1779, *Deudorix mathewi*; *Parantica pumila* [but see notes concerning Erromango, below]; *Euploea leucostictos* (Gmelin, 1790), *E. boisduvalii* Lucas, 1853, *Polyura sacco* and *Vagrans egista*) also occur on islands from Erromango and south in forms different to those on Efaté and north. It is probable that races of *Cepora perimale* (Donovan, 1805) and *Nacaduba* "*mal-*

licollo" on Futuna may also warrant subspecific rank, although insufficient material from adjacent islands is presently available to allow a proper assessment.

The situation on the island of Erromango itself is apparently rather more complex, particularly among the Danainae. For example, although *Parantica pumila* populations from Erromango belong fundamentally with the southern islands, a small percentage of individuals appear very similar to the race which occurs on the central islands whilst, as has already been noted (Ackery et al. 1989: 715), both central and southern forms of *Euploea leucostictos* occur sympatrically on Erromango. It is curious that very similar forms of both *E. leucostictos* and *E. boisduvalii* occur on the southern islands and on the Torres group, with a distinguishable race on the islands in between.

Faunal discontinuity in the north

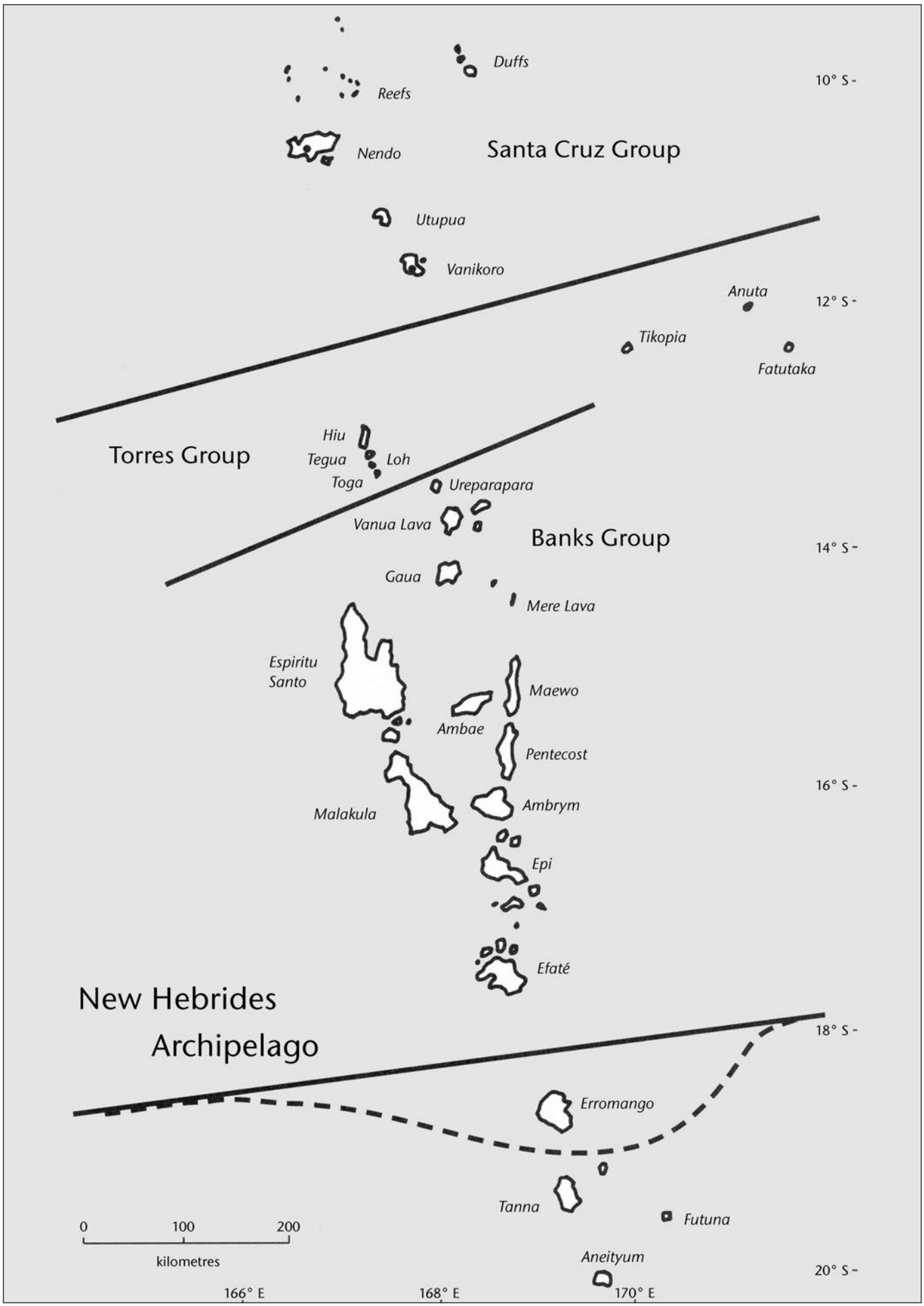
Due no doubt to the fact that the northern and rather remote Torres group of islands has been seldom visited, no faunal discontinuity in the north of the New Hebrides Archipelago appears to have been noted prior to this project. In fact, whilst differences between the Torres and Banks (and other central islands) groups show some clear divergence at subspecies level, there are some unexpected differences in butterfly distribution, even at generic level, between the Torres and Santa Cruz groups (Tennent 2002a).

