



Birds of paradise, vicariance biogeography and terrane tectonics in New Guinea

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Abstract

Aim The subspecies of Paradisaeidae are mapped and the distribution patterns correlated with aspects of New Guinea tectonics.

Location New Guinea, the northern Moluccas, and north-eastern Australia.

Methods Panbiogeographical analysis (Craw *et al.*, 1999).

Results *Pteridophora*, *Loboparadisaea*, *Parotia carolae* and others are notably absent from the Vogelkop, Huon and Papuan Peninsulas, accreted terranes in the north and east of New Guinea. Coupled with this, putative sister taxa in each of *Astrapia*, *Parotia* and *Paradisaea* show massively disjunct affinities between the Vogelkop and Huon Peninsulas: *Astrapia nigra* (Vogelkop) and *A. rothschildi* (Huon Peninsula); *Parotia sefilata* (Vogelkop) and *P. wahnesi* (Huon); and *Paradisaea rubra* (Western Papuan Islands by the Vogelkop) and *P. guilielmi* (Huon Peninsula). In the last two species the males have oil-green throat coloration extending above the eye to cover the front of the crown, the eye is reddish-brown not yellow, the rectrices are longer and the inner vane of the outermost primaries is not emarginate.

Main conclusions The disjunct affinities among the accreted terranes (Vogelkop, Huon, etc.), together with the absences there of groups like *Pteridophora*, are incompatible with usual dispersal models of New Guinea biogeography, but are compatible with recent analyses of vicariance biogeography and terrane tectonics (Michaux, 1994; Flannery, 1995; de Boer & Duffels, 1996a, b; Polhemus, 1996; Polhemus & Polhemus, 1998). Birds of paradise are sedentary forest dwellers with small home ranges and are tolerant of disturbance, and so it is suggested that populations have been caught in the dramatic geological movements (lateral and vertical) of different parts of New Guinea and this has led to fragmentation and juxtaposition of ranges, as well as altitudinal anomalies.

Keywords

Pacific, tropics, rain forest, ecology, evolution.

INTRODUCTION

Major questions remain: Just where are the major distributional breaks on mainland PNG and what causes (or caused) them? (Beehler, 1993).

Birds of paradise (Paradisaeidae) are endemic in the rain forests of New Guinea (thirty-seven species), the northern Moluccas (two species), and north-eastern Australia (four species) (Cooper & Forshaw, 1977; Frith & Beehler, 1998) (Fig. 1). As well as being speciose, these birds show remarkable morphological diversity in their skull, bill, facial wattles and trachea, and show more variation in feather structure and

colour than any other bird family. Paradisaeidae are famous for their beauty and elaborate courtship behaviour, and they have often served as a case-study in influential evolutionary syntheses (Wallace, 1869; Mayr, 1964 [1942]). Ernst Mayr (in Gilliard, 1969) wrote that 'Every ornithologist and birdwatcher has his favourite group of birds... Frankly, my own are the birds of paradise and bower birds. If they do not rank as high in world-wide popularity as they deserve it is only because so little is known about them...'

The disjunct distribution of *Macgregoria* De Vis. (Fig. 9) (formerly regarded as a bird of paradise) is very similar to that of many other plants and animals in montane New Guinea (Heads, 1999) and closely follows the main tectonic division of New Guinea, the former northern margin of the Australian craton (Fig. 3). This observation led to the

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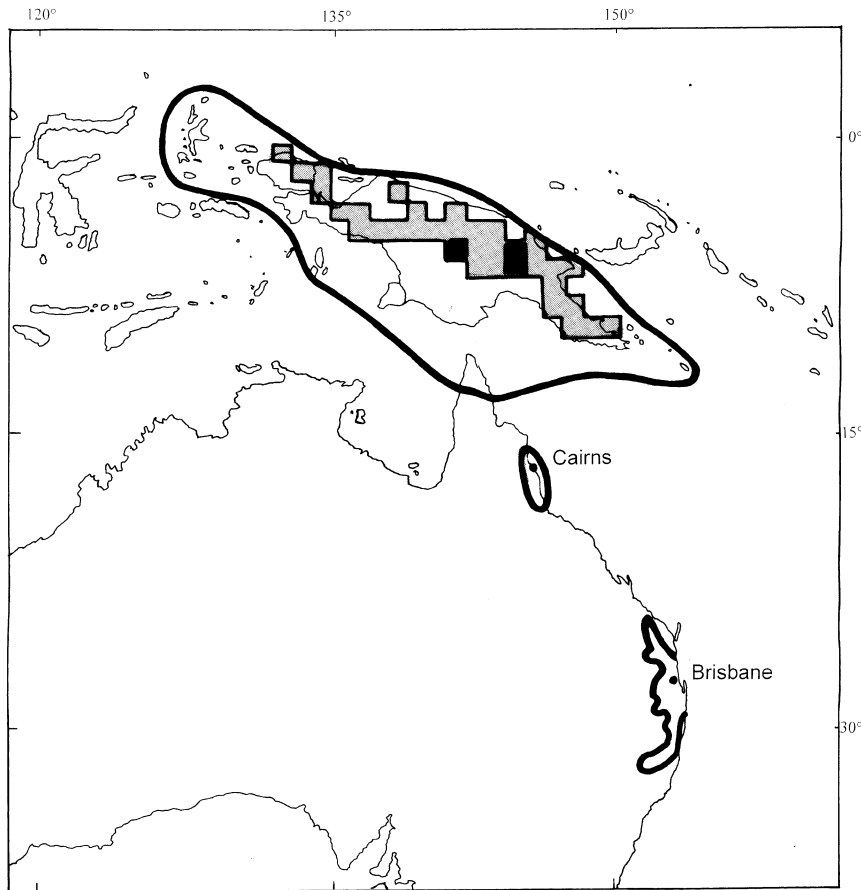


