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Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: a geotectonic explanation

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Abstract

The present-day distribution patterns of the cicadas of Wallacea, New Guinea, and the West Pacific reflect the extremely complex geotectonic history of that area. The patterns found in two unrelated monophyletic groups of cicadas (Insecta, Homoptera, Cicadoidea), the subtribe *Cosmopsaltriaria* and the tribe *Chlorocystini* with its sister tribe *Prasiini*, are analysed and related to data from the geological literature. The two groups have a comparable distributional range over Sulawesi, Maluku, New Guinea, the Bismarck Archipelago, and the East-Melanesian archipelagos, to Tonga and Samoa. The occurrence of endemic species, species groups, and genera in congruently delimited parts of this range made us recognize 14 areas of endemism. The areas of endemism coincide with geological entities, which have been isolated during a considerable period of time. Most of the areas originated from oceanic island arcs, which developed as a result of subduction along the southern and western edges of the Pacific tectonic plate, others are rifted microcontinents. Concentrations of species and especially endemic species of the various cicada genera in different areas of endemism suggest that each of these genera evolved in isolation on one of the afore mentioned geological entities. These entities can therefore be regarded as source areas for the genera. The island arc fragmented as a result of collisions first with the Asian- and later with the Australian tectonic plate and several of its parts reamalgamated at the northern craton of the Australian plate, where they now form the greater part of the island of New Guinea. After reamalgamation of the arc fragments the cicadas of the respective genera that had evolved on these fragments could disperse into adjoining areas, but since cicadas are poor dispersers the source areas of the genera can still be recognized in present-day distribution patterns. The generic relationships in the two groups of cicadas under study indicate area relationships that comply with the latest palaeogeographic reconstructions. The main vicariant speciation events in the cicada cladograms correspond with the presumed sequences of fragmentation of the island arc. Cicada phylogeny and distribution combined reflect the historic area relationships rather than the present ones.

1. Introduction

In 1860 Wallace argued that a line running between Bali and Lombok, between Borneo and Sulawesi, and bending eastward south of the Philippines can be drawn to separate the Indian

or Asian zoological region from the Australian region. Some years later Huxley (1868) introduced the name “Wallace’s Line” for this line of demarcation, and suggested on the basis of his own studies of birds that the Philippines should be included in the Australian rather than the Asian region. Just

half a century after his first publication, Wallace (1910) shifted the presumed borderline between the Asian and Australian biotas to east of Sulawesi and the Philippines. Since then, several new borderlines have been proposed on the basis of studies of the distributions of various groups of animals and plants. Wallace's changing views on the position of this demarcation line were recently discussed by George (1981), while a review of the alternative borderlines was given by Simpson (1977) in a paper he despairingly entitled "too many lines".

In the meantime Dickerson (1928) had proposed the name Wallacea for the geologically unstable area between Asia and Australia. Wallacea included the Lesser Sunda islands from Lombok to Timor in the south, Sulawesi with the Sula islands in the centre, and the Philippines in the north. Wallacea as defined above "was based largely on the available hydrographic and geologic data", but was also interpreted as a transition zone wherein the Asian and Australian groups of animals and plants intermingle (Dickerson, 1928).

As a biogeographer Wallace is often regarded a dispersalist in the Darwinian tradition, though his appraisal of the role of geology in biogeography is also acknowledged (e.g., Nelson and Platnick, 1981; Humphries and Parenti, 1986). Michaux (1991) recently argued that "Wallace did not try to explain distributions patterns by invoking the occurrence of unique events but rather by recourse to general principles". There are indeed many passages, especially in Wallace's "The Malay Archipelago" (1872) and some of his earlier writings (1860, 1863), where Wallace attributed a major role to geological and geophysical changes in the evolution of distribution patterns. Wallace regarded Sulawesi as the most unusual of five biogeographic regions in the Malay Archipelago, unusual because it has a unique but rather impoverished biota, notwithstanding that it lies in the very heart of that archipelago (Michaux, 1991). Wallace (1872: p. 283) supposed that Celebes (Sulawesi) was one of the oldest parts of the archipelago: "It probably dates from a period not only anterior to that when Borneo, Java and Sumatra were separated from the continent, but from that still more remote epoch when the land

that now constitutes these islands had not risen above the sea".

In a recent biogeographic analysis of the entire butterfly fauna of Sulawesi in relation to the fauna of the surrounding islands, Vane-Wright (1991) came to the not unexpected conclusion that there is no sharp division within Wallacea between the Asian and Australian biotas. The lack of success in finding an unambiguous borderline between the Asian and Australian biotas can be explained in our view by the very complex geotectonic history of Wallacea and the adjacent Papuan region. Wallace's Line should be reinterpreted in terms of Asian and Australian derived terranes and microcontinents with their own original biotas, as was recently suggested by Michaux (1994), rather than in terms of differences in dispersal abilities among different groups. Most islands and archipelagos in Wallacea and the Papuan region are of composite geological nature, and comprise parts of microcontinents and island arcs. Many of these geological entities have rifted, collided and slipped past each other, so that the geography of the area has continuously and greatly changed in the course of time. The distribution patterns of animals and plants in Wallacea and the Papuan region must to a great extent have been determined by these complex geotectonic movements. Active dispersal of Asian and Australian animals and plants that occurred when the area had more or less reached its present configuration of islands and archipelagos apparently played a minor role in the distribution patterns.

The complexity of geotectonic movements makes Wallacea, New Guinea, and the west Pacific a challenging area for areacladistic studies, since many of the changes that occurred in the relative positions of the various islands and island parts must have led to vicariant speciations. The taxon-areacladogram of a monophyletic group of a sufficient age, that shows a high rate of endemism in the areas concerned, should reflect that geotectonic history. This paper presents the taxon-areacladograms of two such groups, both in cicadas. We will compare the general biogeographic patterns revealed from these taxon-areacladograms with the palaeogeography of the area.

2. The object of the study, the cicadas

Cicadas form a group of homopterous insects that belongs to the superfamily Cicadoidea. Cicadas are subdivided into two larger and four smaller families (Duffels and Van der Laan, 1985; Duffels, 1993), but the validity of this classification is under discussion. Each of the two largest families, the Cicadidae and the Tibicinidae, is represented in Wallacea and the west Pacific by a large monophyletic species group. The subtribe *Cosmopsaltriaria* of the tribe Dundubiini of the Cicadidae (at present 125 recognized species) is distributed in Sulawesi, Maluku, New Guinea, the Bismarck Archipelago, and some East-Melanesian and Polynesian archipelagos, viz., the Solomon Islands, Vanuatu, Fiji, Tonga, and Samoa (Fig. 1). The *Cosmopsaltriaria* contain the following genera: *Aceropyga* Duffels, *Brachylobopyga* Duffels, *Cosmopsaltria* Stål, *Diceropyga* Stål,

Dilobopyga Duffels, *Moana* Myers, *Rhadinopyga* Duffels and an undescribed genus here indicated as “new genus I”. The other group of study consists of the sister tribes Prasiini and Chlorocystini (sensu stricto) of the Tibicinidae (about 176 recognized species). It has a distribution similar to the *Cosmopsaltriaria*, but is absent from Fiji, whilst small numbers of its species occur farther westward to Java, Sumatra and the Lesser Sunda islands, northward to Borneo and the Philippines, and southward into eastern Australia (Fig. 2). The tribe Prasiini contains the genera *Arfaka* Distant, *Jacatra* Distant, *Lembeja* Distant, and *Prasia* Stål. The tribe Chlorocystini sensu stricto contains: *Adeastria* De Boer, *Baeturia* Stål, *Chlorocysta* Westwood, *Cystopsaltria* Goding and Froggatt, *Cystosoma* Westwood, *Guineapsaltria* De Boer, *Glaucopsaltria* Goding and Froggatt, *Gymnotympana* Stål, *Papuapsaltria* De Boer, *Mirabilopsaltria* De Boer, *Owra* Ashton,

Fig. 1. Distribution of the cicada subtribe *Cosmopsaltriaria* and its presumed sister group the genus *Meimuna*.

