

The Cicadas of the Fiji, Samoa
and Tonga Islands,
their Taxonomy and Biogeography
(Homoptera, Cicadoidea)

by

J. P. Duffels

with a chapter on the geological history of the area

by

A. Ewart



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Preface

My wife and I spent two and a half months in Fiji in 1979 with the object of collecting cicadas for a taxonomic and biogeographic study. This field work enabled us to make a collection of adult cicadas, larvae and exuviae and to study the habitat, ecology and sound-production of several species. I am greatly indebted to my wife, Greet Duffels-van Egmond, for her enthusiastic assistance in the field and for taking photographs of living cicadas and their habitats. Grants from the Netherlands Foundation for the Advancement of Tropical Research (WOTRO, no. WR 87-147) and the Association for Scientific Tropical Research funded part of the field work and a preceding visit to the Bernice Bishop Museum, Honolulu.

During our stay in Fiji we received considerable help from Dr G.H.D. Williams, Conservator of Forests (Suva), Mr R.H. Yarrow, Director of Agriculture (Suva) and the staff of the Koronivia Research Station, Nausori: Mr S.R. Singh, Dr M.K. Kamath, Mr Sada N. Lal and Mr W. Fauoro. Essential assistance in the field work was given by Mr Alec Chang and Mr Waisea Drova (Forestry Station, Colo-i-Suva), Mr Deo Sharan Singh (Department of Agriculture, Waiyevo) and Mr Rupeni Masi (Rewasa, Rakiraki). I wish to express my gratitude for their help.

In a late stage of my taxonomic work on the Fijian cicadas, I decided to include the Samoa and Tonga cicadas in this publication. The cicada fauna of Samoa and Tonga is relatively poor, but in the context of the Fijian fauna it presents some interesting taxonomic and biogeographic interpretations.

The taxonomic work is based upon Fiji material collected by us and upon museum specimens from Fiji, Samoa and Tonga. The following persons and institutions generously lent material in their care: Dr W.J. Knight and Mr M.D. Webb, British Museum (Natural History), London; Mr G. Nishida, Dr F.J. Radovsky and Dr G.A. Samuelson, Bernice P. Bishop Museum, Honolulu; Dr J.F. Lawrence and Mrs Margaret K. Thayer, Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.; Dr J.S. Dugdale and Dr P. Maddison, Department of Scientific and Industrial Research, Auckland; Dr M.K. Kamath and Mr S.R. Singh, Koronivia Research Station, Nausori, Fiji. I am also indebted

to Dr P. Maddison for the opportunity to study the UNDP/FAO material. Dr A.J. Newton, Museum of Comparative Zoology, Harvard University, Cambridge, kindly provided information on the localities in Fiji visited by W.M. Mann. Grants from the Uyttenboogaart-Eliassen Foundation and the Netherlands Organization for the Advancement of Pure Research (ZWO, no. 09-99) supported visits to examine the collections of respectively the Commonwealth Scientific and Industrial Research Organization, Canberra and the Museum of Comparative Zoology, Harvard University, Cambridge.

After completion of the taxonomic and phylogenetic parts of this study it occurred to me that the publication would benefit from a chapter on the geological history of the Fiji — Samoa — Tonga region. I am very grateful to Prof. Dr. A. Ewart, Department of Geology and Mineralogy, University of Queensland, for his willingness to contribute to the enterprise and for suggesting some palaeogeographic and biogeographic implications, which are extremely valuable for understanding the historic biogeography of the southwest Pacific cicadas. Thanks to Prof. Ewart's knowledge of Australian cicadas, I have very much benefitted from a discussion with him on the relationships of the new genus *Fijipsalta* with the Australian cicadas.

I particularly thank Prof. Dr. C. Wilkinson in the Department of Entomology for patiently reading the manuscript leading to many corrections of the English and other improvements. Finally I would like to thank the following persons also in the Institute of Taxonomic Zoology for their continuous help: Mr J. Zaagman for the preparation of the drawings of the whole insects and the maps, Mr L. v.d. Laan for the preparation of the photographs, Mrs Annelies Stoel for typing the manuscript, Mr C.L. Hellegreen and Mr G. Verlaan for preparing material, and Mr A. Rol for his assistance in the preparation of the sonograms.

Amsterdam, August 1987.

J. P. Duffels

Abstract

A total of 24 cicada (sub)species occurring in the Fiji, Rotuma, Samoa and Tonga Islands, are described and illustrated in the adult stage and as far as known in the larval stages and in the exuviae. The species described include 12 new (sub)species. Of the 24 (sub)species 15 are attributed to *Aceropyga*, of which the following, all from Fiji, are described as new: *acuta*, *corynetus monacantha*, *corynetus ungulata*, *egmondae*, *hureka*, *macracantha*, *philorites* and *pterophon*. The infrageneric classification of *Aceropyga* as proposed here, is based upon phylogenetic analysis of the southwest Pacific taxa, not without consideration of the taxa from other areas. The new genus *Fijipsalta* is erected for *F. tympanistria* (Kirkaldy) from Fiji. Two new species are described in *Baeturia*: *rotumae* from Rotuma and *maddisoni* from Tonga and Samoa. Two species are placed in a new generic combination, *Raiateana knowlesi* (Distant) and *R. kuruduadua* (Distant), whereas the latter is sub-

divided in three subspecies of which *bifasciata* from Fiji and *samoensis* from Samoa are new. Keys to the genera and (sub)species, found in the area studied, are presented for the adults and for the 5th larval instars and exuviae. The richest cicada fauna is found in Fiji, where 19 (endemic) (sub)species are known to occur. Rotuma has one (endemic) species. Samoa and Tonga have three and two (sub)species respectively; one species is found in both island-groups, the others are endemic to one group. Aspects of the historical biogeography of the cicadas of the southwest Pacific are discussed on the basis of taxon-area cladograms resulting from the phylogenetic analysis of two groups of the genus *Aceropyga* and the species of the genus *Raiateana*. The biogeographic patterns found in south-west Pacific cicadas are described in relation to the geological history of the area. As a result of field work some information is included on the ecology, behaviour and sound-production of the Fiji species.

Introduction

After my attention was drawn to the Fiji cicada fauna following the study of the widespread western Pacific genus *Aceropyga* (see Duffels, 1977) my wife Greet Duffels-van Egmond and I made a field-trip to Fiji from 15.I to 30.III.1979. We visited the large islands Viti Levu, Vanua Levu and Taveuni, the small island Ovalau east of Viti Levu and the islets of Laucala and Nggamea NE of Taveuni. A list of collecting stations has been published (Duffels, 1979) and fig. 1 gives the localities where we collected. During this trip we made a collection of about 500 adult cicadas, larvae and exuviae. Study of this material and museum specimens from the Fiji, Samoa and Tonga islands led to this faunal study of the cicadas of the SW Pacific island groups.

In the present paper a total of 24 (sub)species of cicadas has been described from Fiji, Samoa and Tonga Islands, of which 12 are described for the first time. The genus *Aceropyga* is represented with 15 (sub)species, of which 8 are new to science. The

study of these *Aceropyga* species led to a better understanding of the phylogenetic relationships of this genus to the other genera of the subtribe Cosmopsaltriaria. The cladogram of the genera of the Cosmopsaltriaria, which was given in a previous paper (Duffels, 1986: fig. 2), partly relied upon the synapomorphies discovered during this study of the *Aceropyga* species of Fiji. This paper presents a new cladogram for the species groups in the genus *Aceropyga*, which gives a much better insight in the interspecific relationships than an earlier cladogram presented (Duffels, 1977: fig. 265).

The taxonomic positions of *Tibicen kuruduadua* (Distant, 1881) from Fiji and Samoa and *Tibicen knowlesi* (Distant, 1907) from Fiji have been clarified by the study of new material of these species. This study concludes that the transfer of these species to the originally monotypic genus *Raiateana* Boulard (type-species *Raiateana oulieta* Boulard, 1979 from the Society Islands) is justified.

ria Stål have been described, one occurring in Samoa and Tonga, and the other on Rotuma Island.

The genus *Fijipsalta* has been erected for the very peculiar *Cicadetta tympanistria* Kirkaldy, 1907 from Viti Levu, Fiji. The taxonomic affinities of

from Fiji and *Moana expansa* Myers, 1928 from Samoa are uncertain, and will probably remain uncertain until new material of these species becomes available.

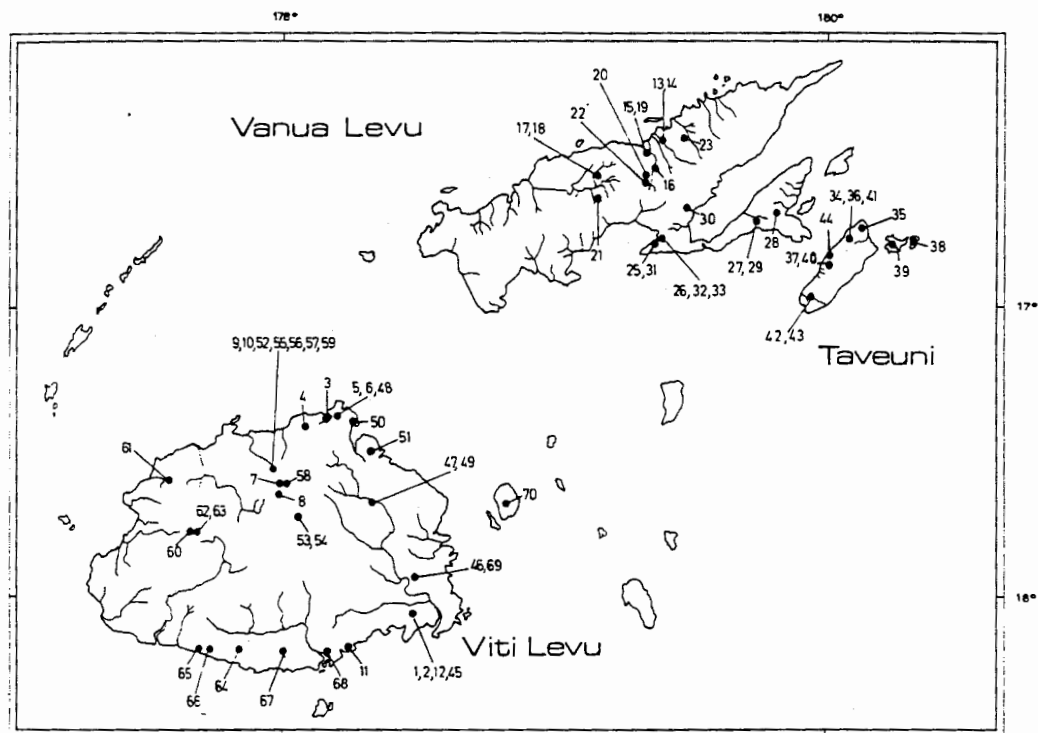


Fig. 1. Localities in Fiji at which cicadas were collected during an excursion from 15.i.1979 to 30.iii.1979 made by J.P. and M.J. Duffels.