Figure 1 Distribution of Paradisaeidae, showing areas with ≥ 10 species (stippled) and ≥ 20 species (black) per $1^\circ \times 1^\circ$ grid cell.

present study of bird of paradise distributions in relation to the composite history of the New Guinea orogen as a craton margin plus accreted terranes. A general review of the group and a study of regional biodiversity in it are published elsewhere (Heads 2001b, c).

Recently DNA studies of Paradisaeidae have begun to appear (Cracraft & Feinstein, 2000), but so far have concentrated on higher-level relationships in the family. Most of the genera have similar, more or less concentric ranges through New Guinea (Fig. 2), like groups in *Rhododendron* L. (Stevens, 1982, Fig. 1), and so their precise cladistic interrelationships are perhaps not as important for biogeographical analysis as the species and subspecies, which divide up New Guinea in highly structured patterns.

Many more collections are needed to resolve problems of intraspecific variation and distribution in birds of paradise (Cracraft, 1992). The subspecies suggest a fertile field for molecular study, although many of the critical populations and clines occur in rugged and remote country and adequate sampling will be difficult. Populations of special phylogeographical interest are highlighted below. These include some that are known but remain uncollected, and also several subspecies proposed by earlier authors such as Stresemann, Greenway, Mayr, Iredale and Gilliard, but not recognized in Cracraft (1992) and Frith & Beehler's (1998) revisions. Mayr (1962) and Gilliard (1969) accepted 111 and 109

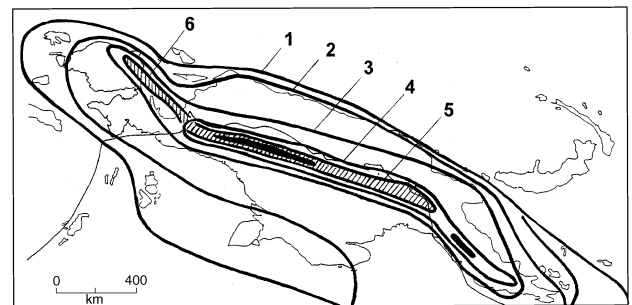


Figure 2 Distribution of twelve New Guinea genera of Paradisaeidae and *Macgregoria* (semidiagrammatic). 1 = *Manucodia* and *Paradisaea* (the latter east to the D'Entrecasteaux Archipelago only), 2 = *Ptiloris* and *Drepanornis*, 3 = *Astrapia*, *Lophorina*, *Parotia* (also in Foya Mts.), and *Epimachus* (not on Huon Peninsula), 4 = *Cnemophilus*, 5 (oblique hatching) = *Pteridophora* and *Loboparadisaea*, 5 plus 6 (vertical hatching) = *Paradigalla*, solid black = *Macgregoria*. Two New Guinea genera are not shown: *Cicinnurus* (Western Papuan Islands and New Guinea, but not on the D'Entrecasteaux Archipelago), and *Seleucidis* (wide on the mainland, but possibly not on the Huon or Papuan peninsulas). Craton margin as fine line.

subspecies, respectively, Cracraft (1992) and Frith & Beehler (1998) recognized only eighty-nine 'species' and ninety-two subspecies, respectively – a reduction of 18%.

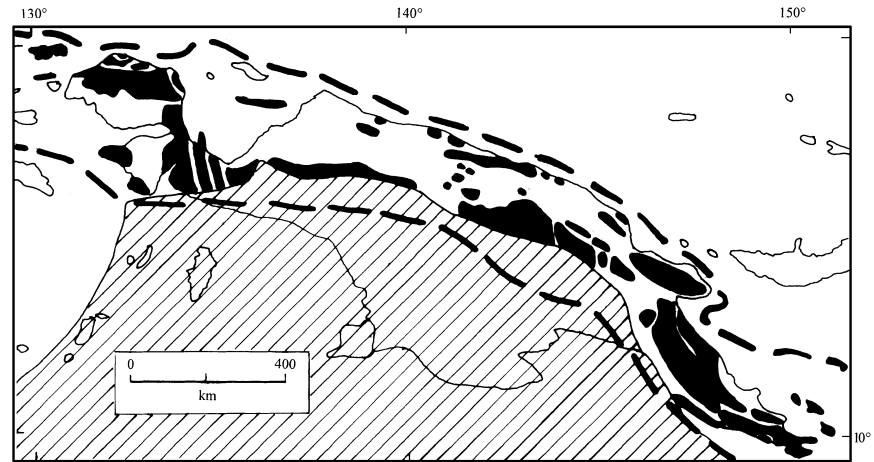


Figure 3 Geological map showing the Australian craton (hatched), the New Guinea orogen (between the heavy broken lines), and the accreted New Guinea terranes (black) (simplified from Pigram & Davies, 1987). Onshore areas of successor basins are unshaded.