The Torres islands mark the northern extremity of Vanuatu and are comprised of four main islands and two smaller ones, lying east of the 8000 m deep Torres Trench. The main islands are Hiu, Tegua, Loh and Toga and, although the author visited only Hiu and Loh (the few butterflies reported on Tab. 3 from Tegua and Toga represent under reporting), the islands are sufficiently close to each other to warrant consideration as a discrete biogeographical entity.

Torres populations of 7 species (*Papilio fuscus*; *Nacaduba novaehebridensis*, *Catopyrops nebulosa* (Druce, 1892), *Jamides celeno* (Cramer, 1775), *Danaus affinis* (Fabricius, 1775), *Euploea leucostictos* and *E. boisduvalii*) occur in a different race to those on the central islands, whilst the Torres might also be the southerly limit of *Hypolimnas pithoeka* (Tennent, 2002c). Other species (*Appias athama* (Blanchard, 1848), *Luthrodes cleotas* (Guérin-Méneville, 1838), *Hypolimnas octocula*), all of which are known from the neighbouring Banks group where the first two may be locally common, appear not to have reached the Torres. Yet further species (*Appias paulina* (Cramer, 1777), *Cepora perimale*, *Catochrysops panormus* (C. Felder, 1860), *Polyura sacco*, *Acraea andromacha* (Fabricius, 1775)) are quite widespread further south, but have apparently not reached the Banks or Torres, whilst at least one species (*Euploea sylvester* (Fabricius, 1793)) is essentially a northern species.

Table 4: Butterflies of the Torres and Santa Cruz groups. — * denotes species which occur on the Torres and Santa Cruz groups as different subspecies.

Species	Santa Cruz	Torres
Hesperiidae		
Badamia exclamationis (Fabricius, 1775)	×	×
Hasora chromus (Cramer, [1780])	×	×
Hasora hurama (Butler, 1870)	×	
Borbo cinnara (Wallace & Moore, 1866)	×	×
Caltoris philippina (Herrich-Schäffer, 1869)	×	
Pelopidas lyelli (Rothschild, 1915)		×
Papilionidae		
Graphium hicetaon (Mathew, 1886)	×	
Papilio aegeus Donovan, 1805	×	
Papilio fuscus Goeze, 1779		×
Pieridae		
Catopsilia pomona (Fabricius, 1775)	×	
Catopsilia pyranthe (Linnaeus, 1758)		×
Eurema hecabe (Linnaeus, 1758)	×*	×*
Belenois java (Sparrmann, 1768)	×	×
Lycaenidae		
Hypochrysops julie Tennent, 2001	×	
Deudorix mathewi Druce, 1892		×
Bindahara phocides (Fabricius, 1793)	×	
Nacaduba dyopa (Herrich-Schäffer, 1869)	×	×
Nacaduba kurava (Moore, 1858)	×	
Nacaduba novaehebridensis Druce, 1892	×*	×*
Nacaduba samsoni Tennent, 2001	×	
Prosotas russelli Tennent, 2003	×	
Nothodanis schaeffera (Eschscholtz, 1821)	×	
Catopyrops nebulosa Druce, 1892	×*	×*
Ionolyce lachlani Tennent, 2001	×	×
group of *Jamides bochus* (Stoll, [1782])	×	×
Jamides amarauge Druce, 1891	×	
Jamides celeno (Cramer, [1775])	×*	×*
Catochrysops taitensis (Boisduval, 1832)	×	×
Euchrysops cnejus (Fabricius, 1798)	×	×
Lampides boeticus (Linnaeus, 1767)	×	×
Zizula hylax (Fabricius, 1775)	×	×
Zizina labradus (Godart, 1824)	×	×
Leptotes plinius (Fabricius, 1793)	×	
Nymphalidae: Danainae		
Tirumala hamata (Macleay, 1827)	×	×
Danaus plexippus (Linnaeus, 1758)	×	×
Danaus affinis (Fabricius, 1775)	×*	×*
Euploea sylvester (Fabricius, 1793)	×	×
Euploea leucostictos (Gmelin, 1790)	×*	×*
Euploea boisduvalii Lucas, 1853	×*	×*
Euploea treitschkei Boisduval, 1832	×	×
Nymphalidae: Satyrinae		
Mycalesis perseus (Fabricius, 1775)	×*	×*
Orsotriaena medus (Fabricius, 1775)	×	
Melanitis leda (Linnaeus, 1758)	×	×
Nymphalidae: other subfamilies		
Parthenos sylvia (Cramer, 1775)	×	×
Doleschallia browni Salvin & Godman, 1877	×	×
Hypolimnas antilope (Cramer, 1777)	×	×
Hypolimnas pithoeka Kirsch, 1877	×*	×*
Hypolimnas alimena (Linnaeus, 1758)	×	
Hypolimnas bolina (Linnaeus, 1758)	×	×
Yoma sabina (Cramer, [1780])		×
Junonia villida (Fabricius, 1787)	×	×
Junonia hedonia (Linnaeus, 1764)	×	
Vagrans egista (Cramer, [1780])	×	×