Historical résumé

The collections made in the Fiji Islands during the voyage of the H M S Herald in Oceania contained the cicadas, whereupon Francis Walker (1858) based the first taxonomic descriptions of cicadas of Fiji. The three cicada species, *Dundubia distans*, *D. subfascia* and *D. lineifera*, described then, are now assigned to *Aceropyga distans*. In 1881 and 1882 W. L. Distant described two new species from the Fiji Islands, *Cicada kuruduadua* (now: *Raiateana kuruduadua*) and *Cosmopsaltria stuarti* (now: *Aceropyga stuarti*), from the collection of the Godefroy Museum, Hamburg. Two more cicadas

from Fiji were added by the same author at the beginning of this century: *Sawda vitiensis* Distant, 1906 (now: *Cosmopsaltria vitiensis*) and *Cicada knowlesi* (now: *Raiateana knowlesi*). *Cicadetta tympanistria* (now: *Fijipsalta tympanistria*), an interesting species with some very peculiar features, was described from Viti Levu, Fiji by G. W. Kirkaldy in 1907. In the same publication two Australian species *Cyclochila australasiae* (Donovan, 1805) and *Macrotristria angularis* (Germar, 1834) were recorded from Fiji, but one year later Kirkaldy (1908) suggested that these species might have been

accidental visitors in Fiji. I have not found any confirmation of the occurrence of these Australian species in Fiji, and I am inclined to believe that the specimens were wrongly labelled.

Cosmopsaltria albostrata Distant, 1888 (now: *Aceropyga albostrata*) was described from the Philippines but later study (Duffels, 1977) proved that this species is an endemic of the Tonga Islands.

A revision of the genus *Diceropyga* led to the description of the new genus *Aceropyga* for the Fiji species *A. distans*, *A. stuarti* and *A. corynetus* Duffels, 1977, the Tonga species *A. albostrata* and some others from the Bismarck Archipelago, Solo-

mon Islands and Vanuatu (Duffels, 1977).

In "Insects of Samoa" Myers (1928) recorded three species from the Samoa Islands: *Tibicen kuruduadua* (now: *Raiateana kuruduadua*), *Baeturia exhausta* Guérin, (now: *Baeturia madisoni* n. sp.) and *Moana expansa* n. gen. sp.. The relationships of *Moana expansa* are unclear since the species is only known from one adult, a severely mutilated male collected from a spider's web, and the exuviae of one male. After the discovery of the very peculiar sound organs Boulard (1976) placed this species in the new subfamily Moaninae.

Phylogeny of three groups of south-west Pacific cicadas

Phylogenetic taxon-analysis provides a basis for historic biogeographical reconstructions. Three more or less resolved taxon cladograms for cicadas of the south-west Pacific can be presented (figs. 2-4). The numbers of the squares in these figures refer to presumed synapomorphies listed in the figure captions. Autapomorphies for the species or

subspecies have not been included. The taxon cladograms are changed into taxon-area cladograms by substituting the taxon names with the island and island group from where the taxon has been recorded. The taxon-area cladograms will be discussed in the biogeography chapter.

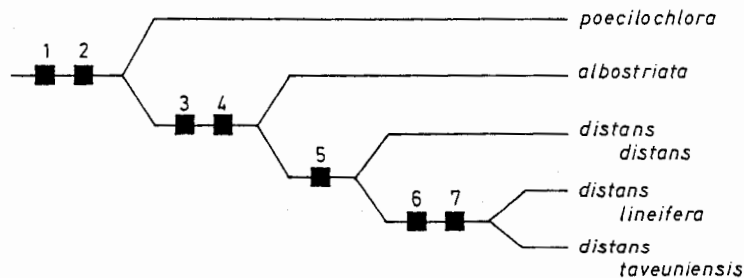


Fig. 2. Cladogram of the *Aceropyga distans* group from the Fiji and Tonga Islands and *A. poecilochlora* from Vanuatu. Presumed synapomorphies:

1. median uncus lobe of male genitalia long
2. claspers of male genitalia strongly reduced
3. shape of male abdomen (see description of the *distans* group)
4. apex of aedeagus with two long, sharply pointed, chitinized appendages
5. marking on mesonotum reddish brown
6. tegmina with marginal spots at the apices of the longitudinal veins
7. tegmina with spots at the bases of the 5th and 6th apical areas

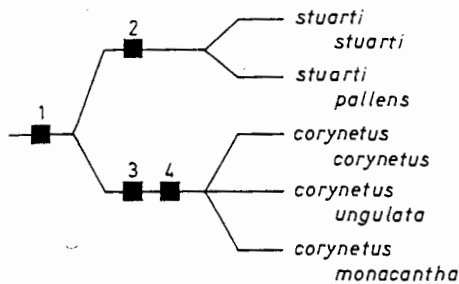


Fig. 3. Cladogram of the *Aceropyga corynetus* group from the Fiji Islands. Presumed synapomorphies:

1. male abdomen with club-shaped apical part formed by segm. 7 and 8
2. male abdomen without marking of dark spots
3. 10th abd. segm. of 5th instar larva and exuviae with strongly developed medio-proximal protrusion
4. blade of tibia of 5th instar larva and exuviae with deep emargination

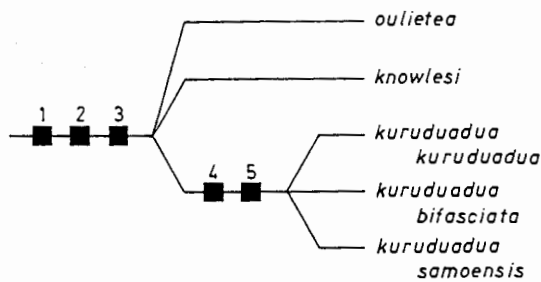


Fig. 4. Cladogram of *Raiateana* from the Fiji, Samoa and Society Islands. Presumed synapomorphies:

1. dorsal ridges on the uncus
2. male abdomen distinctly conical
3. 7th male sternite narrow
4. shape of male operculum as in fig. 155
5. lateral margin of pygofer with strongly developed "shoulder"

Biogeography of the south-west Pacific cicadas

The island groups

Fiji Islands and Rotuma Island

The richest cicada-fauna in the south-west Pacific is found in the Fiji Islands (Table 1). The present study brings the total number of Fiji cicadas to 19 described (sub)species and denotes considerable increase of knowledge of their distribution. As a result of our field-work in Fiji in 1979 five (sub)species have been recorded now from Vanua Levu, whereas previously not a single cicada was known from this island (Duffels, 1977). A total of 12 (sub)species is known from Viti Levu, and three of those have been found also in the small nearby island Ovalau. The other smaller islands of the Fiji archipelago are still very fragmentarily known. One endemic subspecies occurs on Totoya and Maola and one endemic subspecies on Kandavu.

All Fijian cicadas are endemic to the Fiji group at subspecific or specific level. Three species endemic to Fiji are widespread through the archipelago: *Aceropyga distans*, *A. corynetus* and *A. stuarti*. Each has an endemic subspecies on Viti Levu and nearby Ovalau, another subspecies on Vanua Levu and Taveuni, and possibly a different one on one of the other Fiji islands. *Raiateana kuruduadua* is represented in Fiji with two endemic subspecies: one on Viti Levu and another on Vanua Levu and

Taveuni. A third subspecies of *R. kuruduadua* has been found on Samoa. The other known Fiji species are single island endemics, which probably occupy very restricted areas.

Baeturia rotumae is the only (endemic) cicada species recorded from Rotuma Island, situated 500 km north of Fiji.

Samoa Islands

Baeturia maddisoni is apparently a common species on the islands of Western and American Samoa: Upolu, Savaii, Manono, Tutuila and Tau. The two other species recorded from Samoa are endemics to Western Samoa: the very peculiar *Moana expansa* from Upolu and *Raiateana kuruduadua samoensis* from Upolu and Savaii.

Tonga Islands

Aceropyga albostriata is restricted to the southern Tongatapu group, and *Baeturia maddisoni* is recorded from the northern islands of the Tonga chain: Niuatoputapu and Vava'u islands.

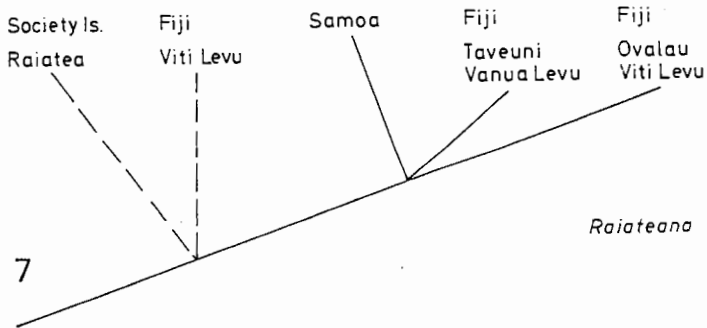
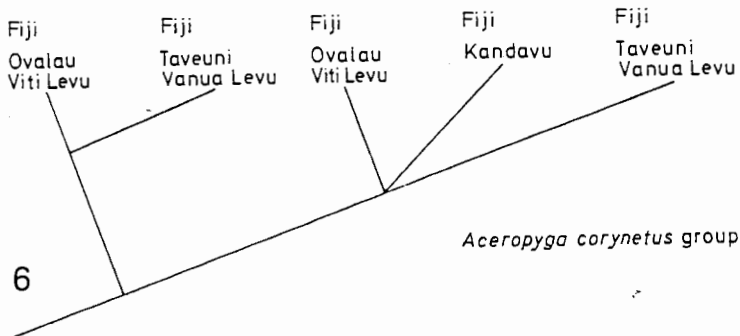
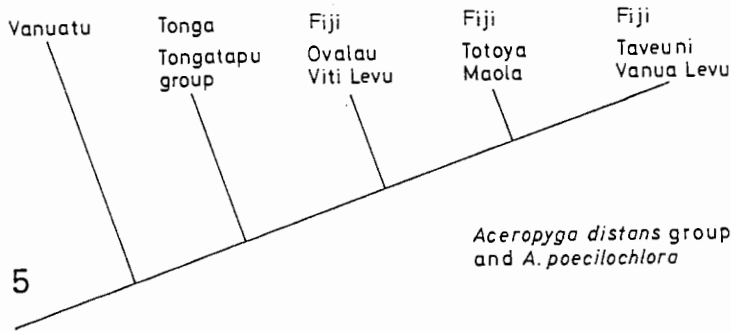
Areas of endemism and their relationships

The methods of cladistic biogeography as outlined

can be recognized on the basis of Table 1 and three taxon-area cladograms (figs. 5-7). Fig. 5 shows the relationships of areas of endemism as recognized in the taxon-area cladogram of the monophyletic group consisting of the *Aceropyga distans* group and *Aceropyga poecilochlora*. The taxon-area cladograms of the *Aceropyga corynetus* group (fig. 6) and *Raiateana kuruduadua* (fig. 7) confirm the biogeographical coherence of Viti Levu and Ovalau, and of Vanua Levu and Taveuni and do not conflict with the relationships found in the *distans*

group and *A. poecilochlora*. Kandavu Island has an undetermined position in the Fiji archipelago, and the relationships of Samoa are uncertain. The taxon-area cladograms together allow the speculation that the Maola and Totoya subspecies (of *A. distans*) and the Kandavu subspecies (of *A. corynetus*) developed after unique speciation events, whereas the speciation event leading to the development of Viti Levu/Ovalau and Taveuni/Vanua Levu subspecies was common to at least four species.