Some subspecies show marked differences in dimensions and colours of parts and in their calls, while others are more subtle and sometimes controversial. The biogeographical analysis given here initially disregards the degree of genetic differentiation and is instead concerned primarily with spatial relationships and differences. Similarly, rates of evolution differ between lineages, and so a common biogeographical pattern may be held by distinct species in one group, good subspecies in another, barely differentiated subspecies in another and identical populations in a fourth, but all may be the result of the same evolutionary phase of modernization. Genetic potential for differentiation differs among groups and this results in different degrees of diversity.

The breaks and disjunctions in many New Guinea distributions have been found to correlate not with ecology but with the major geological boundary in New Guinea, the junction of the former craton in the south and the accreted terranes lying to the north (Heads, 1999, 2001a, b) (Fig. 3). This line is equivalent to the Median Tectonic Lines of New Zealand and Japan. Diversity (number of species of in $1^\circ \times 1^\circ$ squares) in both Paradisaeidae and Ptilonorhynchidae was found to be highest in the Mount Hagen – Wahgi valley – Jimi Valley square (Heads, 2001c). This region is situated right on the craton margin, and is also unusual tectonically as several terranes, including two with ultramafic rocks, are juxtaposed there. This initial work indicated that study of the species and subspecies distributions in relation to the craton and terranes would be of interest.

The results extend the observations of recent authors (Michaux, 1994; de Boer, 1995a; Flannery, 1995; de Boer & Duffels, 1996a,b; Polhemus, 1996; Polhemus & Polhemus, 1998) on terrane tectonics and animal distributions in New Guinea.

GEOLOGY OF NEW GUINEA

The geology of New Guinea has been dominated since the Mesozoic by the interaction of the Australian and Pacific plates, separated by the South Bismarck, Woodlark and

Solomon Sea plates (Bain *et al.*, 1972; Tregoning *et al.*, 1998). The plate boundary in New Guinea followed the craton margin through the Mesozoic and the Tertiary, but currently it lies just north of the north coast in NW Papua New Guinea (PNG), while further east it follows the Ramu and Markham valleys, between the main cordillera and the Huon Peninsula.

Dow (1977) characterized the tectonic structure of New Guinea with reference to three zones which form strips along the axis of the country: (1) in the south, a platform with granitic basement (the Australian craton), (2) in the north, oceanic crust and volcanic island arcs, and (3) between them the Mobile Belt *c.* 150 km wide with intrusive and metamorphic rocks and a great intensity of faulting – ‘the whole belt is best described as a fault zone’.

The Australian craton in New Guinea is overlain by sediments and overthrust belts, except at Mabaduan Hill (New Guinea’s only true inselberg), Saibai Island (by Daru), in the Strickland Gorge, and in the Kubor Mountains. The exposures here represent remnants of a basement high of Palaeozoic granites that extends north from the Great Dividing Range in Australia. Palaeozoic basement is also exposed in Irian Jaya in the Wandammen Peninsula and in the central core of the Vogelkop (Kemum terrane). These represent old fragments of Australian craton. The Kemum terrane at least had detached from the craton by the Early Cretaceous (Pigram & Davies, 1987; Polhemus, 1996).

The margin of the crystalline basement in the Eastern Highlands, Morobe and Gulf Provinces of Papua New Guinea (PNG) is obscured by sediments of the Aure Trough, but more or less coincides with the eastern limit of shelf limestones.

Both vertical and lateral movements on faults have been described from New Guinea. In the Bundi Fault Zone (between the Jimi and Marum terranes) rivers have been displaced right-laterally by about 3 km (Dow, 1977). The Wampit fault, near Lae, has displaced a recent alluvial fan by 400 m, and the Weitin fault in southern New Ireland has displaced a Quaternary coral terrace left-laterally by several kilometres. This is the sort of evidence which led geologists

to infer 480 km of right-lateral movement on the Alpine fault in New Zealand (Heads, 1998).

New ideas on accreted terrane tectonics that were developed originally for western North America have subsequently been used successfully in other areas around the Pacific. Pigram & Davies (1987) gave a radical re-interpretation of the New Guinea orogen, the folded and faulted mountainous spine of New Guinea formed during the Tertiary. They described the orogen as consisting of a southern part (the Australian craton), and a northern part consisting of at least thirty-two tectonostratigraphic terranes (including those of the Mobile Belt) that have formed separately elsewhere and subsequently been accreted to the craton (Fig. 3). In eastern PNG several terranes of diverse origin amalgamated in the Palaeogene resulting in the metamorphism of the proto-Owen Stanley terrane. The New Guinea orogeny was initiated in Oligocene time. The composite eastern PNG terrane then docked with the Australian craton in the Miocene, and finally the Finisterre (Huon Peninsula) terrane, formerly part of an island arc with New Britain and others, was accreted after the early Pliocene. Pigram & Davies (1987) discussed transcurrent movement on faults and suggested left-lateral offsets of up to 300 km along the Ramu–Markham and Bundi Fault Zones.