Map 3: The New Hebrides Archipelago: lines of faunal discontinuity

There are also some interesting comparisons to be made between the Torres and Santa Cruz groups, components of the same "biogeographic province" (Dahl 1984), illustrated in Tab. 4.

It is accepted that perceived faunal differences between localities may be due to a number of reasons and that apparent disparities may be misleading when the possibility/likelihood of under-reporting is taken into account. In this case, the author has spent many months on islands of the Santa Cruz group (Tennent 2002a), and more than two weeks in the Torres at different times of year, and knows the butterfly fauna of both island groups moderately well. Whilst some genera containing small, unobtrusive species, or species which habitually live in the canopy, reported from one group may merely be unrecorded on the other (e.g. *Hypochrysops*, *Deudorix*), there are clear examples of real differences between these two island groups. For example, *Yoma sabina*, a large and colourful nymphaline butterfly, is common on the Torres and all islands to the south, including Aneityum, but has never been reported from Santa Cruz (and is highly unlikely to have been overlooked).

Perhaps the best illustration of differences in distribution between the Torres and Santa Cruz island groups is to be found in the Papilionidae. *Papilio aegeus* is common on Nendo, Utupua and Vanikoro, but is thought to have been accidentally introduced there by man, probably on citrus plants, at some time during the last 200 years (Tennent 1999b, etc.). There is no other obvious explanation for the fact that allied species occur on all the intervening islands between Santa Cruz and Australia/New Guinea, where the nearest populations of *P. aegeus* occur. The species is not known from Vanuatu, where *Papilio fuscus* is common on most islands, including the Torres. It is probable therefore that the genus *Papilio* has not naturally spread further north than Hiu in the Torres group. Conversely, *Graphium hicetaon* occurs on the main islands in the west of the Santa Cruz group (Nendo, Utupua and Vanikoro), but is not known from Vanuatu, where the only report of the genus consists of unconfirmed reports of *Graphium sarpedon* from Espiritu Santo and Erromango as a result of the RSE (Gross 1975: 417). Both *Papilio* and *Graphium* species are large and conspicuous butterflies, unlikely to be overlooked.

Of 5 genera (*Hypochrysops*, *Bindahara*, *Prosotas*, *Nothodanis*, *Orsotriaena*) reported from Santa Cruz but not from the Torres, and 4 genera (*Pelopidas*, *Graphium*, *Deudorix*, *Yoma*) recorded from the Torres, but not Santa Cruz, some may be treated with caution, since they include species that are likely to be under-recorded (*Pelopidas*), or known from very few specimens (*Bindahara*), or only recently recorded and known from further afield (*Prosotas*). Even so, there certainly appear to be significant differences, even at generic level, between these island groups.