Fig. 2. Distribution of the cicadas of the sister tribes Chlorocystini and Prasiini and their presumed sister group the genus *Muda*.

Scottotympana De Boer, *Thaumastopsaltria* Stål, and *Venustria* Goding and Froggatt.

The following remarks can be made concerning the distribution of these two groups. The great majority of the species (and subspecies) is found on the two largest islands; Sulawesi has 22%, and New Guinea 52%, of all species. Both groups show a high rate of endemism. Practically all cicadas that occur on Sulawesi are restricted to this island (the distribution area of a small number of species includes some of the small nearby islands), and all but one of these Sulawesi endemics are restricted to only a part of that island. A similar situation is found in New Guinea where none of the cicadas are widely distributed all over the island. Of the New Guinea cicadas 59% are endemic to restricted

parts of the island, others are more widespread within New Guinea sometimes including adjacent islands. The number of cicada species considerably decreases to the east of New Guinea: the Bismarck Archipelago has 19 species of which 10 are endemics, the Solomon Islands have 26 species of which 23 are endemics, Vanuatu has 3 species with 2 endemics, the 15 species of Fiji are all endemic to that island group, the Tonga and Samoa islands have one species in common, while each of these latter island groups also has one endemic species.

The high rate of endemism found in cicadas of Wallacea, New Guinea, and the West Pacific must presumably be explained mainly by the complex geotectonic history of the area, but the poor dispersal abilities of cicadas is another factor favour-

ing endemism in this group. This can probably be explained by the peculiar life-cycle of these insects. As soon as the eggs are hatched, the young larvae fall to the ground and dig themselves in within a few minutes (Dubois, 1966). The insect then passes through five larval stages, which are all subterranean (Boulard, 1965; Chandler, 1972, 1973; Dubois, 1966; Ito and Nagamine, 1974a,b; Kuniata and Nagaraja, 1992; Monsarrat, 1966; Nagamine and Teruya, 1976). The larvae feed by sucking on plant roots. They presumably stay within the root system of a single plant (Dubois, 1966) and hardly move about horizontally. The final, 5th, instar larvae emerge from the soil and metamorphosis takes place. The cicada life cycle usually takes 2–8 years, although a few species are annual (Chandler, 1972, 1973; Moulds, 1990; Nagamine and Teruya, 1976), whilst the species of the genus *Magicicada* Davis on the other hand live for 13 or 17 years (Simon, 1988). The winged adults live 2–4 weeks at the most, but sometimes for only 3 or 4 days (Kuniata and Nagaraja, 1992; Monsarrat, 1966; Moulds, 1990). The short adult life might provide an explanation for the apparent poor dispersal abilities of cicadas.

3. Areas of endemism

The high rate of endemism of cicadas in Wallacea, New Guinea, and the West Pacific led to the recognition of several potential areas of endemism (Duffels, 1986). The tentatively recognized areas of endemism were related to geological entities as recognized in the palaeogeographic reconstructions of the Pacific available at that time, specifying the relevance of barriers, island arcs and land connections. Some years later the potential areas of endemism could be properly defined as based on the congruent distributional limits of two or more species or higher taxonomic categories, when data from the cicada work in progress (e.g., Duffels, 1988a; De Boer, 1989) and from biogeographic studies on moths (Holloway, 1984, 1987; Holloway and Jardine, 1968), butterflies (Vane-Wright, 1990), and marine waterstriders (Andersen, 1989a,b) were combined (Duffels and De Boer, 1990). In 1990 we recognized the

following 7 areas of endemism: Sulawesi, the Moluccas, three parts of New Guinea (the Birds Head, central New Guinea, and northern New Guinea), the Bismarck and Admiralty Islands, and the Solomon Islands. Four island groups in the South-West Pacific, viz., Vanuatu, Fiji, Tonga and Samoa, had been recognized before as being areas of endemism (De Boer, 1989; Duffels, 1988a). In addition to his taxonomic and phylogenetic studies on the plant genus *Guioa* Cav., Van Welzen (1990) analysed the historical biogeographic patterns of Malesia by combining data on *Guioa*, cicadas, and some other groups of animals and plants. Van Welzen arrived at the conclusion that: “although some of the historical distribution patterns contradict each other, all more or less indicate the same areas as areas of endemism”. In his analysis Van Welzen (1990) principally used the areas of endemism as recognized by Duffels (1986)—though some were subdivided—and assigned an “area of endemism” status to the remaining parts of New Guinea: the Papuan Peninsula and southern New Guinea (Van Welzen, 1990: fig. 49).

The analysis of the historical biogeographic patterns found in cicadas presented here forced us to expand the number of areas of endemism to 14 (Fig. 3). These areas can be recognized on the basis of the distributions of all species, species groups, and genera, attributed to the Cosmopsaltriaria, the Chlorocystini, and the Prasiini (see literature in Duffels, 1986 and Duffels and De Boer, 1990, and the following later publications: De Boer, 1990, 1991, 1992a,b, 1993a,b, 1994a–d, 1995a,b; Duffels, 1990a, b, 1993; Duffels and Van Mastrigt, 1991). Several of these areas of endemism enclose areas of endemism of a lower rank, which are characterized by the congruent distributions of monophyletic subgroups or single species.

Sulawesi (including some of the nearby islands such as Buton, Muna, and Salayer) is an area of endemism, characterized by several endemic genera. The distribution of monophyletic species groups on Sulawesi indicates that the various arms of that island might be separate areas of endemism of a lower rank (Duffels, 1990a).

Only some fairly widely distributed species occur all over Maluku and the islands of the Banda arcs.

Fig. 3. Areas of endemism in Wallacea, New Guinea and the West Pacific.

This area as a whole should therefore not be regarded as an area of endemism. North Maluku is an area of endemism for several species groups, while South Maluku is also regarded as an area of endemism since several endemic species occur here. Two species groups show sister area relationships between North and South Maluku indicating that Maluku as a whole also can be considered as an area of endemism.

The island of New Guinea as a whole is not an area of endemism for cicadas; no cicada species or monophyletic species group restricted to New Guinea occurs in all parts of that island. The Birds Head, central New Guinea, northern New Guinea including the Huon peninsula, and the Papuan peninsula are all distinct areas of endemism, with endemic genera, species groups and species. The Huon peninsula may form an area of endemism of a lower rank; it has several endemic species, but no endemic species groups or genera. A few species are apparently endemic to parts of south New Guinea, but because that area is presumably undercollected, south New Guinea as a whole is regarded here as a single area of endemism.

The Bismarck Archipelago has relatively few endemic species, but some of these form small

monophyletic species groups. New Britain and New Ireland, possibly together with the Admiralty islands, are therefore regarded as an area of endemism.