All the terranes, whatever the rock type, are more or less covered with high rain forest, but each is faunistically and floristically distinct with much local endemism. The boundary faults between the terranes are often major landscape features, for example, the contact between the Bowutu and Owen Stanley terranes (aerial photograph in Pieters, 1982).

SPECIES AND SUBSPECIES DISTRIBUTIONS

The subspecies distributions as mapped here are based on the species maps and subspecies notes in Frith & Beehler (1998) (and also Gilliard, 1969; Diamond, 1972) and are approximate only. The maps also show the craton margin (Pigram & Davies, 1987). Locality maps of the island of New Guinea and the PNG Highlands are given in Figs 4 and 5.

Subfam. *Cnemophilinae* Mayr

Cracraft & Feinstein (2000) indicated this group to be the sister to Corvidae + Paradisaeidae + Artamidae, which would make it a family if the others are maintained at that rank. The three species in *Cnemophilus* De Vis. and *Loboparadisaea* Rothschild are notably absent from the Vogelkop and Huon Peninsulas for no apparent ecological

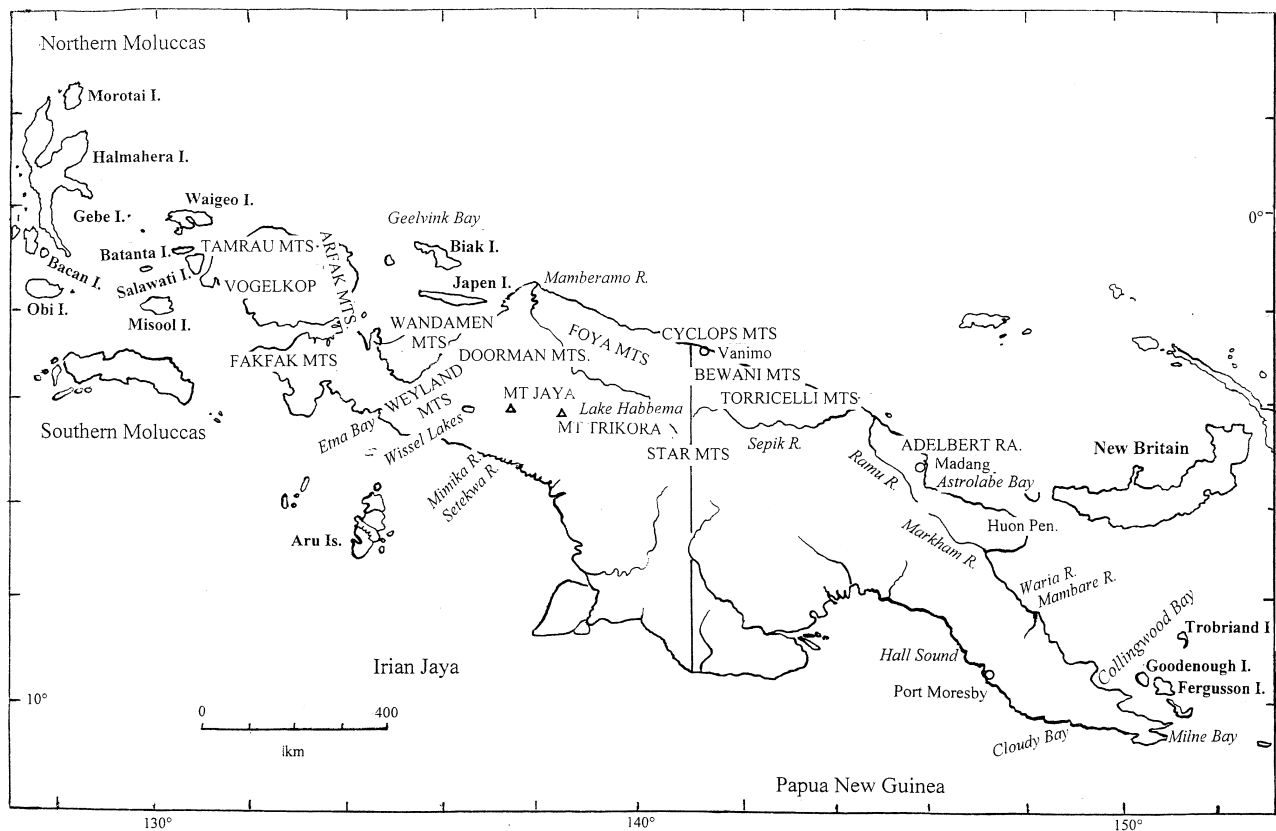
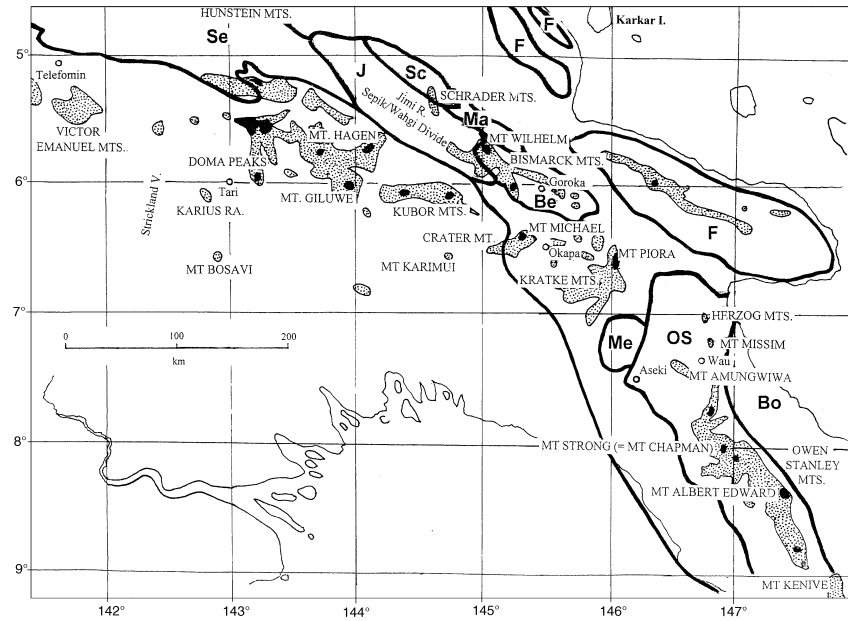