Fig. 5 shows the Tongatapu group, the most



Figs. 5-7. Taxon-area cladograms for three groups of cicadas from the south-west Pacific obtained by substitution of the taxon names in the cladograms of figs. 2-4 with the island and island group names.

Table 1. Distribution of the Cicadoidea recorded from the Fiji Is., Rotuma I., Tonga and Samoa Is.

	Fiji						Tonga			Samoa		
	Viti Levu	Ovalau	Kandavu	Vanua Levu	Taveuni	Totoya, Maola	Rotuma	Tongatapu-group	Ha'apai-group	Yava'u-group	Western Samoa	American Samoa
<i>Aceropyga</i> Duffels, 1977												
<i>distans distans</i> (Walker, 1858)	+	+										
<i>distans lineifera</i> (Walker, 1858)						+						
<i>distans taveuniensis</i> Duffels, 1977				+	+							
<i>albostrata</i> (Distant, 1888)								+				
<i>huireka</i> n. sp.				+								
<i>stuarti stuarti</i> (Distant, 1882)	+	+		+								
<i>stuarti pallens</i> Duffels, 1977				+	+							
<i>corynetus corynetus</i> Duffels, 1977	+	+										
<i>corynetus monacantha</i> n. subsp.			+									
<i>corynetus ungulata</i> n. subsp.				+	+							
<i>philoritis</i> n. sp.	+											
<i>acuta</i> n. sp.	+											
<i>macracantha</i> n. sp.	+											
<i>egmondae</i> n. sp.	+			+								
<i>pterophon</i> n. sp.	+											
<i>Cosmopsaltria</i> Stål, 1866												
<i>vitiensis</i> (Distant, 1906)	+											
<i>Moana</i> Myers, 1928												
<i>expansa</i> Myers, 1928											+	
<i>Raiateana</i> Boulard, 1979												
<i>kuruduadua kuruduadua</i> (Distant, 1881)	+											
<i>kuruduadua bifasciata</i> n. subsp.				+	+							
<i>kuruduadua samoensis</i> n. subsp.											+	
<i>knowlesi</i> (Distant, 1907) n. comb.	+											
<i>Baeturia</i> Stål, 1866												
<i>rotumae</i> n. sp.							+					
<i>maddisoni</i> n. sp.									+	+	+	
<i>Fijipsalta</i> n. gen.												
<i>tympanistria</i> (Kirkaldy, 1907) n. comb.	+											

by Platnick & Nelson (1978), Rosen (1978) and Humphries & Parenti (1986) are applied to investigate the island interrelationships in the SW Pacific. Prerequisites to apply the methods are according to Schuh & Stonedahl (1986): 1) monophyletic groups whose included taxa have restricted distributions and 2) cladistic analyses for those groups that resolve the interrelationships of the included taxa at the level at which they are endemic.

Reconstruction of taxon cladograms and substi-

tution of taxon names in the taxon cladograms with their areas of distribution provide taxon-area cladograms. The congruencies in these taxon-area cladograms are thought to reflect the relative recency of interconnections between areas of endemism. The results obtained thus from phylogenetic taxon reconstruction can be compared with geological data to derive a better understanding of historic processes in biogeography.

The areas of endemism in the south-west Pacific

Geological history of the Fiji - Tonga - Samoan region of the S. W. Pacific, and some palaeogeographic and biogeographic implications

(by A. Ewart)

The understanding of the geology of the region necessitates the recognition of the fact that the region has evolved from of a complex series of island arc - marginal basin "events", occurring along the northeastern boundary of the Australian-Indian plate, where it converges and interacts with the Pacific plate. Before outlining the sequence of geological events, as currently understood, it is necessary to note the major physiographic-tectonic elements of the region (Fig. 9):

(1) The Fijian islands, the subaerially exposed portion of a slightly larger suboceanic crustal mass constituting the Fijian platform (or microplate). (2) Extending initially southeastwards and then southwards from Fiji is a long linear submarine ridge some 2400 km long, which joins with the New Zealand North Island; this is the Lau-Colville Ridge, the Lau portion being defined as north of latitude 28°S (Woodall, 1985). The emergent features of the Lau ridge constitute a large number of islands (the Lau Islands), including both atolls and dissected volcanic cones. (3) Immediately to the west of the Lau-Colville Ridge is the extensional back-arc (marginal) South Fiji basin, roughly triangular shaped, and bounded to the north by the Fiji plateau and Vanuatu trench, and by the Loyalty and Three Kings rises to the west. Davey (1982) has interpreted the South Fiji basin as initiating during the Oligocene; it is floored by oceanic crust. (4) To the east of the Lau-Colville ridge is a younger, still active (Pliocene-Recent) back-arc basin, the Lau-Havre basin (e.g. Malahoff *et al.*, 1982) of which the northern portion is specifically the Lau Basin; this again is floored by oceanic crust, but near its northern end occurs the volcanically active island of Niua fo'ou. (5) The eastern boundary of the Lau-Havre basin is the submarine Tonga-Kermadec ridge, which itself is bounded to the east by the Tonga-Kermadec trench, interpreted as the present locus of westward subduction of the Pacific plate. The northern end of the Tonga trench curves westwards and connects with the Vitiaz Trench lineament and

the North Fiji fracture zone, the latter passing just northwards along the northern margin of the Fiji platform, and thus also defining the northern margin of the Lau basin. Prior to the formation of the Lau-Havre basin, the Lau-Colville and Tonga-Kermadec ridges were joined as a single ridge. The Lau-Colville ridge thus constitutes a remnant arc (Karig, 1970), while the Tonga-Kermadec arc is the frontal arc that includes the presently active line of volcanoes forming the Tofua arc. (6) West of the Fiji platform, extending westwards to the Vanuatu (New Hebrides) island arc, is a third extensional basin, the North Fiji Basin (Falvey, 1978), now considered as initiating during the Pliocene, i.e. probably contemporaneous with the Lau basin (Whelan *et al.*, 1985). (7) The Samoan islands, and including the linear series of seamounts and shallow banks extending to the northwest. These have a geological origin which is quite different from the previous ridges, arcs, and backarc basins listed, representing the phenomenon of oceanic island volcanism, now believed to be hot spot related.

Most syntheses of the S.W. Pacific conclude that Vanuatu (New Hebrides), Fiji, and Tonga-Kermadecs were initially joined into a once continuous island arc (the Vitiaz arc; e.g. Gill and Gorton, 1973; Coleman and Packham, 1976; Duncan *et al.* 1985), that existed along the convergent north-eastern boundary of the Australia-India plate. It is inferred that westward subduction of the Pacific plate occurred along this boundary, but the evidence is not conclusive. The cause of the eventual fragmentation of this early arc system is unknown, but is thought to have, at least in part, resulted from collisions with Pacific plate seamounts (Gill *et al.*, 1984). Brocher (1985a) suggests that the former site of subduction of the Vitiaz arc is now seen as the Vitiaz trench lineament, consisting of a series of short, narrow basins connecting the Vitiaz trench with the Tonga trench (Fig. 9). Brocher further notes that the most likely current location of fragments of the former Vitiaz arc is within the Vanuatu

southern group of the Tonga Islands, as the sister group of the Fiji Islands. On the other hand the distribution of *Baeturia maddisoni* suggests some coherence between the northern islands of the Tonga chain and Samoa.

Biogeographic coherence and the relationships between areas of endemism in the south-west Pacific can be further elucidated by consideration of taxa with a wide distribution in the area (fig. 8).

The distribution of the genus *Aceropyga* as a whole extends from the Bismarck Archipelago to the Tonga Islands: two species are endemic to the Bismarck Archipelago, one is endemic to the Solomon Islands, one is found on Vanuatu and the remote island of Kusaie, East Carolines, 14 (sub)species are found in Fiji, and one species is endemic to southern Tonga. This distribution is regarded as an island chain distribution along the eastern part of the Outer Melanesian Arc with a most conspicuous radiation in Fiji (Duffels, 1983a, 1986). Following further study of the relationships of the *Aceropyga* species of the Bismarck Archipelago and Solomon Islands, which all belong to the *A. aluana* group, the area cladogram of fig. 5 can hopefully be extended to the Solomon Islands and Bismarck Archipelago.

Cosmopsaltria vitiensis is the only species of *Cosmopsaltria* in the south-west Pacific, but it is provisionally allocated in the genus. *Cosmopsaltria* evolved mainly in Central New Guinea (Duffels, 1983a), which forms the continental Inner Melanesian Arc part of New Guinea. However, a group of 3 species, the *gracilis* group, is found in the North Coast mountains of New Guinea and the Papuan Peninsula, which form the western part of the oceanic Outer Melanesian Arc (Duffels, 1983a, b; 1986).

Raiateana shows a distributional pattern connecting Fiji (ssp. *kuruduadua* and *bifasciata* of *R. kuruduadua*, and *R. knowlesi*) and Samoa (*R. kuruduadua* ssp. *samoensis*) with Raiatea I. in the Society Is. (*R. oulieta*). The probable sister group of this genus is formed by the genera *Nggeliana* Boulard and *Heteropsaltria* Jacobi from the Solomon Is. (Duffels, 1986). No relatives of these three genera are found in the Bismarck Archipelago, New Guinea, Sulawesi, or Maluku.

The distribution of the genus *Baeturia*, in Japan, Ryukyu Islands, Maluku, New Guinea, Queensland, Solomon Is. and Samoa (De Boer, 1982), Vanuatu (Boulard, 1979) and now recorded from Rotuma Island and the northern Tonga islands seems interesting from a historic biogeographical point of view.