The East-Melanesian archipelagos together (e.g., the Solomon Islands, Vanuatu, Fiji, Tonga, and Samoa) combined with the Bismarck Archipelago, form a definite area of endemism of higher rank characterized by the occurrence of two endemic sister genera. Each of the above mentioned East-Melanesian island groups forms an area of endemism on its own and many of the individual islands of the Solomon and Fiji groups have their own endemic species.

If the cicada fauna of Wallacea and the Papuan region evolved exclusively as a result of vicariance, the phylogeny of the endemic taxa should reveal the historic relationships between the areas of endemism. However, it must be assumed that the reamalgamation of terranes in Sulawesi and New Guinea will also have had its effects on the distribution patterns of the cicadas on these islands. Active dispersal between reamalgamated terranes has probably obscured many of the patterns of endemism determined by vicariance. Nevertheless it seems that the vicariant patterns can still be recog-

nized. The phylogenetic relationships of the cicadas often indicate area relationships that differ from what one would expect from the present-day relative geographic positions of these areas. In many instances, areas appear to be more closely related to geographically farther removed areas than to the immediately adjacent ones. The distribution of the genus *Gymnotympana* (De Boer, 1995a), for example, suggests a relationship of northern Maluku to eastern New Guinea, rather than to western New Guinea or the Birds Head. The monophyletic *Baeturia bloetei* group (Fig. 4), which is distributed in Maluku, northern New Guinea, the Bismarck Archipelago, and East Melanesia (De Boer, 1989), shows that a species in northern New Guinea may be more closely related to a species from Samoa than to a *Baeturia* species from, for example, central or southern New Guinea. This indicates a closer geological relationship between northern New Guinea and the East Melanesian archipelagos than between northern New Guinea and central or southern New Guinea.

These peculiar area relationships can be largely explained by the present knowledge of the geotectonic history of the area, a resume of which is given in the following section.

4. Geology

4.1. Geological history

The geotectonic evolution of New Guinea and adjacent areas is extremely complex. The island itself is an assemblage of numerous island arc fragments and microcontinents which at various geological times collided with the northern craton of the Australian tectonic plate. It is no wonder therefore, that geologists have not reached consensus on a detailed palaeogeographical reconstruction of the tectonic movements in and around New Guinea. However, consensus grows where the main trends of these movements are concerned. The following pages present a short and simplified review of the geotectonic evolution of the distribution area of the cicada taxa under study; a more detailed discussion on the palaeogeography of this area will be given elsewhere (De Boer, 1995d).

To understand the geological history of Sulawesi, New Guinea, and the adjacent archipelagos of Maluku and East Melanesia, it is necessary to go back in time to the mid-Mesozoic break-up of Gondwana. After the separation of India and Australia–Antarctica from Africa (about 180 m.y. ago), the Indian subcontinent moved northward towards Asia, while Australia–Antarctica kept an eastern course (Dietz and Holden, 1970; Nishimura and Suparka, 1990; Daly et al., 1991). The collision between India and Asia (50 m.y. ago) caused a clockwise rotation of southeast Asia, which in turn might be responsible for the almost simultaneous change in the direction of movement of the Pacific tectonic plate, from initially northward to westward (Hamilton, 1979; 1986; Daly et al., 1991). This change of direction can be read from the angle between the Emperor Seamount Chain and the Hawaii Chain, which chains developed from one and the same “hotspot”. As part of the general plate readjustments, which include the above mentioned changes, the Philippine Sea plate separated from the Pacific plate at about 42 m.y. ago (Nishimura and Suparka, 1990).

Australia, which by now had become separated from Antarctica by the opening of the Tasman Sea (95 m.y. ago), had changed its course northward (Daly et al., 1991; Honza, 1991). As a result of these changes in relative plate motions the Australian plate was now obliquely advancing on the Pacific plate. The floor of the Tethys Sea, which initially separated the Australian and Pacific plates was forced to subduct under that of the Pacific, and the volcanic activity accompanying this subduction gave rise to a volcanic island arc on the southern and western edges of the Pacific plate. This arc is henceforth referred to as the West Pacific island arc. The West Pacific island arc is not identical to the Outer Melanesian arc (see the end of this paragraph). Remnants of this West Pacific island arc have been recognized and are as follows: the central Philippines, northern, central and southeastern New Guinea and the Bismarck Archipelago. Daly et al. (1991) indicate that parts of northern and eastern Sulawesi also originate from this arc, from a position between the central Philippines and central New Guinea, but this is not widely accepted among geologists. Hall (1996)

Fig. 4. Distribution of the species of the *Baeturia bloetei* group: *macgillavryi* (1), *bloetei* (2), *papuensis* (3), *bismarckensis* (4), *manusensis* (5), *mussauensis* (6), *brandti* (7), *sedlaceorum* (8), *reinhoudti* (9), *cristovalensis* (10), *gressitti* (11), *bilebanarai* (12), *mendanai* (13), *marginata* (14), *boulardi* (15), *eduberti* (16), *rotumae* (17), *maddisoni* (18).

proposes a southern hemisphere origin for eastern Sulawesi, possibly related to the Birds Head microcontinent, while in his view northern Sulawesi was formed more or less in place. The Solomon Islands, Vanuatu, Fiji, and Tonga, which in the present-day configuration seem to be a continuation of this island arc, are supposed to be of a different origin; these archipelagos developed at the edge of the Australian rather than the Pacific plate (Gill and Gorton, 1973; Packham, 1973; Ewart, 1988) in an island arc which is henceforth referred to as the South-West Pacific island arc. Only a part of the northern Solomon arc might be an extension of the West Pacific island arc.

Since the Pacific plate continued to move westward, the island arc on its edges advanced on, and finally collided with, the Asian continent. This collision must have occurred about 40–42 m.y. ago, somewhere along the eastern margin of the Asian plate, and caused the West Pacific island arc to fracture. The northwestern part of the arc started rotating clockwise, which made the central Philippines collide with the continental western Philippines, while fragments of northern and eastern Sulawesi swept past the northwestern corner of the still advancing Australian continent towards Borneo (Rangin et al., 1990a,b; Daly et al., 1991; Honza, 1991).

The more eastern parts of the West Pacific island arc continued moving westward until Australia reached the subduction zone of the Tethys Sea and a part of the West Pacific arc, known as the Sepik Arc, collided with the northern craton of that continent, in the first of a series of collisions between arc fragments and the Australian continental margin (Pigram and Davies, 1987). However, several slivers of Australian continental crust, or microcontinents, had preceded Australia in reaching the subduction zone and were incorporated in the island arc fragments before these fragments in turn collided with Australia. The arc fragments which eventually amalgamated with the Australian continent were thus already of a composite nature. Other such microcontinents, which either lay just north of Australia, or became detached as a result of the approaching Sepik Arc collision, were pushed westward by the advancing Sepik Arc terrane and are now situated in Maluku.

The islands of Buton, Sula, Banggai, Obi and Bacan, and the submerged Banda ridges are all of such microcontinental origin (Hamilton, 1979, 1986; Silver and Smith, 1983; Silver et al., 1985; Pigram et al., 1985; Lee and McCabe, 1986; Katili, 1989; Hartono, 1990; Daly et al., 1991; Smith and Silver, 1991). Concerning Maluku, only Halmahera-Morotai is, at least partly, of island arc origin; the Halmahera arc evolved far to the east of its present position along a fracture in the Pacific plate to which possibly also eastern Mindanao, Waigeo island, and the Mariana, Yap, and Palau arcs are connected (Hall and Nichols, 1990; Honza, 1991).