Figure 4 Locality map of New Guinea and the Moluccas. Available literature for Irian Jaya (West Papua) often cites the old Dutch place names, and so many of these are used here. For reference, the three highest mountains in Irian Jaya are Mt Carstensz = Mt Sukarno = Mt Irian = Mt Jaya; Mt Wilhelmina = Mt Trikora; and Mt Goliath = Mt Mandala (western Star Mountains).

Figure 5 Locality map of the PNG Highlands, showing land over 2400 m (stippled) and land over 3600 m (black) and geological terranes (Be = Benabena, Bo = Bowutu, F = Finisterre, J = Jimi, ma = marum, me = menyamya, Sc = Schrader, Se = Sepik, OS = Owen Stanley).



reason. However, this zone of absence is a zone of endemism for related species pairs in *Astrapia* and *Paradisaea* (see below).

Cnemophilus loriae (Salvadori) (Fig. 6). *Cnemophilus l. inexpectata* (Junge). Weyland Mountains east to the Victor Emanuel Mountains. The boundary between this and the next subspecies is unclear but possibly lies just west of the Doma Peaks, a common point of distributional break in the family.

Cnemophilus l. amethystina (Stresemann). Mount Bosavi and Doma Peaks east to the Bismarck Mountains.

Cnemophilus l. loriae. Papuan Peninsula (i.e. the 'tail' of southeast New Guinea, east of the Huon Peninsula).

Cnemophilus macgregorii De Vis. (Fig. 7). The two subspecies have ranges rather like those of the last species; both show a subspecies break near Goroka and the craton margin. *Cnemophilus macgregorii* and *Paradisaea rudolphi* are 'equally anomalous' (Frith & Beehler, 1998) in that both are widespread on the cordillera but do not extend to its western limit at the Weyland Mountains (separated from the main ranges by the Wissel = Paniai Lakes). Frith and Beehler wrote that 'An explanation for these truncated ranges is not readily forthcoming...', but the Weyland Mountains, here noted as a centre of absence, are also a centre of endemism in other birds of paradise (subspecies of *Astrapia* and *Parotia*).

Cnemophilus m. sanguineus Iredale (incl. *C. m. kuboensis* Mayr and Gilliard). Lake Habbema (by Mount Wilhelm) to near Goroka.

Cnemophilus m. macgregori De Vis. South-east of the last. A skin in a head-dress seen near Goroka and said to have been shot in the Kratke Mountains appeared to have had paler upper parts like *C. m. macgregori* (Gilliard, 1969), as mapped here, or it may be intermediate between this and

C. m. sanguineus. (C.B. Frith, *in litt.* 22 August 2000, kindly confirmed that the Kratke Mountains record of *C. loriae* on the species map in Frith & Beehler, 1998 should be deleted, and one for the Kratke Mountains added to the map of *C. macgregorii*.)

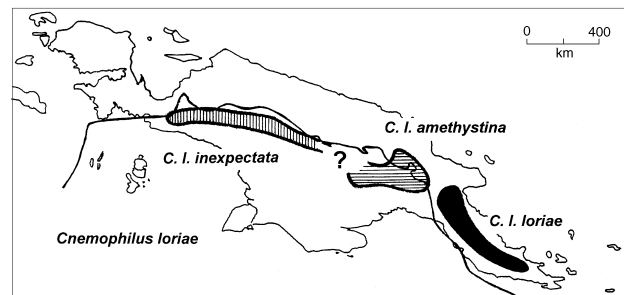


Figure 6 The distribution of *Cnemophilus loriae* (this and subsequent maps show the former craton margin as a line).