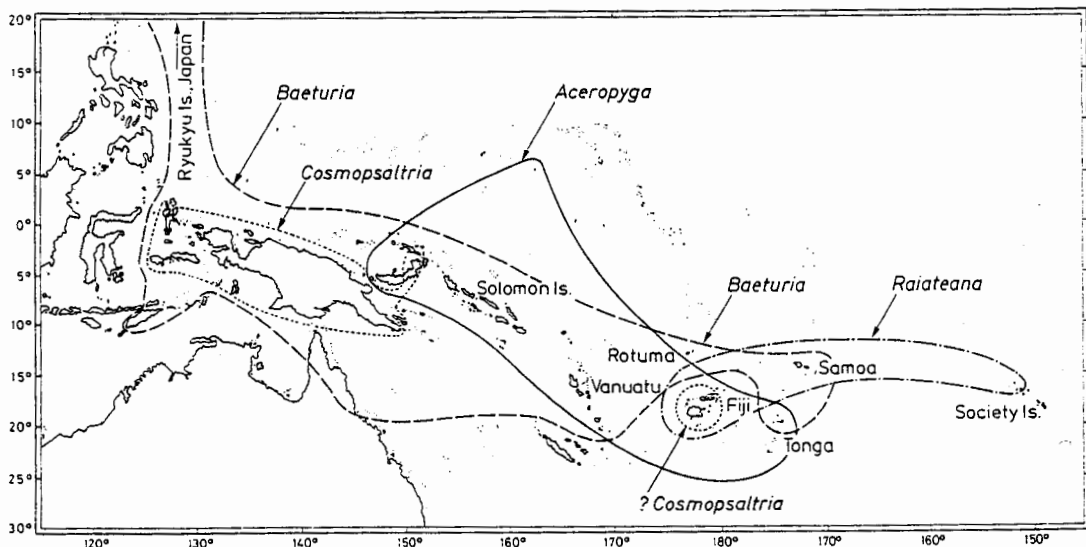


Fig. 8. Distribution of the genera *Baeturia*, *Aceropyga*, *Cosmopsaltria* and *Raiateana*.

that a well evolved volcanic arc existed in middle Oligocene, but its date of inception is unknown. Dates of 33 ± 2 Ma are, however, well established for mafic volcanic lavas and an associated intrusive pluton. A further phase of igneous activity is recognised in early to middle Miocene, in which arc tholeiite lavas are intercalated with reefal and volcanoclastic sediments, widely occurring in Viti Levu. This phase is dated at 10 ± 2 Ma; similar ages (12-14 Ma) are found for the western Lau islands, as noted later. Gill *et al.* (1984) interpret available dates as indicating that deformation, *uplift*, intrusion of trondhjemite and gabbro plutons, and low-grade metamorphism all occurred during the middle Miocene, but do note that this does not necessarily coincide with the timing of the breakup of the Vitiaz arc.

Mature Arc Stage (10-5.5 Ma). The beginning of this stage is correlated with the "Tholo (or Colo) Orogeny". This, however, possibly only represents a time of unusually intense volcanic and plutonic igneous activity, and upwarping, in Fiji alone (rather than being more widespread throughout the region). During this time, widespread volcanism certainly occurred across Fiji (especially Viti Levu) and more than a dozen of the Lau islands and the Yasawas, and is associated with widespread intrusions of plutons and epiclastic sedimentation. Moreover, the chemistry of the volcanism showed a marked increase in diversity. Gill *et al.* (1984) conclude that there is no convincing evidence for the breaking of the Vitiaz arc occurring before 8Ma (mid-late Miocene) and only weak evidence that it began before 5.5 Ma (latest Miocene). A rather unique, but voluminous, phase of high-silica (rhyolitic) volcanism occurred 6.9 ± 0.5 Ma ago, from E-W submarine vents in northeastern Vanua Levu, within 50 km of the present rifted margin. This type of volcanism is interpreted as due to crustal melting, accompanying initial crustal thinning, itself a likely precursor to rifting.

Early Rifting Stage (5.3-3 Ma). This period coincided with (i) contemporaneous formation of the North Fiji and perhaps initiation of the Lau back-arc basins; (ii) the development of extensional stress regimes in at least northern Viti Levu and in Lau; (iii) a distinct change in the chemistry of the volcanism, in which basaltic lavas become predominant; these are dated from 5.5 to 3.0 ± 0.3 Ma, having erupted from more than 30 centres. Included are the Ba and Koroimavua volcanic groups of Viti Levu and the Macuadrove super-group of Vanua Levu; Tavua, the largest volcano (situated in north central Viti Levu), evolved during the period 4.5-3.5 Ma.

Late Rifting Stage ($< 3.0 \pm 0.3$ Ma). At this stage,

Fiji was surrounded by back-arc basins. The volcanism had now totally changed to lavas dominated by alkali olivine basalt, quite different from the earlier Fijian volcanism, and indeed quite distinct from the modern Tongan volcanism. The focus of the volcanism has migrated and converged on the Koro Sea perimeter during the past 1Ma. A rather distinct, but again relatively voluminous dacitic volcanism has occurred in the Kadavu island group of southwesternmost Fiji.

A major change that had now occurred, of strong biogeographic relevance, was the separation of Fiji (i.e. the Lau ridge) from the Tonga-Kermadec ridge, and the initiation of the eastern subduction zone, currently seen as the Tonga-Kermadec trench; this produced the widening Lau basin, a process still continuing.

The Rotational History of Fiji. It is now recognised that the Fijian Islands have been rotated anticlockwise; Whelan *et al.* (1985) specifically suggest $21-60^\circ$ rotation during the past 5-3 Ma (i.e. $5-12^\circ$ per m.y.); the process is inferred to be continuing. The 5Ma date is favoured for the initial opening of the back-arc basins, which is coupled to the rotation.

Periodicity of volcanism. The new K-Ar dates (Whelan *et al.*, 1984) show a distinct peaking in the intensity of volcanicity between 2-4.8 Ma, the main peak occurring at 3.8 Ma. This peak was widespread throughout Fiji, and coincided with active major rifting (breakup) of the Vitiaz arc.

Lau Islands

These represent the emergent features of the Lau ridge, and include both atoll reefs and islands, the latter surrounded by barrier and fringing reefs. Many of the islands represent maturely dissected cones of middle to late Miocene, or early Pliocene age. Erosional remnants of limestone form covering deposits on many islands, representing raised Miocene-Pliocene reefs. Some dissected Pliocene volcanoes are not reef covered. The following notes outline the major geological events so far recognised (Woodhall, 1985):

Middle Miocene. Andesite-dominated volcanism that formed the islands of Yacata and Nayau are considered to have been an extension of the New Hebrides western volcanic belt at this time. Dates of 13.95 and 12.7 Ma are reported for the volcanics from these two islands, respectively (Whelan *et al.*, 1985).

Late Miocene. Andesite volcanism continued to be widespread through the Lau group between ap-

and Fiji-Lau arcs (or perhaps more correctly, ridges).

The available data further indicate that Oligocene and early Miocene volcanism, and associated contemporaneous sedimentation, took place on the former Vitiaz arc. Older Middle to late Eocene volcanics are recognised at 'Eua (Tonga) and within the Lower Wainimala group in S. Viti Levu; Woodhall (1985), however, suggests that these may predate the formation of the former outer Melanesian (Vitiaz) arc, and instead may have formed as parts of an *inner* Melanesian arc that would have included the Norfolk, New Caledonia, and D'Entrecasteaux ridges. This implies an eastward movement of these remnants, as a result of back-arc basin evolution that included the South Fiji basin, in Oligocene time (Woodhall, 1985). If correct, this interpretation adds a further dimension to the com-

plexity of the geological evolution of the arc systems of the S.W. Pacific.

The following account summarises the major phases of development of the major islands, and island groups, within the area of biogeographic relevance to this work.

Fijian Islands

The following summary is based mainly on Gill (1970), Gill *et al.* (1984), and Whelan *et al.* (1985), this latter paper providing the most comprehensive collation and evaluation of available K-Ar dates on the Fijian and Lau islands. The sequence of stages listed below follows those recognised by these authors:

Early Arc Stage (>10Ma). Available dates confirm

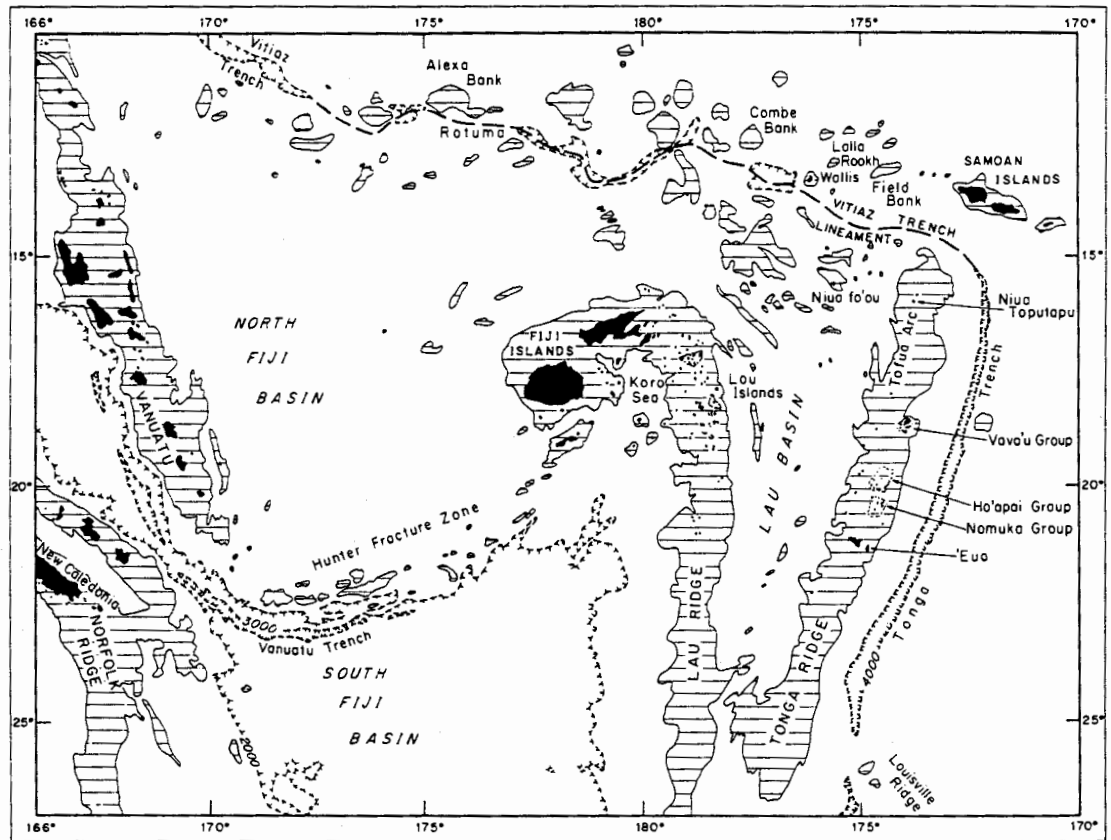


Fig. 9. Bathymetric map of the Fijian-Vanuatu-Samoan region showing the major morphological and tectonic boundaries and features. The solid continuous contours represent the 1000 fathom contour, and show the major features of positive relief. Other contour figures are also in fathoms. Solid areas are exposed islands.

proximately 5.5-9 Ma. As no contemporaneous volcanism is recognised in the New Hebrides, Woodhall (op. cit) suggests that the Lau and New Hebrides ridges may have commenced to separate at this stage. This phase of activity correlates with the Fijian "Colo"orogeny. Following the cessation of volcanicity, near 5.5 Ma ago, submergence of the volcanic cones evidently occurred, allowing reef growth to occur; the cause of submergence may be due to both tectonic changes and sea-level changes.