The greater part of the Birds Head peninsula of New Guinea is also continental, but its origin is not unambiguous. According to Pigram and Panggabean (1984) the Birds Head consists of two microcontinents, Kemum (which forms the nucleus of its northern half) and Misool (consisting of Misool island and the Onin and Kumaua peninsulas), of which the first one became detached from near central Papua New Guinea and the second one probably from an area east of Queensland. These microcontinents collided and moved as a single block westward, just north of the continent, by the same process that moved other microcontinents into the Moluccan area, and they collided again with the continent (about 10 m.y. ago) at their present position. Hall (1996), however, supposes the Birds Head to have rifted from western Australia, close to its present position.

The collision between the Sepik Arc and the Australian continent had three major effects. It caused: (1) an inversion of the subduction zone from initially northward (the Tethys Sea plate under the Pacific plate) to southward (the Pacific plate under the Australian Plate), (2) orogenesis in central New Guinea (the Sepik Arc terrane, together with parts of the Australian plate margin, developed in what are now the central mountain ranges of New Guinea), and (3) the development of a foreland basin (the weight of the accreted terrane pressed down the northern parts of the Australian continent, e.g., southern New Guinea and northern Queensland, so that these became submerged) (Pigram and Davies, 1987; Pigram et al., 1989; Daly et al., 1991).

To the east of the Sepik Arc terrane several terranes, initially forming an archipelago, had amalgamated to a single block, the East Papua Composite terrane, which collided (about 15 m.y. ago) with a part of the Australian continent just to the east of the amalgamated Sepik Arc terrane (Pigram and Davies, 1987). This block, that now forms the Papuan peninsula and initially included the terranes of the D'Entrecasteaux islands, the Louisiade Archipelago, and of Woodlark island, remained for a long time (possibly until the amalgamation of the Finisterre terrane see below) separated from other parts of New Guinea by a deep sea trough, the Aure Trough (Dow, 1977; Pigram and Davies, 1987). The opening of the Woodlark Basin, which separated Woodlark island and the D'Entrecasteaux islands from the Papuan peninsula, prevented other arc fragments to amalgamate in this area. More eastern parts of the West Pacific island arc, which were still moving westward on the Pacific plate, were led past the Papuan peninsula towards the Australian continent and accreted to the north of the Sepik Arc terrane. The terranes that now form the northern mountain ranges of New Guinea (e.g., the Gauttier, Torricelli, Mt. Turu, and Prince Alexander terranes) accreted about 10 m.y. ago to New Guinea and soon after this event the accretion of the Finisterre terrane (the Huon peninsula), with in its rear the Bismarck Archipelago, started (Pigram and Davies, 1987). The accretion of the Finisterre terrane was not completed until about 2 m.y. ago, when some smaller arc fragments like the Cyclops mountains and the Arfak mountains had also collided with northern New Guinea and the Birds Head, respectively (Pigram and Davies, 1987).

The East Melanesian archipelagos, which initially formed a continuous South-West Pacific island arc with Vanuatu linking the Solomons to Fiji (Packham, 1973; Ewart, 1988), had moved northward along with the Australian continent and collided (9–12 m.y. ago) in the Solomon area with the Ontong Java plateau, which was earlier interpreted as a submerged continental fragment in the Pacific plate (Packham, 1973; Honza, 1991), but is now understood to consist of large buildups of basaltic volcanoes (Pigram, pers. comm.). As a result of this, and the simultaneous collisions in

the New Guinea area, the South-West Pacific island arc broke up. Vanuatu rotated clockwise, Fiji rotated anticlockwise, and the Tonga-Kermadec ridge rifted from the Lau-Colville ridge (Gill and Gorton, 1973; Green and Cullen, 1973; Packham, 1973; Silver and Smith, 1983; Ewart, 1988; Honza, 1991). By 3 m.y. ago this rifting and rotating had caused a complete isolation of Fiji.

The palaeogeographic reconstruction presented here differs in some fundamental respects from earlier reconstructions that have been used to interpret the historic biogeography of the Pacific. In earlier biogeographic publications we assumed the existence of two separate arcs, the continental Inner Melanesian Arc and the oceanic Outer Melanesian Arc (e.g. Duffels, 1983, 1986). The inner arc was supposed to consist of central New Guinea, New Caledonia, and New Zealand, although its continuity was doubted. The outer arc included northern New Guinea, the Bismarck Archipelago, Solomon Islands, Vanuatu, Fiji, and Tonga. Sulawesi did not form a part of these Melanesian arcs. In the new palaeogeographic reconstruction presented above, the central Philippines, Sulawesi, and central New Guinea are supposed to originate from the same arc as northern New Guinea, the Huon peninsula, the Papuan peninsula and the Bismarck Archipelago. To avoid confusion this arc is referred to as the West Pacific island arc. Eastern Melanesia is supposed here to have formed a different arc, which consisted of the Solomon Islands, Vanuatu, Fiji, and Tonga. This arc we named the South-West Pacific arc.

The use of the term "arc" is not unambiguous here, since it consists of true oceanic arc elements and microcontinental fragments of Australian origin.

Michaux (1994) introduced the names inner and outer Melanesian rifts, emphasizing the rifted microcontinental elements of Australian origin that became incorporated within these arcs. The Australian elements in the inner and outer Melanesian arcs can be used to explain distribution patterns of Papuan groups that originate from Australia.

4.2. *Geological cladogram*

The fragmentation of the West Pacific island arc can be summarized in the cladogram-like graph of

Fig. 8. This geological cladogram is rooted in southeast Asia, which represents the 40–42 m.y. ago collision of the West Pacific arc with the Asian continent. The various areas branch off in the order in which they are supposed to have lain in that arc; for the New Guinean parts this is the same order in which these parts collided with the Australian continent. The terranes of the Birds Head and the East Melanesian island groups are not included in the cladogram, since they are of different geological origin than the West Pacific island arc terranes; in biological terms: they do not form a monophyletic group.

5. Area cladistic analysis

5.1. Island arc patterns in cicadas

The geotectonic history discussed above shows that many of the areas of endemism which could be recognized from the distributions of cicadas and other groups (Fig. 3) coincide with areas which went through a period of geographic isolation, either as microcontinents or as island arc fragments. The fact that most of the areas of endemism recognized by the analysis of the distribution patterns of the *Cosmopsaltria* and the *Chlorocystini*+*Prasiini* coincide with island arc fragments suggests that the Pacific island arcs functioned as a route of dispersal for these groups and that the fragmentation of the West- and South-West Pacific island arcs determined the main vicariant speciation events in both cicada groups. By far the greater portion of cicadas still occur in areas directly derived from these arcs. The fact that the New Guinean genera are generally concentrated in different parts of the island (compare for example *Aedeastria* (Fig. 5) concentrated in western New Guinea with *Cosmopsaltria* (Fig. 6) centred in central New Guinea, and *Gymnotympana* (Fig. 7) with most species in eastern New Guinea) suggests that these genera arrived traveling on different geological fragments on New Guinea.