Discussion

The New Hebrides Archipelago lies on the western edge of the Pacific tectonic plate, which is in the process of being subducted under the eastern edge of the Australian plate (Falvey & Greene 1988), and changes in the relative geographic positions of Vanuatu, Fiji, Lau, Tonga and Samoa as a result of complex plate boundary evolution continue today (Ewart 1988). The islands of Vanuatu are young in geological terms (Lee 1975) and were formed in four distinct phases of tectonic/volcanic activity (Mallick 1975). Mawson (1905) carried out the first geological survey of at least some of the islands of Vanuatu, but it was not until the 1960s and 1970s that more detailed explorations began. Subsequent work (Greenbaum et al. 1975, Ash et al. 1980) suggests the Torres group, together with parts of Espiritu Santo and Malakula, are significantly older (ca. 36 million years old) than the neighbouring Banks groups (ca. 1–2 million years old), whilst central and southern islands are also much more recent in origin (ca. 2–11 million years old). As was noted in discussing Solomon Islands biogeography (Tennent 2002b), the geological record is fundamentally a marine one (Hall 1998), and geologists have been reluctant, or attached low importance, to identifying areas that were above sea level at any time (Holloway 1998). Thus, although ages of rocks and physical features on islands can be dated by geologists with, in many cases, a high degree of accuracy, age data relating to subaerial/submarine existence of islands are rather more problematic. The age of rocks themselves may be of limited relevance in assessing the subaerial age of islands and evolution of their faunas.

It seems certain that islands like the Torres group were considerably more distant from their neighbours in relatively recent times than they are at present. The reasons for differences in butterfly distribution in the New Hebrides Archipelago probably lie in a combination of distances between individual islands, and the geological history of the islands themselves. It is believed that some 20% of the present land area of Vanuatu surfaced within the last 200 000 years.

Of the 79 butterfly species known to occur in the New Hebrides Archipelago (including the Santa Cruz group), 9% (at least 7) are endemic. This compares with levels of endemism of 11% (birds), 17% (bats), 20% (reptiles) (Lord Medway & Marshall 1975), 50% (earthworms), 42% (termites) and 31% (earwigs) (Gross 1975). Diamond & Marshall (1976) recognised Vanuatu as an important faunal crossroads in bird distribution, and found that racial differences in the Santa Cruz islands suggested close affinity with islands further south, rather than with the Solomons Archipelago or other neighbouring island groups. The Santa Cruz group was thus considered to be an impoverished outlier of Vanuatu, with admixtures from the Solomons and Fiji (Diamond & Marshall 1976: 191). So far as butterflies are concerned, the New Hebrides Archipelago does not seem particularly impoverished, supporting a respectable number of species for an

oceanic island archipelago some distance from potential faunal sources (New Guinea, Australia etc.).

The butterfly fauna of Vanuatu comprises 84 subspecies of 69 species in 42 genera. These are fundamentally widespread genera and species, many of which have shown an ability to disperse widely throughout the Pacific (e.g. *Badamia* Moore, [1881], *Catopsilia* Hübner, [1819], *Eurema* Hübner, [1819], *Deudorix* Hewitson, [1863], *Nacaduba* Moore, [1881], *Jamides*, *Famegana*, *Zizula* Chapman, [1910], *Zizina* Chapman, [1910], *Danaus* Kluk, 1802, *Euploea* Fabricius, 1807, *Doleschallia* C. & R. Felder, 1860, *Hypolimnas* Hübner, [1819], *Junonia* Hübner, [1819], *Vagrans* Hemming, 1934 etc.). There are no endemic genera, and two endemic species (*Deudorix mathewi* and *Polyura sacco*). Some 26 described subspecies (31%) are endemic to Vanuatu. Additional taxa (*Prosotas russelli* Tennent, 2003, *Ionolyce lachlani* Tennent, 2001, *Jamides bochus*-group species) are endemic to the New Hebrides Archipelago (i.e. found also on the Santa Cruz group).

Gressitt (1961: 25) said of Vanuatu: "The New Hebrides present a puzzle on account of the poverty of their fauna as compared with the very rich Solomons just to the northwest and with the fairly rich Fiji islands to the east and New Caledonia to the south. One would expect the fauna to be much richer from the close proximity of the islands to a rich subcontinental fauna like that of the Solomons. To find them poorer than Fiji and New Caledonia which are further from the source areas is still more surprising ..." More recent work suggests that the insect (or at least the butterfly) fauna of Vanuatu is by no means impoverished in comparison with neighbouring islands and island groups, and that earlier assessments were based on inadequate data.

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