Early Pliocene. Reef development on the eroded volcanoes is considered to have been restricted by a global sea-level low stand estimated to have occurred some 5.5-6.5 Ma ago (Vail *et al.*, 1977). A reversal of this sea-level trend, approximately 5 Ma ago, can plausibly account for the uniformly transgressive early Pliocene limestones (included within the Tokalau limestone group), which cover the older subaerial volcanoes. Volcanism, of basaltic type (i.e. changed from the early phases), occurred between 2.7-4.5 Ma, but was less widespread than previously.

Late Pliocene-Quaternary. Sporadic alkaline basaltic volcanism occurred between 0.3-2.2 Ma (Mago Volcanics), accompanied by tensional rifting and block faulting. One consequence has been the emergence of the early Pliocene reefs. Formation of marine terraces on these newly emerged reefs is interpreted by Woodhall (op. cit) to have occurred in late Pliocene during the eustatic sea-level falls that followed the early Pliocene high sea-level stands (Vail *et al.*, 1977). The intensity of the rifting process decreased southwards along the Lau ridge.

The Tongan Islands

The Tongan ridge (or forearc) has been the site of an active plate boundary since Eocene. As previously described, successive back-arc basins have opened behind it (i.e. to the west), rafting the forearc eastwards to its present position. An age of middle to late Eocene is indicated for the basement of the Tonga forearc, based on volcanic exposures on 'Eua (Stearns, 1971; Ewart *et al.*, 1977; Duncan *et al.*, 1985; Cunningham and Ansdcombe, 1985).

A further complicating factor on the modern evolution of the Tonga ridge is the occurrence of the large, aseismic Louisville ridge on the Pacific plate; this trends obliquely to the axis of the Tonga ridge (Fig. 9), with which it is currently colliding, and is thus evidently being subducted beneath the forearc.

The Tongan islands comprise two, essentially parallel chains of NNE-SSW trending islands, the western group comprise the active volcanoes (the Tofua arc), lying some 160 km west of the Tonga

trench axis. The eastern island chain lies some 95-130 km west of the trench, situated on the central part of the Tonga ridge, and comprise limestone covered islands, currently volcanically inactive.

A closer investigation of the eastern Tongan islands indicates two general types: (a) limestone islands of Pliocene to Holocene age built on older volcanic piles (e.g. Vava'u and Tongatapu); (b) islands that expose older (pre-Pliocene) rock successions (e.g. Nomuka group and 'Eua). Geographically, the eastern islands naturally cluster into four distinct groupings, each representing the summit of a localised topographic "summit" (or block) along the Tonga ridge, and each separated by major WNW-ESE faults. The groups, from north to south, are: the Vava'u group; the central Ha'apai and Nomuka groups, and the Tongatapu group (Fig. 9).

The Tofua Arc. The active volcano arc was initiated in the (?) late Pliocene (Herzer & Exon, 1985) although the exposed volcanic islands would represent the later Pleistocene-Recent volcanicity. The notable exception is one of the northern volcanoes, Niua Toputapu, for which a tentative data of ca. 3 Ma has been obtained (Cunningham and Ansdcombe, 1985), suggesting this to be either a remnant cone from the pre-rifted Lau-Tonga ridge, or a volcano developed during initial rifting. These volcanoes have dominantly erupted basaltic andesites, with rarer andesites and dacites (Ewart *et al.*, 1973; Ewart, 1976).

Vava'u Group: Outcropping sequences comprise Quaternary subhorizontal terraces of coral limestone, lying unconformably on ? Pliocene limestones, these probably resting on an older volcano with associated caldera (Cunningham and Ansdcombe, 1985).

Ha'apai Group: The eastern islands simply comprise a raised coral platform constituting a discontinuous barrier reef along the Tongan platform. The western islands consist of raised Quaternary coral limestone and/or pyroclastic sediments.

Nomuka Group: This group has been uplifted further than surrounding blocks, thus exposing sequences of early to late Miocene volcanoclastic sediments, indicating extensive, relatively close volcanicity during the Miocene; the volcanic products were quite extensively reworked to form the deposits. These volcanoes would have been similar to those of the modern Tofua arc. Miocene, and on some islands, raised Quaternary reefs overlie the Miocene volcanoclastic sediments.

Tongatapu Group: The islands of Tongatapu and 'Eua provide the most complete geological sections although interestingly, the geological histories of

these two islands differ. Extensive drilling in Tongatapu has revealed a succession of strata showing a history of nearly continuous volcanism and/or sedimentation from late Eocene to early Pliocene; depths of sedimentation varied, there being evidence of shallow water in middle upper Miocene. The exposed rocks on Tongatapu are Pleistocene limestones.

Eua: Here, a middle Eocene volcanic basement (Duncan *et al.*, 1985; Ewart and Bryan, 1972) is ex-

posed, which when forming, would almost certainly have been exposed subaerially, as now. Overlying this basement are middle Eocene conglomerates, grading up into late Eocene-Oligocene limestones, deposited in shallow shelf environments. Considerable erosion of the Eocene-Oligocene limestones subsequently occurred, indicating uplift and an erosional or non-depositional gap developing in late Oligocene. Middle Miocene to early Pliocene volcanoclastic sediments follow unconformably,

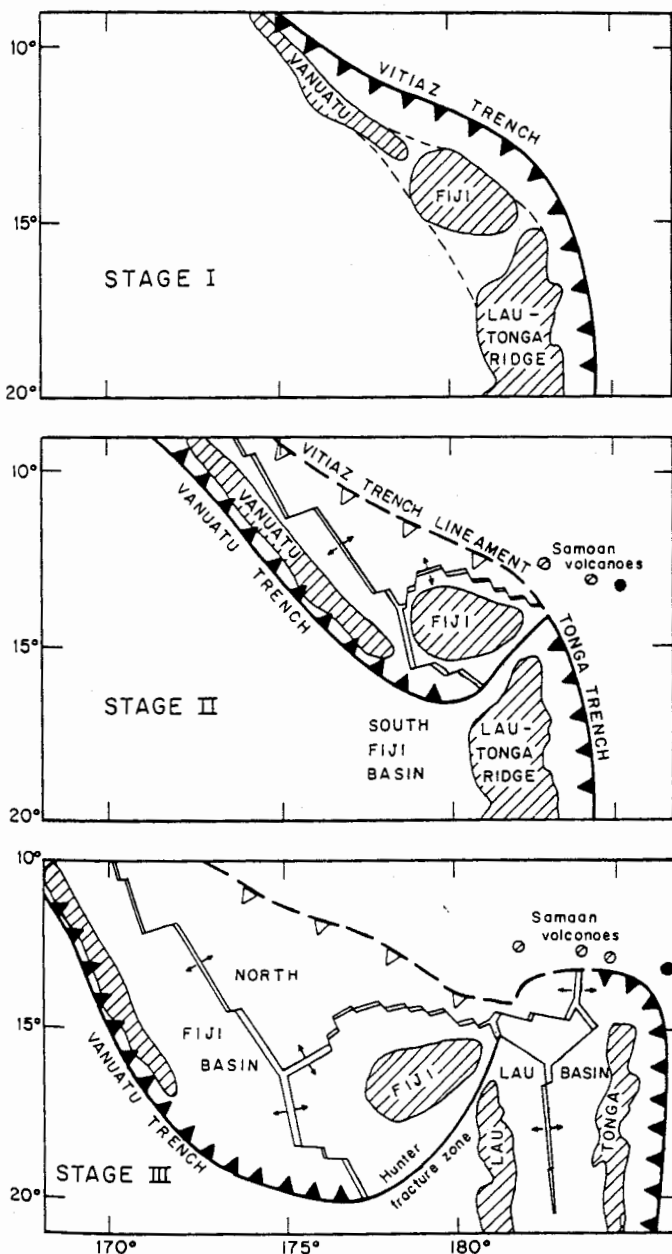


Fig. 10. Highly schematic sketches illustrating the current interpretations of the break-up and subsequent tectonic evolution of the island arcs and basins of the S.W. Pacific. Stage I would correspond broadly to late Eocene-Oligocene; Stage II to Miocene; Stage III, Pliocene to Pleistocene. Active subduction zones are shown with the solid triangular ticks; failed subduction zones by dashed lines and hollow triangular ticks. Redrawn and slightly modified from Falvey (1978) and Brocher (1985a).

the volcanoclastic supply ceasing in early Pliocene. A further succession of coral and foraminiferal limestones, of ?early Pliocene age, overlies disconformably the previous volcanoclastic sediments. The final phases have been late Pliocene tilting and faulting, and Pleistocene-Recent intermittent uplift and growth of limestone marine terraces.

Summary of Tongan evolution (Fig. 10)

1. The middle Eocene volcanic basement of Tonga, as seen on 'Eua, represented part of a volcanic chain, subaerially exposed, which predated the South Fiji basin, and would have formed part of a single Lau-Tonga ridge; this may have been located near, or attached to, the Norfolk-New Caledonia ridge.

2. Late Oligocene saw the opening of the South Fiji basin, with the rafting of the Lau-Tonga ridge eastwards. There is evidence of volcanicity continuing through from the Eocene; this was also a period of possible widespread emergence of the ridge, brought about by a eustatic sea-level drop (Vail *et al.*, 1977) and tectonic uplift. Herzer and Exon (1985) suggest that the uplift in fact began somewhat earlier, possibly even late Eocene.

3. An active volcanic island arc certainly existed through the Miocene, west of the Tonga ridge, and was situated on what is now the Lau ridge. Most of the Tonga ridge was submerged during this period. Late Miocene marked a decline in volcanicity. Large fault systems began to develop at the end of the Miocene to early Pliocene, causing widespread uplift and creating regional unconformities; this period is interpreted as related to the opening of the Lau basin, splitting the Lau and Tonga ridges, and causing further eastwards rafting of the Tonga ridge.