The sister groups of both our groups of cicadas are distributed in east and southeast Asia. The genus *Meimuna* Distant is regarded as the sister

group of the *Cosmopsaltria* (Fig. 1), whilst the genus *Muda* Distant is the supposed sister group of the sister tribes *Chlorocystini* and *Prasiini* (Fig. 2). This means that the ancestors of both the *Cosmopsaltria* and the *Chlorocystini*+*Prasiini* presumably invaded the West Pacific island arc from the Asian continent, after this arc had collided with southeast Asia. The West Pacific island arc presumably never formed a continuous land-mass, but has always been a string of islands and archipelagos, with continuously changing interconnections. The first speciation events might well have occurred as a response to these changing interconnections and well before the arc finally fragmented, but the present-day generic differentiation most probably does result from this final fragmentation. The collisions of several of the arc fragments at various times and places with northern Australia may provide an explanation why the various New Guinean genera are concentrated in different parts of the island. Of course, when such a fragment collided and was added to New Guinea, the cicada fauna on that particular fragment could more or less freely disperse into other parts of the island, while those species already present on New Guinea could disperse into the newly accreted terranes. Several species have done so, since none of the genera are strictly endemic to any one fragment, but most species obviously have not dispersed, which accounts for the present-day concentrations of endemics.

If the above reasoning is correct and the fragmentation of the island arcs is responsible for the generic diversification, the phylogeny of the two groups of cicadas should reflect the order in which the arcs fragmented. This can be tested by area cladistic analysis, provided we rule out the recent dispersal events and reduce the area of distribution of a genus to its original source area as microcontinent or island arc fragment.

5.2. Island arc fragments as source areas

We postulate that fragmentation of island arcs caused vicariant speciation events, which are responsible for the present-day generic differentiation in the cicadas under study. This means that the various cicada genera evolved on different

Fig. 5. Distribution of the species of the cicada genus *Aedeastria*: *cobrops* (1), *sepia* (2), *digitata* (3), *kaiensis* (4), *latifrons* (5), *waigeuensis* (6), *cheesmanae* (7), *hastulata* (8), *moluccensis* (9), *obiensis* (10), *bullata* (11), *dilobata* (12).

geological entities as island arc fragments and, possibly, microcontinents. These geological entities can then be seen as the source areas for the genera. Due to the poor dispersal abilities of cicadas these source areas can still be traced from the present-day distribution patterns of the genera.

The following fragments and microcontinents must be taken into account as the main possible source areas: (1) the arc fragments in Sulawesi, (2) Maluku, (3) the microcontinents in the Birds Head peninsula, (4) central New Guinea (the Sepik Arc terranes), (5) the Papuan peninsula (the East Papua Composite terrane), (6) northern New Guinea, (7) the Huon peninsula (the Finisterre range), (8) the Bismarck Archipelago, and (9) the east Melanesian archipelagos (the South-West Pacific island arc).

Several characteristics in the distribution patterns of the genera give an indication as to what is the most probable source area of a particular genus. A concentration of strictly endemic species in any of the above listed areas indicates that area

as source area; *Gymnotympna* (Fig. 7) for example definitely has most endemic species in the Papuan peninsula. When no concentration of endemics exists, a concentration of co-occurring species might indicate the source area; *Cosmopsaltria* (Fig. 6) shows such a concentration of co-occurring species in the central mountain ranges of New Guinea. Species that occur outside the area where their genus is concentrated very often have a comparatively wide distribution which generally includes that concentration area and some adjacent areas. Such species obviously are better dispersers than the strictly endemic ones, and are supposed to have recently dispersed from the source area into adjacent areas. This is best illustrated by the genus *Gymnotympna* (Fig. 7); the species of *Gymnotympna* that occur in northern New Guinea or New Britain all have a relatively wide distribution and two of them occur in the Papuan peninsula as well. In this way a comparison of distribution patterns of genera can be helpful to trace the source areas; genera that

Fig. 6. Distribution of the species of the cicada genus *Cosmopsaltria*: *doryca* (1), *lata* (2), *halmaherae* (3), *gracilis* (4), *huonensis* (5), *gestroei* (6), *gigantea* (7), *mimika* (8), *aurata* (9), *signata* (10), *meeki* (11), *satyrus* (12), *personata* (13), *bloetei* (14), *emarginata* (15), *capitata* (16), *loriae* (17), *delfae* (18), *papuensis* (19), *retrorsa* (20), *toxopeusi* (21), *waine* (22), *kaiensis* (23).

evolved on the same arc fragment must have had the same opportunities to disperse into adjacent areas, and will show similar patterns in their more widely distributed species. In some instances genera show concentrations of species or monophyletic subgroups in more than one area; *Gymnotympana* (Fig. 7) has a monophyletic subgroup of three species in northern Maluku, while other endemics concentrate on the Papuan peninsula. In this case both areas together are regarded as the source area.

5.3. The genera and their source areas

In this section the most probable source areas of the Prasiini and the various genera of the *Cosmopsaltria* and the *Chlorocystini* will be discussed. For full particulars about the distributions of the species is referred to earlier revisionary work (see Section 3 for references).

The most probable source areas of *Gymnotympana* and *Cosmopsaltria* were already

indicated above. The source area of *Gymnotympana* has been discussed before in relation with that of the genera *Diceropyga* and *Thaumastopsaltria* (see De Boer, 1995a). *Gymnotympana* (Fig. 7) is distinctly concentrated in eastern New Guinea (De Boer, 1995a), and is especially numerous in the Papuan peninsula: of the 20 species of this genus, 15 are found in Papua New Guinea, 12 of these occur in the Papuan peninsula and 6 are endemic there. The strictly endemic species that occur outside the Papuan peninsula are found in central New Guinea (2 species), Australia (2 species), and North Maluku (a monophyletic group of 3 species). The distribution pattern of *Gymnotympana* shows several similarities with those of *Thaumastopsaltria* (De Boer, 1992a) and *Diceropyga* (Duffels, 1977, 1988b). As far as the New Guinean species are concerned, these genera also show a distinct concentration in the eastern parts of the island. All three genera have widespread species in northern New Guinea, and occur in Queensland (*Thaumastopsaltria* and

Fig. 7. Distribution of the species of the cicada genus *Gymnotympana*: *varicolor* (1), *rufa* (2), *hirsuta* (3), *olivacea* (4), *verlaani* (5), *montana* (6), *viridis* (7), *dahli* (8), *streptans* (9), *rubricata* (10), *langeraki* (11), *nigravirgula* (12), *parvula* (13), *stenocephalis* (14), *membrana* (15), *minoramembrana* (16), *phyloglycera* (17), *stridens* (18), *subnotata* (19), *obiensis* (20).

Diceropyga are both represented there by one single widespread species that also occurs on New Guinea). *Diceropyga*, like *Gymnotympana*, has a species group in northern Maluku. Although there are also remarkable differences in distribution between these three genera—*Diceropyga*, for example, has several endemic species on the Solomon Islands and an endemic species group on the Bismarck Archipelago—the similarities in these genera indicate a similar source area. For *Gymnotympana* this source area presumably consists of the East Papua Composite terrane and part of northern Maluku, presumably the Halmahera arc. The two *Gymnotympana* species endemic to the eastern parts of the central mountain ranges are probably the result of a recent westward dispersal following the closure of the Aure Trough and similarities in distribution of the Australian species with the Australian species of *Thaumastopsaltria* and *Diceropyga* suggests that they result from a dispersal during one of the Pleistocene or Pliocene glacial periods. The East

Papua Composite terrane is presumably the source area of *Thaumastopsaltria*, but *Diceropyga* must have had a larger source area, which included the East Papua Composite terrane, the Bismarck Archipelago, the Halmahera arc, and at least part of the Solomon Islands.