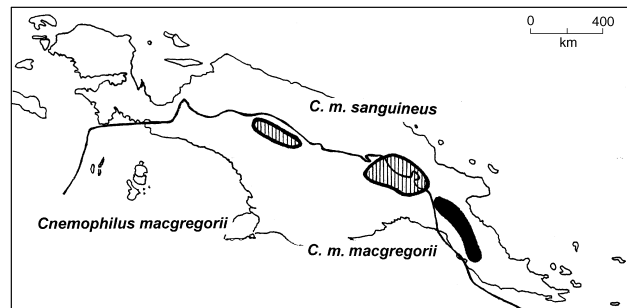


Figure 7 The distribution of *Cnemophilus macgregorii*.

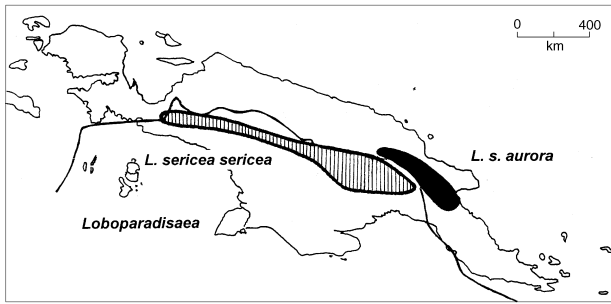


Figure 8 The distribution of *Loboparadisaea*.

Loboparadisaea Rothschild. (Fig. 8). Like *Cnemophilus*, this is absent from the Vogelkop and Huon Peninsulas. The boundary between the two subspecies tracks the craton margin precisely.

Loboparadisaea s. sericea Rothschild. Weyland Mountains east to Kubor Mountains and Karimui/Soliabeda.

Loboparadisaea s. aurora Mayr. Upper Jimi River and Mount Wilhelm area, Okapa, Aseki, Herzog Mountains and Wau.

Subfam. Paradisaeinae

Macgregoria De Vis. (Fig. 9). This has been treated as a bird of paradise by most authors (e.g. Frith & Beehler, 1998). However, Iredale (1956) observed living birds and indicated that *Macgregoria* is instead a member of Meliphagidae. Cracraft & Feinstein (2000) also came to this conclusion (without citing Iredale, 1956). *Macgregoria* seems bound to be removed from Paradisaeidae, but whatever the outcome the distribution is noteworthy, as it is absent from the Vogelkop and Huon Peninsulas like *Cnemophilus* and *Loboparadisaea*. The disjunction between the subspecies correlates well with the craton margin:

Macgregoria p. carolinae (Junge). Mounts Carstensz and Wilhelmina to the Star Mountains by Telefomin.

Macgregoria p. pulchra De Vis. Mounts Strong (Chapman), Albert Edward, Scratchley, Victoria and Batchelor.

Macgregoria, disjunct between the Star Mountains and the Owen Stanley Mountains, favours the 'fruit' of *Dacrycarpus compactus* (Wasscher) de Laub., disjunct between Telefomin and around Mount Wilhelm (Heads, 1999). As

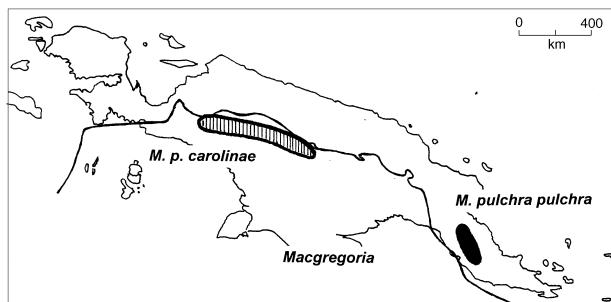


Figure 9 The distribution of *Macgregoria*.

Archbold & Rand (1935) pointed out, the distribution of the two may perhaps be correlated. However, rather than the bird distribution being a simple effect of the plant distribution (the plant is considerably more widespread than the bird), both disjunctions may be the result of similar tectonic/biological development along the craton margin, for example through massive lateral fault movement. Another mountain bird, *Amalocichla sclateriana* De Vis. (Eopsaltriidae) (2700–3900 m) with a similar disjunction (*A. s. occidentalis* Rand in the Snow Mountains, *A. s. sclateriana* in the Owen Stanley Mountains) lives on insects and spiders – not podocarps. The disjunction also occurs in other birds such as *Melidectes ochromelas*. This was mapped by Diamond (1973) who attributed the gap to 'checkerboard exclusion' as it is filled by vicariants. This is probably a more profitable line of enquiry than his other suggestion that the pattern is because of 'irregular geographical variation', especially as the same disjunction is frequently seen in plants. For example the thirteen species of *Vaccinium* sect. *Neojunghuhnia* (Koorders) Sleumer (Stevens, 1982) have a total range almost identical to that of *Macgregoria*, as does *Kelleria patula* Merr. & Perry (Heads, 1990).

Lycocorax pyrrhopterus (Bonaparte) (Fig. 10). Northern Moluccas. This surrounds the range of the only other bird of paradise on the Moluccas, *Semioptera* Gray (Fig. 27), which is on Halmahera but not Morotai or Obi.