4. The Pliocene to Holocene period seems to have been a period of continuing tectonic instability, with faulting, and differential uplift and subsidence occurring due to continuing spreading of the Lau basin. An additional complicating factor is the subduction of the Louisville ridge which is believed to have also caused doming along the Tonga ridge (Herzer and Exon, 1985).

Finally, the establishment of the active Tofua arc commenced during (?late Pliocene, representing the third major volcanic phase in the geological evolution of Tonga.

5. The island of Niua fo'ou lies in the northern Lau basin, geographically being part of Tonga. It is an active basaltic volcano, and petrologically quite distinct from the Tofua arc volcanoes (e.g. Ewart and Hawkesworth, 1987), being an ocean island volcano developed within the spreading Lau basin.

The subaerial portion is almost certainly no older than later Pleistocene.

Samoan Islands

The Samoan islands are oceanic island volcanoes. There are four main islands, or island groups; these are, from west to east, Savai'i, Upolu, Tutuila, and the Manua group. The islands increase in size westwards, and a particularly striking feature is that this island chain has active volcanism at both its north-west and southeast ends, all of which make them unique amongst Pacific volcano chains. Extensive subaerial volcanism occurred in Savai'i early this century, while submarine eruptions occurred within the Manua group in 1866.

To understand Samoan volcanism further, the history of the volcanism needs to be viewed in two distinct stages (Natland, 1980; Natland and Turner, 1985): (a) The formation of shield volcanoes; these are now found to progress in age from west to east, from Savai'i to Upolu, thence to Tutuila, to Ofu-Olosega, and finally to the youthful Ta'u. The lavas erupted are dominantly tholeiitic basalts initially, grading to alkaline basalts prior to the formation of the major calderas. Post-caldera lavas are often very differentiated, including trachytes. (b) Voluminous outpouring of basaltic lavas from numerous vents, principally oriented along a rift zone trending 110° in Upolu and Savai'i, but also extending to a few vents in Tutuila. These eruptions occurred long after extinction of the shield volcanoes and are referred to as the post-erosional volcanism; they include strongly undersaturated basaltic lavas such as nephelinites.

The post-erosional volcanism is attributed to bending of the Pacific plate southwards as it interacts around the westerly trending portion of the northern termination of the Tonga trench; it is inferred that this causes rifting, and this rift propagates eastwards along the Samoan ridge as the Pacific plate motion carries the Samoan archipelago westwards past the Tongan trench "corner" (Natland and Turner, *op. cit.*).

The Age Progression of the Samoan Shield Volcanoes and Seamounts

Natland and Turner (1985) report new K-Ar dates for two Samoan islands as follows: Tutuila 1.03-1.40 Ma; Upolu 1.54-2.80 Ma. These are from the shield volcanoes of Pago and Taputapu (Tutuila) and Fagaloa (Upolu). Palaeomagnetic data also confirm an upper limit of 1.7 Ma for the Tutuila shield volcanism. K-Ar dates are not currently available for the other islands. Palaeomagnetic data for

Savai'i, however, are consistent with an upper limit of shield volcanism of 2.4-3.4 Ma (Keating, 1985), while field and palaeomagnetic data suggest an age < 0.7 Ma for the Manua group (Natland and Turner, 1985; Keating, 1985).

Thus, the data suggest that the main shield building phases of the Samoan islands become progressively younger towards the east, as also found in other Pacific volcano chains, such as Hawaii. Shield volcanism on Upolu is estimated to have lasted at least 1 Ma, and on Tutuila 0.4-0.8 Ma.

Stretching broadly westwards from the Samoan islands are a complex series of seamounts, ridges, and islands (Fig. 9). Three seamounts, in particular, continue the WNW trend of the Samoan chain, and recent dredging and K-Ar dating has been carried out (Duncan, 1985), with the following results:

Field Bank 5.4 ± 0.2 Ma.

Lalla Rookh Bank 10.0 ± 0.3 Ma.

Combe Bank 13.5 ± 0.9 Ma.

Thus, these data, plus the new Samoan islands dates, indicate that the Samoan volcanism can be confidently traced at least as far west as the Combe Bank, and that a progressive linear ageing occurs to the west (i.e. the Seamount chain extends 1700 km WNW from Samoa). This suggests a "hot-spot" volcanic phenomenon, as found in other Pacific volcanic chains, and the Samoan volcanic trend is subparallel to these other Pacific "hot-spot" chains. Duncan (1985) calculates a migration rate of 7.7 ± 2.5 cm/yr from the various age data, with the "hot-spot" located approximately 150 km east of Tutuila. Brocher (1985b) has shown that these submarine seamounts are flat topped edifices with shallow banks, although Combe Bank is somewhat larger; their general morphology, lithospheric subsidence (as shown by deep terraces), and sedimentary cover on the edifices are, however, consistent with the predicted westward age progression (Brocher, 1985b). The petrology of these seamounts is also consistent with the Samoan magmatic province (Sinton *et al.*, 1985).

One question, however, concerns the relative spatial relation between the Samoan volcanoes and northern Tonga ridge and trench. Fixed "hot-spot" volcanism implies a relatively deep, fixed position of the source of the volcanic magmas, with the overlying Pacific plate moving westwards across this fixed frame of reference, thus producing progressively older volcanic islands westwards along the chain. In this way, islands will be born, mature, eventually erode, and ultimately subside as they move across, and eventually past, the "hot-spot" source. As the Tonga arc is interpreted to have been

rafted eastwards as a consequence of late Pliocene to Recent Lau basin opening (see previous description), it would imply that the northern end of Tonga has progressively approached the Samoan islands (e.g. Duncan, 1985), in which case, the Tonga trench would have been some 400 km west of its present position 3 Ma ago. Natland and Turner (1985), however, suggest that the Samoan shield volcanoes have built at approximately the same distance from the "corner" of the Tonga trench (and ridge) for the past 13.5 Ma. They note that the calculated volcano migration rate (7.7 ± 2.5 cm/year) is slower than predicted for motion over a fixed "hot-spot" at this Pacific latitude, and this raises the question of the development of possible convective-thermal disturbances at the northern "corner" of the Tonga trench which may be contributing to the shield volcanism. Such complications have certainly been important in the Samoan post-erosional volcanism, but their role is much less certain in the more important shield-building volcanism of the Samoan volcanic chain. Thus, this aspect is at present unresolved.

It should be also noted that a number of additional seamounts and exposed volcanic islands occur west and south of Combe Bank, and these considerably complicate the general appearance of the Samoan volcano migration (Fig. 9). It seems likely that seamounts originating from mid-plate volcanism along the Tuvalu (formerly Ellice) islands, of Cretaceous age, have occurred, and these have partially overlapped with the Samoan seamounts (e.g. Brocher and Holmes, 1985). Alexa Bank is the most westerly major seamount, and is dated by Duncan (1985) at 36.9 ± 0.5 Ma, which does not obviously fit the Samoan seamount migration data. A number of volcanic islands occur north of the Fijian islands, towards the Vitiaz trench lineament, notably Rotuma and Wallis islands. Wallis is assigned to the Tuvalu island chain and its mid-Pleistocene volcanism (erupted on to an older volcanic edifice) is correlated with its collision with the Vitiaz trench lineament (Brocher and Holmes, 1985). Quaternary alkali basalts also occur on Rotuma (as on Fijian islands) and are generally attributed to reorganisation of the complex plate boundaries in the region north of Fiji in the past few million years (Sinton *et al.*, 1985), although the edifice possibly formed by subduction-related volcanism (Brocher and Holmes, 1985).

Some biogeographic and paleogeographic implications

Fiji-Lau-Tonga: An active volcanic island arc chain

certainly existed in the S.W. Pacific in the middle Eocene, although its position (and original continuity) with respect to either the present Fijian or New Caledonian regions is still unknown. Furthermore, a well evolved volcanic island arc chain existed in the middle Oligocene (33 ± 2 Ma) constituting an early volcanic phase of the Vitiaz arc, it being possible that the Eocene volcanism continued through to Oligocene. The relative extents of the resulting land masses cannot yet be properly evaluated except to note the occurrences of volcanic chains in the region during this period of geological time. It does appear, however, that widespread late Oligocene emergence of the Tonga ridge occurred. A particularly widespread and important phase of island arc volcanicity is recognised to have occurred in the early to middle Miocene (10-14 Ma), extending to late Miocene (5.5 Ma); the various products of this volcanic chain are found in the Fijian, Lau, and older Tongan islands, again indicating the development of an emergent volcanic island chain. A further important event was the inferred middle Miocene emergence of the Fijian area; although the initial exposed landmasses must have been smaller, and more disconnected than now, the evidence suggests that not only did the archipelago persist through to the present time, but presumably grew and coalesced by continued volcanicity; particularly intensive volcanicity occurred in the Pliocene

(Fig. 11). Considerable topographic fluctuations of the evolving Fijian landmass would, however, have been caused by erosion, eustatic sea level changes (see below), and, of course, the instability and catastrophic short term changes resulting from volcanic eruptions.

Miocene emergence is also indicated for the Lau ridge and its volcanoes. In contrast, the Tonga ridge was evidently largely submerged during much of this period, with rifting and uplift, however, starting in late Miocene to early Pliocene.

The Pliocene evidently saw widespread transgression on the Lau ridge, while the Tongan ridge continued to be a period of considerable tectonic instability, with differential uplift and subsidence, which continued through the Pleistocene to today; 'Eua probably emerged during late Pliocene. The late Pliocene to Quaternary in the northern Lau islands was marked by sporadic volcanicity and tectonic disturbances resulting in emergence of older eroded volcanic edifices and their superimposed reefs. The final major volcanic phase was the (?) late Pliocene development of the Tofua arc along the western Tongan ridge, although the emergence of the volcanoes presumably did not occur until late Pleistocene, and in fact, is still occurring (e.g. the active Falcon and Metis shoals).

It is thus evident that the Lau and Tongan islands have not provided the same degree of longevity or long term stability as the Fijian archipelago, with respect to suitable migration environments. Survival and speciation in such environments would require extensive "island hopping", although the periods of emergence and subsidence do evidently occur on time scales of at least of the order of 1 to 2 million years. Successive "reinvansion" from a more extensively stabilised Fijian biota would also represent a plausible scenario in such circumstances.