Cosmopsaltria (Fig. 6) is distinctly concentrated in the central mountain ranges of New Guinea; 12 of the 23 species occur there. These are found mainly above an altitude of 1000 m, while *C. signata* is recorded from altitudes between 1800 and 3400 m only (Duffels, 1983, 1986, 1988c,d; Duffels and Van Mastrigt, 1991). Many of the central mountain range species have a fairly wide distribution from the Wissel lakes to well into the Papuan peninsula, though some are recorded from very restricted areas in the central mountains only. The number of co-occurring species in the Papuan peninsula decreases eastward. There is no distinct concentration of strictly endemic species in any of the other source areas mentioned above. Considering these facts, the Sepik Arc fragment of

the West Pacific island arc is presumably the source area of *Cosmopsaltria*.

The source area of *Aedeastria* is even more tricky to trace. This genus has definitely most species in western New Guinea and shows endemism on the islands adjacent to the Birds Head peninsula (De Boer, 1990, 1993b). *Aedeastria* and the genus *Rhadinopyga* (Duffels, 1985), which is endemic to the Birds Head and some adjacent islands, are the only genera with endemic species on the Birds Head and the islands of Waigeo and Misool (Fig. 5); the endemic occurrence of *Thaumastopsaltria adipata* on Misool is regarded as questionable (De Boer, 1995a). One or both of the microcontinents that now form the Birds Head presumably form the source area of *Rhadinopyga*. Although *Aedeastria* has only one endemic species on the Birds Head itself, the similarities in distribution with *Rhadinopyga* suggest that that genus is of similar microcontinental origin.

By similar reasoning as given above for the genera *Gymnotympana*, *Cosmopsaltria*, and *Aedeastria*, it is possible to allot a most probable source area to all the remaining genera of the Chlorocystini and Cosmopsaltriaria, and to the Prasiini as a whole. These taxa and their presumed source areas will only be discussed briefly, as a more elaborate discussion on the distribution patterns of the various genera is published elsewhere (De Boer, 1995d).

Brachylobopyga (Duffels, 1982, 1989) and *Dilobopyga* (Duffels, 1977, 1990a,b) are endemic to Sulawesi and presumably originate from the arc fragments that now form part of that island.

The Prasiini at present contain four genera. *Arfaka* (3 species) is endemic to the Birds Head peninsula of New Guinea (M.R. de Jong, pers. comm.). *Jacatra* (2 species) occurs on Java and Sumatra (M.R. de Jong, pers. comm.). *Lembeja* (approximately 40 species) is widely distributed. It has most species on Sulawesi, but also occurs on Borneo and the Philippines (1 species), New Guinea (about ten species, most of which are undescribed), and Australia (2 species) (De Jong and Duffels, 1981; De Jong, 1982, 1986, 1987), while a monophyletic subgroup from the Lesser Sunda islands, the *L. harderi* group, (3 species) presumably forms a separate genus (M.R. de Jong,

pers. comm.). *Prasia* (7 species) is endemic to Sulawesi (De Jong, 1985). The revision of the Prasiini is not completed and several of the phylogenetic relationships are still obscure. Since most of the species of the Prasiini are endemic to Sulawesi, it seems likely that the Prasiini as a whole originate from the arc fragments that now form part of that island. The occurrences on Borneo, the Philippines, the Lesser Sunda islands, and even possibly on Java and Sumatra might be explained by recent dispersals from Sulawesi, but the occurrences of several groups on New Guinea and Australia, which together do not form a monophyletic group, seem to contradict the here discussed island arc dispersal. A phylogenetic reconstruction of the Prasiini might solve this problem, for now the Prasiini are considered to originate from Sulawesi.

The monophyly of *Mirabilopsaltria* (De Boer, 1995b) and *Papuapsaltria* (De Boer, 1995c) is doubtful (see also De Boer, 1995e) and the distributions of these genera in both cases do not indicate a single source area. *Papuapsaltria* has most endemic species in the western half of the Papuan peninsula, but a monophyletic subgroup of five species is endemic to northwestern New Guinea. The source area of *Papuapsaltria* is probably the East Papua Composite terrane, but part of the genus might have evolved on the northern New Guinea terranes. *Mirabilopsaltria* has two endemic species in northern New Guinea, one in the Huon peninsula, and one in the Papuan peninsula. A fifth species might be endemic to the Bismarck Archipelago, but a female that possibly belongs to that species was collected in northern New Guinea, and a sixth species is widely distributed in northern New Guinea and the Papuan peninsula. The source area of *Mirabilopsaltria* is presumed to be northern New Guinea, although part of the genus might originate from the East Papua Composite terrane.

Six of the eight species of *Guineapsaltria* (De Boer, 1993a) occur in northern New Guinea, but only two are endemic there. The others have a fairly wide distribution along the northern mountain ranges and the Huon peninsula to the western half of the Papuan peninsula. The fact that these species do not reach farther eastward suggests a dispersal from northern New Guinea into the

Papuan peninsula. One species is endemic to the western half of the Papuan peninsula, and one to the eastern half. The latter is the sister species of a widely distributed and therefore presumably easily dispersing species, which even reaches into Queensland, and might have reached the eastern half of the Papuan peninsula by dispersal. The terranes of northern New Guinea presumably form the source area of *Guineapsaltria*.

Baeturia is a large genus with over 60 species, distributed all over Maluku, New Guinea, and East Melanesia (De Boer, 1982, 1986, 1989, 1992b, 1994a–d). The genus can be subdivided into seven species groups, six of which have a total of 13 endemic species in northern New Guinea. The numbers of endemic species and co-occurring subgroups in the other parts New Guinea and elsewhere are remarkably lower. Two groups are found in Maluku, but only one has (three) endemic species there. Two groups occur with a total of four endemic species in the central mountain ranges. Three groups occur in south New Guinea, but only two have a total of three endemic species there. Four groups occur on the Papuan peninsula with a total of only five endemic species. Only one group, the *bloetei* group, has endemic species in the Bismarck Archipelago and reaches eastward to Samoa and Tonga (Fig. 4). The Birds Head has no endemic *Baeturia* species. This all seems to indicate that the terranes of northern New Guinea form the source area of *Baeturia*.

The descriptions of the three *Scottotympana* species are based on a total of eleven specimens from five different localities in the northern parts of New Guinea, a record from New Britain was considered uncertain (De Boer, 1990). Although these data are too few in number to allow any definite conclusions, all data available indicate either the northern New Guinea or Finisterre terranes as the source area of this genus. Moreover, a fourth, undescribed, species also comes from northern New Guinea.

The sister genera *Aceropyga* (Duffels, 1977, 1988a, 1993) and *Moana* (Duffels, 1988a, 1993) are distributed in the archipelagos of East Melanesia. *Aceropyga* is, apart from one widely distributed species in Vanuatu and Kusaie and one species in Tonga, endemic to Fiji. The latter island

group is probably the source area of *Aceropyga*. *Moana* is distributed in the Bismarck Archipelago, Solomon Islands, and Samoa. Most species are found in the western part of this area; the Solomon Islands or possibly the Bismarck Archipelago presumably form the source area of this genus.

A new genus I (Duffels, in prep.) is endemic to the Solomon Islands. It contains 6 new species, which are mainly island endemics: 3 species are endemic to Bougainville, one species is endemic to Santa Isabel, one is endemic to Malaita, and one is found in Guadalcanal and New Georgia.