Lycocorax p. pyrrhopterus. Halmahera, Bacan and Kasiruta Islands.

Lycocorax p. obiensis Bernstein. Obi and Bisa Islands.

Lycocorax p. morotensis Schlegel. Morotai and Rau Islands.

Manucodia Boddaert. Four of the five species in this genus are mainly northern, while the first, *M. atra*, has an unusual disjunction.

Manucodia atra atra (Lesson) (Fig. 11). North and south New Guinea, but absent in the southeast from most of Morobe and Oro Provinces, also the D'Entrecasteaux and Trobriand Islands.

Manucodia a. subaltera Rothschild and Hartert. The distribution is 'Disjunct and biogeographically inexplicable' (Frith & Beehler, 1998): there are records on the craton at Aru Islands, and also north of the craton margin in the far

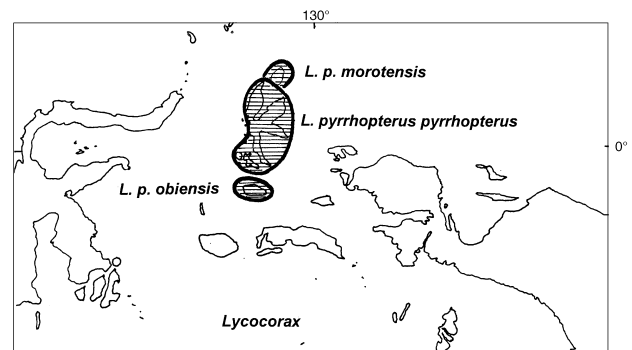


Figure 10 The distribution of *Lycocorax*.

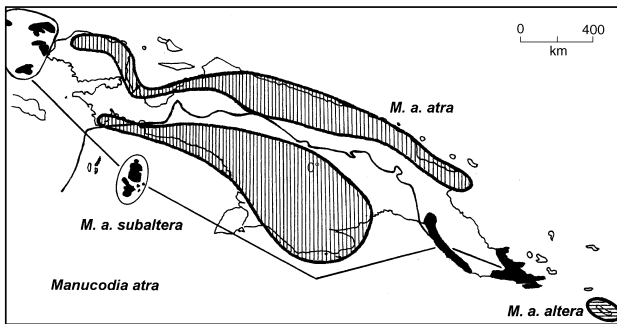


Figure 11 The distribution of *Manucodia atra*.

west (Western Papuan Islands), and in the east on the Papuan Peninsula. This pattern does seem uncommon; the usual connection of the Aru Islands with the New Guinea mainland is with the Mimika-Setekwa or Digul-Fly regions.

However, the cicada *Gymnotympana strepitans* Stål has an identical disjunction between Aru Islands and Port Moresby eastwards (de Boer, 1995b) and a possible parallel is also seen in the mistletoe genus *Cyne* Danser (Loranthaceae), which has two species around Port Moresby (Sogeri, Isuarava), one in the southern Moluccas, and the remaining three in the Philippines (Barlow, 1993). Similarly, the *Bledius lucidus* Sharp group of staphylinid beetles is disjunct between the southern Moluccas (Buru) and Kokoda (Herman, 1986), although the connection may not be direct as the group is also in Taiwan. A similar Timor-Torres Strait disjunction is illustrated by the *B. bellicosus* Fauvel group (Herman, 1986).

However, as well as a possible standard biogeographical connection: Aru Islands – Port Moresby, there is a more common link between the Vogelkop and SE New Guinea. Vogelkop – Huon ties are shown below in *Astrapia* Vieillot and *Paradisaea* L., and Vogelkop – Wau ties are also known. Similarly, after analysing specimens of *Meliphaga* (*Xanthotis*) *flaviventer* (Lesson), Diamond (1972) arrived at ‘the unexpected result’ that birds from both the Karimui area and Okasa (near Okapa, Eastern Highlands Province of PNG) are closest to *rubiensis*, the Weyland Mountains race; ‘One might have expected them to be *giulianettii*, the southern watershed race both to the east and to the west...’

These disjunctions are members of a series which follow the craton margin between the Vogelkop/Weyland Mountains and PNG.

The distribution of *M. a. subaltera* would be resolved if the ties of the Aru Islands birds are with the Western Papuan Islands populations, rather than with those around Port Moresby. The real disjunction would then be between the Western Papuan Islands and Moresby region, following a standard pattern. The two possible alternatives: Western Papuan Islands – Aru Islands – Port Moresby, or Aru Islands – Western Papuan Islands – Port Moresby, could be evaluated by molecular study.

Manucodia a. altera Rothschild and Hartert. Endemic to Sudest (Tagula) Island, which lies within the orogen and comprises metamorphic rocks of the Owen Stanley terrane.