Samoan Islands: As previously described, these are still active at both ends of the group in part due

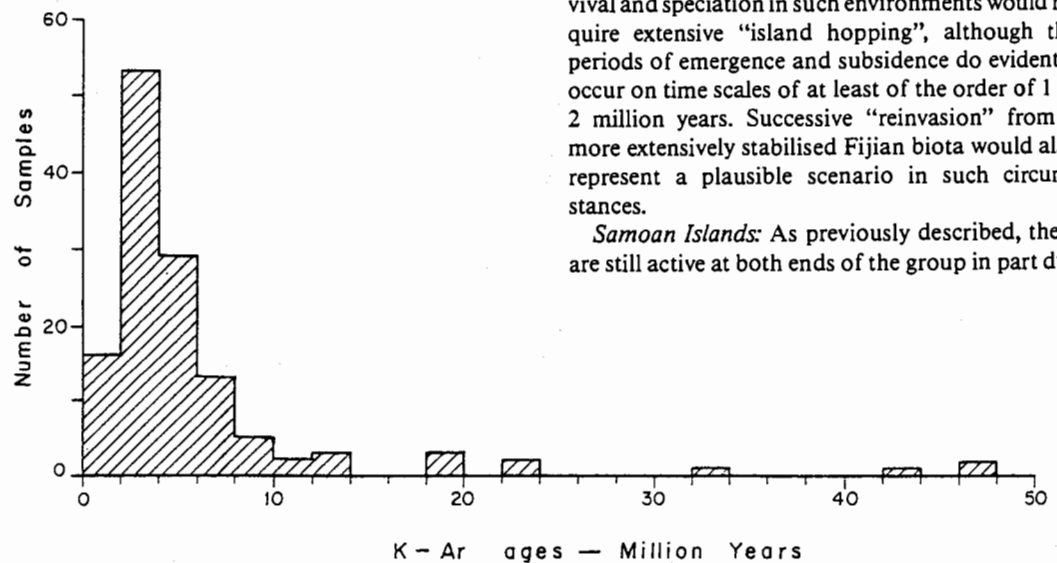


Fig. 11. Histogram showing distribution of K-Ar ages determined from volcanic rocks of the Fiji, Lau and Tongan Islands. Data from Whelan *et al.*, 1985; Duncan *et al.* 1985; Ewart *et al.*, 1977. Note that the histogram cannot be used as a measure of relative volumes of the volcanic episodes, particularly the older stages.

to post-erosion volcanism. It is evident, however, that the age of the oldest exposed shield volcano groups on Savai'i is currently estimated to be 2.4-3.4 Ma. The age of the Samoan chain is, however, much older, at least 13.5 Ma, based on the Tomba Bank. This indicates that subaerial volcanic islands have existed in the Samoan area for the past 13.5 Ma; the islands themselves have, however, emerged, grown, eroded, and eventually subsided in an east to west progression, to some extent as seen in the modern Samoan island group. Thus, a relatively old fauna existing on one of the "proto-islands" 13.5 Ma ago, in order to persist to today, would have to have undertaken periodic eastward inter-island migration as the archipelago continued to evolve. The history of Samoa, however, does allow the possible presence and "in situ" evolution of an island biota whose original Samoan island parentage is significantly older than the currently exposed Samoan islands.

Some General Considerations: (a) Changes in the relative geographic positions of Vanuatu, Fiji, Lau, Tonga, and Samoa have occurred as a result of the very complex plate boundary evolution of this region during the Tertiary, and these "readjustment" processes are still clearly continuing today. These changes are shown in a generalised way in Fig. 10. Perhaps the most important in terms of the more recent biogeographic consideration, is the eastwards rifting of the Tongan ridge from the Lau ridge during the past 3 Ma, with the opening of the Lau basin, obviously resulting in increasing isolation of any relict Tongan biota during this phase. The question of the relative geographic relationship of northeast Tonga and Samoa, is as previously discussed, currently unresolved. If the Samoan shield volcanism is due to a fixed "hot-spot", then the two island groupings will have converged during the past 3 Ma; if the Samoan volcanism is coupled in some way to the northern Tongan subduction zone, then the two island groups have had similar and correlated eastward migration paths.

(b) Although the history of emergence and subsidence of the various islands and island groupings in the S.W. Pacific has been dominantly controlled by the interaction between tectonic, volcanic, and erosion processes, a further complicating factor has been eustatic sea-level changes. The data of Vail *et al.* (1977) suggest that major low sea-level stands occurred during middle Oligocene (26-30 Ma) and late Miocene (3.5-6.5 Ma) of about 250 and 200 m, respectively, below present sea-level. The data also indicate four sea level falls during the Pleistocene, of the order of 150-200 m, respectively, below present sea-level. Higher sea-levels occurred during

middle Miocene and early Pliocene (4-5.5 Ma, or the order of 100 m), with three smaller rises during the Pleistocene. Apart from the obvious effect of accentuating the appearance and/or disappearance of island masses, such sea level changes will alter the areas and relative elevations of "stabilised" islands, thus resulting in very significant ecological changes. Modern bathymetry suggests that the sea level drops would not, however, have allowed the main Fijian islands or the Lau-Fijian islands, respectively, to directly join, and thus provide direct land bridges within each of these island groupings. In Samoa, however, Savai'i and Upolu would presumably have joined during lowered Pleistocene sea-level stands.

(c) Volcanicity and general tectonic (and sea-level) emergence cause two general types of islands, the latter tending to comprise relatively flat, low lying islands, typically limestone covered, even though the base of these islands may be older eroded volcanic edifices. The volcanic islands may attain much greater elevations, but are, of course, much more unstable, and yet also more diverse ecologically. Such contrasts are well shown by the modern eastern and western Tongan island groupings, as previously discussed, and may favour rapid localised selection amongst immigrant populations.

(d) A final geological consideration which may have significant indirect biogeographic consequences is the chemical nature of the volcanic products. As has been described, the earlier volcanicity of the Fijian, Lau, and Tongan islands was of the island arc type, as is continuing today in the modern Tongan volcanoes. The lavas erupted are typically dominated by basaltic andesites, and less common more silica-rich types. In contrast, the younger volcanicity on Fiji, Lau, (and also, such outlying islands as Rotuma) is dominated by alkaline basalts. The Samoan islands have built from basaltic volcanism throughout their history. There are important geochemical differences between the andesite and basaltic lavas, both in terms of major element chemistry (for example, magnesium), and minor and trace element chemistry (for example, phosphorus). In general terms, the andesite lavas are geochemically more "depleted" (e.g. Ewart, 1982). These geochemical differences will presumably be reflected in soil nutrients, and thus are likely to effect vegetation patterns. Moreover, there seems to be a tendency for basaltic soils to develop more rapidly than these from andesitic lavas (although many other factors, such as climate and the physical nature of the volcanic ejecta are clearly also important here).

Historic biogeography of south-west Pacific cicadas

The species of the genus *Aceropyga* are distributed along the eastern part of the Outer Melanesian Arc (= Vitiaz Arc). The development of this arc from an early volcanic phase to an emergent volcanic chain occurred in early to middle Miocene (10-14 Ma), extending to late Miocene (Ewart, this paper). The Outer Melanesian Arc was situated along the present location of the Vitiaz Trench Lineament until the Miocene. Geological data indicate a middle Miocene emergence of the Fijian archipelago, that persists through to present time. Formation of the North Fiji and Lau basins in the late Miocene and Pliocene separated the main Fiji Islands and the Lau group of Fiji from Vanuatu and the Tonga Islands (Ewart, this paper fig. 10).

I am inclined to believe that the ancestors of the *Aceropyga*-species of Fiji reached these islands when Vanuatu, Fiji and Tonga were joined into a continuous island arc. This would date the colonization of Fiji by *Aceropyga* before the breaking of the Vitiaz Arc in the mid-late Miocene (8 Ma) or the latest Miocene (5.5 Ma), and before the consequent isolation of Fiji from Vanuatu. The existence of a continuous dry land in the Fiji archipelago since middle Miocene seems to be reflected in the rich cicada fauna of these islands (19 (sub)species).

The phylogenetic reconstruction of *Aceropyga* (fig. 13) shows that the Fiji species of the genus belong to two monophyletic groups: the *corynetus* complex and the *distans* group. The *corynetus* complex comprises 12 (sub)species, which are all Fiji endemics. The ancestor of the *corynetus* complex probably colonized Fiji from one of the more western islands of the Outer Melanesian Arc. The *distans* group contains one species with three subspecies from Fiji and one species from Tonga. The western origin of the *distans* group is suggested by the occurrence of its sister group, formed by one species, in Vanuatu.

Dispersal along the Outer Melanesian island-arc by island-hopping is probably much facilitated by low sea-level stands. When the Outer Melanesian Arc was open as a route of dispersal for Asian immigrants in the Pacific by the early Miocene, as Duffels (1983b) supposed, the low sea-level stand of the middle Oligocene (Ewart, this paper) played no role in the distribution of West-Pacific taxa. However, a major low sea-level stand of 200 m below the present level in the late Miocene (Ewart, this

paper) would have shaped a more continuous, sub-aerial, Outer Melanesian Arc that facilitated the distribution of land animals and plants over the islands of the south-west Pacific.

The relationships between the groups recognized in the Fijian *Aceropyga corynetus* complex is unknown. Although the *philorites* group and the *corynetus* group are characterized by synapomorphies, we have not been able to recognize their inter-relationships with *Aceropyga huireka*. The *philorites* group is recorded from Viti Levu (5 species), one species being also recorded from Vanua Levu. *A. huireka* is endemic to Vanua Levu, and the *corynetus* group has a wider distribution in the Fiji archipelago.

A. huireka and the species of the *philorites* group occur in rather restricted areas, mostly on one island only. However, the records of *A. egmondiae* from small areas in Viti Levu and Vanua Levu suggest the possibility of a wider actual range, which is under collected.

An interesting pattern is presented in the taxon-area cladograms of figs. 5-7. The biogeographical coherences of Viti Levu and Ovalau, and of Vanua Levu and Taveuni is apparent in the distributions of four cicada-species. The occurrence of a subspecies of *A. corynetus*, *A. distans*, *A. stuarti* and *Raiateana kuruduadua* on Viti Levu and Ovalau, and another subspecies of each of these taxa on Taveuni and Vanua Levu, probably reflects the existence of land bridges between the islands of each pair by sea-level fall in the recent past. The three taxon-area cladograms (figs. 5-7) also suggest a sister group relationship between Viti Levu-Ovalau and Vanua Levu-Taveuni, which might be related to a vicariant event of sea-level rise separating the two island-pairs after a period of connection. Geological data indicating four Pleistocene falls of sea-level in the order of 150-200 m, interspersed by three smaller rises (Ewart, this paper), provide ample explanation for the biogeographic patterns discussed. The island of Kandavu, and Maola and Totoya, are separated from the main Fiji islands by sea more than 2000 m deep. The occurrence of a subspecies of *corynetus* in Kandavu and a subspecies of *distans* in Maola and Totoya could be the result of dispersal over sea.