Six small genera belonging to the Chlorocystini and comprising a total of nine species (*Chlorocysta*, *Cystopsaltria*, *Cystosoma*, *Glauropsaltria*, *Owra*, and *Venustria*) are endemic to parts of eastern Australia (Moulds, 1990). Ancestors of these genera must have invaded Australia from parts of the island arc, since the Chlorocystini as a whole probably originate from southeast Asia. However, since these Australian genera no longer occur in parts of the arc, it is not possible to determine their source areas from their actual distributions.

5.4. Taxon-area cladograms

The distribution of characters in a species group enables us to reconstruct the phylogenetic relationships among the species of that group. Shared characters which are otherwise unique are taken as an indication of relationship. Instead of assuming that a character evolved independently in all species that share the character, it is supposed that the character evolved only once in the common ancestor of those species that have that character. Relationships among species or higher taxonomic groups can be visualized in a dichotomous tree or cladogram. A phylogenetic analysis of the Chlorocystini (De Boer, 1995e) resulted in a cladogram of which a simplified version to genus level is used here. A paper discussing a phylogenetic analysis of the *Cosmopsaltria* is in preparation. The preliminary results of that analysis are used in the present paper.

The phylogenetic relationships between the genera of the two groups of cicadas in combination with the presumed source areas of these genera allow us to investigate the historic relationships between the source areas as far as indicated by the

cicadas. For this purpose the names of the genera in the two available cicada cladograms are substituted by the names of their presumed source areas, following the areacladistic method as outlined by Platnick and Nelson (1978) and Humphries and Parenti (1986). The cladograms of areas thus obtained are taxon-areacladograms (Figs. 9–10), which reflect the biological historic relationships between areas as found in the cicadas. By combining taxon-areacladograms that are based on several unrelated groups a general areacladogram can be obtained. In our view the area cladograms for the two groups of cicadas available provide an insufficient basis for constructing such a general areacladogram. We have preferred here to compare each of the cicada areacladograms with the geological cladogram.

6. Comparison between the geological cladogram and the taxon-areacladograms

If the fragmentation of the West Pacific arc played a major role in the evolution of the cicada

genera in Wallacea, New Guinea, and the West Pacific, the two taxon-areacladograms should reflect the sequences in which the arc fragmented. At first sight the congruence between the geological cladogram and the taxon area cladograms is striking, although there are also some remarkable differences. The area relationships as indicated by the phylogeny and distributions of cicadas and the historical proximities they suggest are visualized in Fig. 11. This figure is intended to help the reader to follow the ensuing discussions.

6.1. Vicariance and fragmentation of the West Pacific island arc

The occurrences of both *Meimuna* (Fig. 1), the sister group of the *Cosmopsaltria*, and *Muda* (Fig. 2), the sister group of the *Chlorocystini* + *Prasiini*, in East Asia, with an overlap in the Ryukyu islands, suggest the collision between the island arc and the Asian continent occurred somewhere to the north of the Philippines.

Fig. 8. Geological areacladogram showing the fragmentation sequences in the West Pacific island arc.

Fig. 9. Taxon-areacladogram of the genera *Cosmopsaltria*. The areas mentioned behind the genus names are the supposed source areas of these genera (see text).

Fig. 10. Taxon-area cladogram of the Chlorocystini-Prasiini. The areas mentioned behind the genus names are the supposed source areas of these genera (see text).

The Central Philippines form the first fragment of the West Pacific island arc that became detached (the first branch in Fig. 8). However, neither the *Cosmopsaltria* nor the *Chlorocystini-Prasiini* have an endemic group in the Philippines. This might mean that the cicadas used an alternative dispersal route by-passing the Central Philippine fragment of the island arc, or simply, that that fragment has been submerged during some period prior to its collision with the continental West Philippines.

Both groups of cicadas, the *Cosmopsaltria* and the *Chlorocystini-Prasiini*, show a vicariance between Sulawesi and New Guinea including the west Pacific. This corroborates the view of some geologists (see above) that parts of Sulawesi indeed originate from the West Pacific island arc and that these parts were, after the Central Philippines, the next to become detached.

The next branch in the geological cladogram leads to the Sepik Arc terrane. This corresponds perfectly well with the next branch in the *Cosmopsaltria* cladogram (*Cosmopsaltria*), which leads to its presumed source area: central New Guinea. The *Chlorocystini-Prasiini*, however, which at this stage have segregated into three subgroups [(1) the *Cystopsaltria-Mirabilopsaltria*

group, (2) the *Papuapsaltria-Guineapsaltria* group, (3) the *Owra-Scottotympana* group) apparently miss a central New Guinean group. Instead, two of these three subgroups have a basal group of genera in Australia. The third subgroup, consisting of *Papuapsaltria* and *Guineapsaltria*, apparently lacks such a basal group altogether; the vicariance between northern New Guinea and the Papuan peninsula as indicated by these two genera corresponds with a similar vicariance higher up in the cladogram of both other subgroups (see below). The presence of the two groups in Australia and their relative positions in the cladogram in comparison to the *Cosmopsaltria* cladogram suggest that their ancestors dispersed into Australia from the Sepik Arc terrane. This might have occurred directly after the Sepik Arc collided with the Australian continent (20 m.y. ago) and prior to the development of the foreland basin, which must have effectively isolated the New Guinea orogen from the Australian continent. It indicates that during some short period the Sepik Arc terrane has been in contact with the Australian mainland. The question why these groups shifted to Australia, and why *Cosmopsaltria* did not, is hard to answer, but we must remember that the development of the central mountain ranges was extremely rapid.

Fig. 11. The historical biogeography of two groups of cicadas visualized. The map shows the fragments of the West Pacific island arc (1–3, 5–8), the Halmahera arc (9) and the Birds Head microcontinents (4) in their historic and present-day position, and the archipelagos of the South-West Pacific arc in place. The cladograms of the Cosmopsaltria and the Chlorocystini–Prasiini are plotted on this map. The branches lead to the genera and the geological entities which are regarded as their source areas.

The fact that *Cosmopsaltria* could follow this development might be more remarkable than that other groups could not. A hypothetical sister-group of *Guineapsaltria* and *Papuapsaltria* might have become extinct during this orogenesis.

The next branch in the geological cladogram leads to the East Papua Composite terrane, or the Papuan peninsula. The next branch of the *Cosmopsaltria* area cladogram leads to *Diceropyga*, of which the source area includes the Papuan Peninsula. Each of the three subgroups of the Chlorocystini too (see above) have their next groups (*Thaumastopsaltria*, *Papuapsaltria*, and *Gymnotympana*) centred in the Papuan peninsula. These genera, that originate or partly originate from the Papuan peninsula, indicate a variety of relationships of the Papuan peninsula to other areas. The extensive speciation in the Papuan peninsula and the different area relationships that are indicated, must presumably be explained by the relatively long isolation of the Papuan peninsula from other parts of New Guinea by the Aure Trough, and by the fact that the Papuan peninsula terranes (= East Papua Composite terrane) have formed an archipelago of islands, which may at various times have had different relationships to other parts of the West Pacific arc system.

Three pairs of genera, (1) *Thaumastopsaltria*–*Mirabilopsaltria*, (2) *Papuapsaltria*–*Guineapsaltria*, and (3) *Gymnotympana* + *Venustria*–*Baeturia* + *Scottotympana*, indicate a vicariance between the Papuan peninsula and northern New Guinea, which perfectly corresponds to the 5th and next branching in the geological cladogram.

6.2. Relationships of the West Pacific island arc terranes to other terranes

Many of the area relationships between the fragments of the West Pacific island arc and of these fragments to areas of a different geological origin can be explained when we assume a historic configuration of terranes as visualized in Fig. 11. In this figure, the terranes of the West Pacific island arc are plotted on a present-day map in the order in which they are presumed to have lain. For the New Guinean terranes this is also the order in which these terranes collided to the

Australian plate. Furthermore, the Birds Head terranes and Halmahera are fitted in in a way that explains their biological area relationships. The terranes of the South-West Pacific island arc are kept in their present-day position, but may initially have lain more to the south of the West Pacific island arc terranes.

South-West Pacific Island arc

The South-West Pacific island arc (Vanuatu, Fiji and Tonga), including the Solomon Islands and possibly the Bismarck Archipelago, form the sister area of a part of the West Pacific island arc (the Papuan peninsula and Bismarck Archipelago) together with Maluku (the Halmahera arc) and the Birds Head, as indicated by the vicariant sister group relationship of *Moana* + *Aceropyga* to *Diceropyga* + *Rhadinopyga* + new genus I. Such a vicariance is not found in the Chlorocystini–Prasiini. The terranes of the South-West Pacific island arc were not included in the geological cladogram since they are presumed to be of a geological origin different from the West Pacific island arc terranes. The above mentioned vicariance, however, indicates a historical proximity between the South-West Pacific island arc (presumably parts of the Solomon Islands), and the Papuan peninsula terranes (Fig. 11). The position of the Bismarck Archipelago is problematic. Based on the cicada distributions this terrane can be included in the West Pacific island arc as well as in the South-West Pacific island arc. The vicariance between *Aceropyga* and *Moana* is supposed to reflect the rotation and subsequent isolation of Fiji relative to other parts of the South-West Pacific arc.

The *Baeturia bloetei* group (Fig. 4) shows a relationship between the terranes of the South-West Pacific island arc and northern New Guinea plus Maluku. This group however, is supposed to have evolved and dispersed eastward fairly recently, after the South-West Pacific island arc had more or less reached its present-day position near the Bismarck Archipelago (De Boer, 1989; Duffels and De Boer, 1990)

Solomon Islands

The Solomon Islands and the Birds Head are sister areas, as is indicated by the relationship

between *Rhadinopyga* and the new genus I. Furthermore, the distribution of the genus *Diceropyga* suggests an area relationship of the Solomon Islands, first to the Papuan peninsula and farther back to Maluku and the Bismarck Archipelago; one species group of the genus *Diceropyga* has several endemics in the Solomons and in the Papuan Peninsula, while the other species groups of *Diceropyga* are found in Maluku and the Bismarck Archipelago. A third relationship, that of the South-West Pacific island arc including the Solomon Islands to the West Pacific island arc, is demonstrated by the vicariance discussed in the section South-West Pacific island arc.

The area relationships of the Solomon Islands indicate the existence of either land connections with, or proximity to, the East Papua Composite terrane, the Bismarck Archipelago, and the Birds Head, possibly in different geological periods.

Bismarck Archipelago

The *D. obliterans* group, the sister group of all other *Diceropyga* species is endemic to the Bismarck Archipelago. This relationship suggests a historical proximity between the Bismarck terranes and the East Papua Composite terrane plus the Solomon Islands. The occurrences of the widely distributed *D. gravesteini* Duffels and two other species of Papuan genera in the Bismarck Archipelago (*Gymnotympana dahli* (Kuhlgatz) (Fig. 7) and *Thaumastopsaltria spelunca* De Boer), presumably result from a more recent dispersal. This may also be the case for the three species of the *Baeturia bloetei* group (Fig. 4). The South-West Pacific island arc group *Aceropyga* + *Moana* also occurs on the Bismarck Archipelago which might indicate a recent dispersal or a historic relationship between the Bismarck Archipelago and that arc (see above the section South-West Pacific island arc).

Maluku

Both, *Diceropyga* and *Gymnotympana* have a monophyletic group of species in Maluku, but these genera are otherwise distributed farther eastward; *Gymnotympana* mainly in the Papuan peninsula and *Diceropyga* in the Papuan peninsula Bismarck Archipelago and Solomon Islands.

Gymnotympana is restricted to northern Maluku, but the Moluccan distribution of *Diceropyga* includes Buru and Seram. The occurrences of these two groups are supposed to reflect the eastern origin of the Halmahera arc and indicate a historical proximity between parts of Halmahera and the East Papua Composite terrane, the common factor in the area relationship between the species groups in these two genera.

Australia

Apart from the Australian genera of the Chlorocystini, which are supposed to indicate a relationship between Australia and the Sepik Arc (see above), several other genera have reached Australia. One species of *Diceropyga* and one of *Thaumastopsaltria* extend from the Papuan peninsula through southern New Guinea to northern Queensland. *Gymnotympana* has two species which are endemic to northern Queensland and the monotypic genus *Venustria*, which is possibly closely related to the Australian species of *Gymnotympana*, is also restricted to northern Queensland. It is supposed that these species dispersed into Australia during the ice age related Pliocene–Pleistocene lower sea levels. It is curious that, apart from the extremely widely distributed *Guineapsaltria flava*, only species that belong to genera of a presumed Papuan origin have been able to reach Australia by this route. These species are all restricted to the Cape York peninsula; descendants of the earlier invaders of Australia (see above) have reached farther south into northern New South Wales (De Boer, 1995d).

Birds Head

The Birds Head is apparently related to the Solomon Islands (as indicated by the sister group relationship between *Rhadinopyga* and the new genus I) and farther back to the Papuan peninsula, Bismarck Archipelago, and Maluku (indicated by the sister group relationship between *Rhadinopyga* + the new genus I and *Diceropyga*). A similar area relationship, one between the Birds Head and the eastern fragments of the West Pacific island arc is suggested by the phylogenetic relationships of *Aedeastria*. *Aedeastria*, *Mirabilopsaltria*, and *Thaumastopsaltria* show a vicariance between

the Birds Head and an area comprising the Papuan peninsula and northern New Guinea.

These relationships corroborate the assumption of an eastern origin of the Birds Head microcontinents and suggest that at least one of these microcontinents has had contact with the East Papua Composite terrane, before the latter became isolated from the remaining arc fragments and from the terranes of the South-West Pacific island arc.

7. Conclusions

From the high degree of congruence between the geological cladogram and the two taxon-area cladograms we conclude that it is highly probable that vicariance caused by the fragmentation of a West- and a South-West Pacific island arc is responsible for most of the present-day generic diversification. The area-relationships indicated by geological data, are often corroborated by the distributions and relationships of cicadas. Furthermore, cicada data add information in the form of biological area relationships, which may eventually contribute to a refined palaeogeographic reconstruction of the arcs in question and a better understanding of the historical connections to surrounding areas (Fig. 11). In two instances we recognize a relationship between areas of a different geological origin that are not recognized in the geological literature, for the very reason that these relationships are not of a geological nature. These are the relationships between the Birds Head (continental) and the Solomon Islands–Papuan peninsula region (island arcs) and the one between northern Maluku (Halmahera arc) and the Papuan peninsula (West Pacific arc). Cicada data contradict an origin of the Bismarck Archipelago (advanced on geological grounds) as an eastern extension of the northern New Guinea terranes in the West Pacific island arc. We recognize a relationship between the Bismarck Archipelago, the Papuan peninsula and the South-West Pacific island arc.

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