The presence of the sister species *A. albostrigata* and *A. distans* in Tonga and Fiji, respectively, can

be explained by active dispersal. An alternative, vicariant, explanation is found in the partition of Fiji (i.e. the Lau Ridge) from the Tonga Kermadec Ridge by the formation of the Lau Basin (3 Ma) (Ewart, this paper).

The cicada-fauna of the islands of the Lau-group of the Fiji and Tonga chain is relatively poor. The Lau-group has only one species, *Aceropyga distans*, whilst the Tonga chain has one species, *Aceropyga albostrigata*, in the southern islands (Tongatapu and Eua), and one species, *Baeturia maddisoni*, in the northern islands (Niuatoputapu and Vava'u). The paucity of the fauna of these islands can be explained by the absence of long term, geological, stability, especially emergence and subsidence occurring on time scales of 1 to 2 million years (Ewart, this paper).

If *Cosmopsaltria vitiensis* from Fiji really belongs to the *Cosmopsaltria gracilis* group, recorded from the New Guinea part of the Outer Melanesian Arc, then it is surprising that the genus is not also recorded from the Solomon Islands and Vanuatu, these being potential stepping-stones along the island-arc from New Guinea to Fiji.

When the characters of the monotypic genus *Moana* and the genus *Aceropyga* are interpreted correctly, *M. expansa* from Samoa forms the alleged sister-group of the genus *Aceropyga* or a group of *Aceropyga*-species. This implies a probable early immigration of an ancestor of *Moana* in the Samoan islands. Emergent volcanic islands have existed in the Samoan area for the past 13.5 Ma (Ewart, this paper). A relatively old fauna existing on one of the "proto-islands" may have undertaken an eastward inter-island migration, so that the original Samoa island fauna may be older than the currently exposed islands, as Upolu, where *M. expansa* was collected. The WNW trend of the Samoan chain of islands running from the now exposed Samoa islands to Field Bank (5.4 Ma), Lalla Rookh Bank (10.0 Ma) and Combe Bank (13.5 Ma) suggests an old island-chain connection with parts of the Outer Melanesian Arc.

The genus *Raiateana* from Fiji, Samoa and the Society islands, and its sister-group comprising the genera *Nggeliana* Boulard and *Heteropsaltria* Jacobi from the Solomon islands form one monophyletic group (Duffels, 1986), which is distributed along the eastern part of the Outer Melanesian Arc and further east to the Society islands. No relatives of this probably monophyletic group of genera have been found in the Bismarck Archipelago and New Guinea. Hayashi (1987) suggests a relationship of this group of genera to the temperate genus *Tibicen* Berthold.

The distribution of the genus *Baeturia* shows congruence with that of *Aceropyga* in Bismarck, Solomon, and Vanuatu islands. However, east of Vanuatu *Aceropyga* is found in Fiji and southern Tonga, whilst *Baeturia* occurs in Rotuma island, northern Tonga, and Samoa (Duffels, 1986). The most remarkable aspects of the distribution of *Baeturia* are the absence of the genus in Fiji, the presence of an endemic species in Rotuma, which is a small island in the Vitiiaz Trench Lineament (Ewart, this paper: fig. 9), and the occurrence of another endemic in the northern Tonga islands and Samoa. This distribution suggests dispersal along the remnants of the Vitiiaz Trench Lineament and further east to Samoa, after the latest Miocene (5.5 Ma) when Fiji was already isolated from Vanuatu; the close resemblance of the Rotuma species to the Tonga and Samoa species favours the idea of dispersal and speciation in the recent past.

Such a distribution including Rotuma and Samoa, but excluding Fiji, has also been found in Macrolepidoptera (Robinson, 1975; Holloway, 1983). Robinson (1975: 340, map 15) states that "during the lowered sea levels of the last glaciation Rotuma lay among a long string of islands running from west to east and forming a bridging archipelago between the Santa Cruz Is. and Samoa".

Speculations on the relationship of the Fiji genus *Fijipsalta* Duffels to Australian and New Caledonian genera of the tribe Cicadettini, as presented in the taxonomy chapter of this paper, do not allow a cladistic biogeographical approach.

Ecology

Cicadas are phytophagous insects. The larval and adult stages feed on nutrient-poor xylem fluids (White & Strehl, 1978). The larvae are subterranean

and exploit the sap-stream in the roots of their host-plants.

No developmental times are known for any

Fijian species, but the rate of growth is very slow so that the development from the first larval instar to the full-grown nymph requires several years. According to the Fijian legend of the Nanai, the Fiji cicada *Raiateana knowlesi* appears every eight years in vast numbers (see *R. knowlesi* for further details). This implies a periodic appearance for the adults of this species. Further data on periodicity in the south-west Pacific cicadas are not available.

The adults of most cicada species collected in Fiji were seen feeding on trunks and branches of trees, with a preference for those with diameters of 8-15 cm. Larvae and nymphs of several species collected, were found feeding on tree-roots. The only Fiji cicada which does not feed on trees is the very small cicada *Fijipsalta tympanistria*, which lives in open glades with small trees, shrubs and herbs. This species was observed feeding on the stems of an unidentified herb of the family Labiatae.

Most Fijian cicadas have a preference for an undisturbed, rain-forest habitat. Many of them are endemics of relatively small areas (fig. 118). Two species, *Aceropyga stuarti* and *Raiateana kuruduadua*, are found in very different vegetation types: rain-forest, dry forest, secondary growth and plantations. *Aceropyga distans* shows some preference for creek-sides and other wet areas in primary and regenerating rainforest. The species with a wide ecological amplitude have an apparently wide distribution range within the islands and over the Fiji archipelago as a whole. The dry areas of the main islands, the western part of Viti Levu and the Savu Savu area of Vanua Levu, have a much lower diversity of cicada-species than the wetter parts. During a survey of underground pests in the Tonga Islands in 1977 Dr. C.A. Edwards collected larvae of *Baeturia maddisoni* in plantations on the roots of

coffee and other crops. The natural habitat of this species is unknown.

Some cicada species seem to have a preference for certain tree-species. The chorus of the adults of *R. kuruduadua* in Fiji is often heard from the canopy of high trees of *Alstonia vitiensis* Seemann and *Geissois ternata* A. Gray, and many exuviae of these cicada-species have been found on trunks of these trees. So they seem to have a preference for these trees. An exclusive host-plant preference was perhaps found for *Aceropyga pterophon*. Adults of this species were found on trunks and branches of *Girroniera certidifolia* Gaud., and larvae and nymphs were collected from the roots. Other host plant records are presented in the ecology paragraphs of each species.

The adult cicadas studied in the field in Fiji were often aggregated in groups of many or a small number of individuals. *A. stuarti* and *R. kuruduadua* were usually heard singing in large groups in the canopy of one or a group of trees. *A. stuarti* also occurs in smaller trees at heights of some meters above the ground, but *R. kuruduadua* is never found in such low places. *A. distans* and *A. corynetus* aggregate in groups of 3-6 and 10-20 individuals respectively, often with several together on one tree trunk. Both species were usually found at levels of 1-6 m above the ground. The aggregation of cicadas of one species in groups and the spacing of these groups in the forest becomes most apparent during the dusk chorus, in which probably all male cicadas participate.

These scattered observations suggest some habitat preference and spatial partition in the local environment by the different cicada species occurring in the same habitat.

Local names of cicadas in Fiji

Different local names are used for the cicadas in the islands of Fiji. The general name for cicadas in Viti Levu is "Maka". The species *Raiateana knowlesi* from this island, which is a great delicacy and a traditional gift in the Sigatoka Valley of Viti Levu, bears the special name "Nanai" (see the legend of the Nanai after the description of *R. knowlesi*). In

the Lambasa area of Vanua Levu, cicadas are called "Nakali", whereas "Kakalu" is used in Savu Savu, South Vanua Levu. Our guide in Savu Savu used the name "Kakalu" only for the large species *Raiateana kuruduadua*. The name "Kaka" is used in the island of Taveuni.

Methods

The methods used for the examination of male and female genitalia are described in my earlier publications (Duffels, 1977, 1983a). The terminology also follows these publications. Morphological terms for the features of larvae and exuviae are for the greater part taken from Boulard (1965) and Kudryasheva (1970). The structures of the foreleg of larvae and exuviae are identified in fig. 12. The measurements were taken as described in Duffels, 1983a.

Sound recordings were made in a natural habitat with an AKG D 202 ES microphone and an Uher 4000 Report-L portable recorder at a tape speed of 19 cm/sec.; the combination having a frequency response limit at about 16.000 Hz.

For our field work in Fiji we used maps of Viti Levu, Vanua Levu and Taveuni Is. on a scale of 1:250.000 (3rd edition, 1973), contour maps of these islands on a scale of 1:50.000 (2nd edition, 1960-1961) and forest types maps on a scale of 1:50.000 (1st edition, 1972). All maps mentioned are available from the Department of Lands and Mineral Resources, Suva, Fiji, and from Edward Stanford Ltd., London.

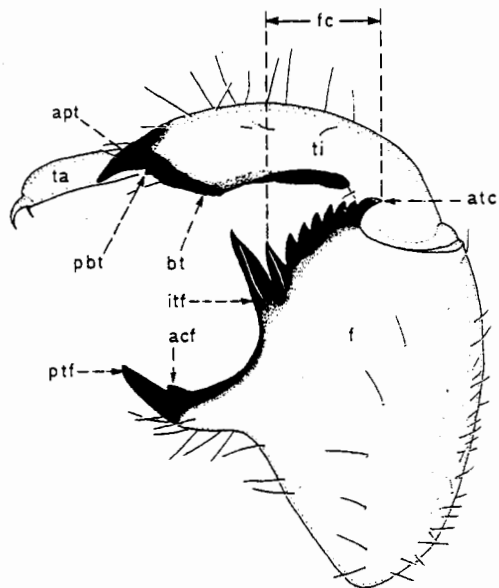


Fig. 12. Fore leg of *Aceropyga distans*. acf, accessory tooth of femur; apt, apical tooth of tibia; atc, anterior tooth of femoral comb; bt, blade of tibia; f, femur; fc, femoral comb; itf, intermediate tooth of femur; pbt, point of blade of tibia; ptf, posterior tooth of femur; ta, tarsus; ti, tibia.

Depositories

The abbreviations given below have been used in the lists of material and throughout the text:

BMNH British Museum (Natural History), London

BPBM Bernice P. Bishop Museum, Honolulu

CSIRO Commonwealth Scientific and Industrial Research Organization, Canberra, Aus-

tralia
DSIR Department of Scientific and Industrial Research, Auckland

MCZ Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.

ZMA Instituut voor Taxonomische Zoölogie (Zoölogisch Museum), Amsterdam