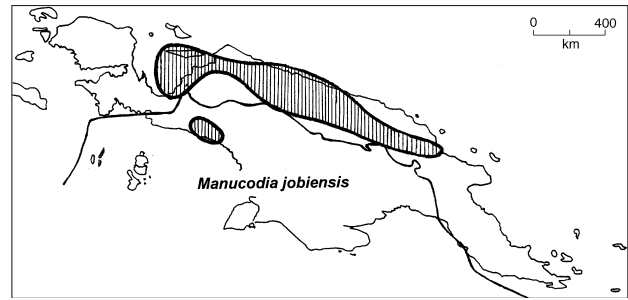


Figure 12 The distribution of *Manucodia jobiensis*.

Manucodia jobiensis Salvadori (incl. *M. j. rubiensis* Meyer from Geelvink Bay) (Fig. 12). Northern New Guinea from Japen Island to Madang, and south of the craton margin at Mimika and Setekwa Rivers only. This range recalls that of the frog *Platymantis* Guenther, which has many species in the Bismarck Archipelago, the Solomon Islands and on the New Guinea mainland north of the craton margin, and records south of the craton margin only at the Mimika and Setekwa Rivers (Zweifel, 1969: Fig. 5). A similar pattern is also seen in the skink *Tribolonotus* Duméril and Bibron (Allison, 1996: Fig. 3), and the plant *Parsonsia alboflavescens* (Dennst.) Mabb., ubiquitous through Malesia except southern New Guinea east of Mimika/Setekwa Rivers (Middleton, 1997).

Manucodia chalybata (Pennant) (Fig. 13). Misool Island and the New Guinea mainland from the Vogelkop to Alotau. Absent from the Western Papuan Islands of Waigeo and Batanta, and also from the Milne Bay islands. It occurs at higher altitudes than *M. jobiensis*. Following Frith & Beehler (1998), it is widespread in northern New Guinea but not in the south (unlike *M. atra*). In very different maps, Gilliard (1969) and Cooper & Forshaw (1977) accepted it as wide in the south. Species delimitation and identification in *Manucodia* is more difficult than in any other paradisaeid genus. Is the single remaining locality of *M. chalybata* in the south (lower Fly) questionable? If not, it represents a striking disjunction 200 km away from the nearest population, on Mount Bosavi. Other altitudinal anomalies in this region are discussed in Heads (2001b) and attributed to tectonic movement.

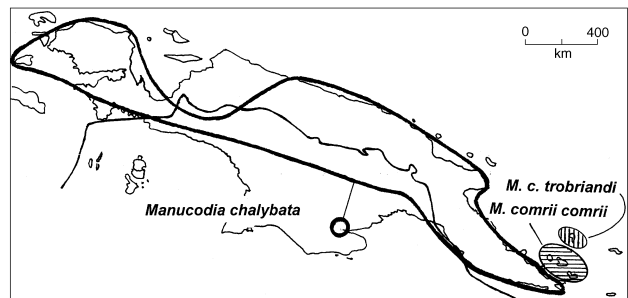


Figure 13 The distribution of *Manucodia chalybata* and *M. comrii*.

Manucodia comrii Sclater. (Fig. 13). This replaces the last two species on Milne Bay islands which lie within the New Guinea orogen. New Britain and New Ireland to the north lie outside the orogen (Fig. 3), and do not have birds of paradise (or bowerbirds – Ptilonorhynchidae) despite being covered with mountainous rain forest.

Manucodia c. comrii. D'Entrecasteaux Archipelago (Good enough, Fergusson and Normanby Islands).

Manucodia c. trobriandi Mayr. Trobriand Islands.

Manucodia keraudrenii (Lesson and Garnot) (Fig. 14). This is one of the most widespread birds of paradise, but despite having six subspecies outboard of the craton and two on it (cf. *Paradisaea*, below) it is absent from the Western Papuan Islands, Huon Peninsula, and also the outer islands of Milne Bay (Trobriands, Sudest) where it is replaced by *M. comrii* and *M. atra*. The craton margin is an important boundary separating the subspecies in the west and in the PNG Highlands.

Manucodia k. keraudrenii. Vogelkop to Mamberamo River, with only one record possibly south of the craton margin, at the Wissel Lakes.

Manucodia k. aruensis Cracraft. Aru Islands.

Manucodia k. jamesii (Sharpe). Southern New Guinea south of a line Mimika River – Karimui. Present at Port Moresby but the subspecific status of populations further south-eastward towards Milne Bay is uncertain (see query in Fig. 14).

Manucodia k. neumanii (Reichenow). Bewani and Lordberg Mountains above the Sepik Valley, to Jimi and Baiyer River catchments (Schrader Mountains, Sepik-Wahgi divide).

Manucodia k. adelberti (Gilliard and LeCroy). Adelbert Mountains.

Manucodia k. diamondi (Cracraft). Okapa, Kassam Pass, northern Kratke Mountains (Cracraft, 1992).

Manucodia k. purpureoviolacea (Meyer). Wau, south-east through the Owen Stanley Mountains.

Manucodia k. hunsteini (Sharpe). D'Entrecasteaux Archipelago (Goodenough, Fergusson and Normanby Islands), only in upland forest.

Manucodia k. gouldii (Gray). Cape York Peninsula (northern Queensland).

Paradigalla Lesson. (Fig. 15) Present on the mountains of central New Guinea and the Vogelkop but absent from the

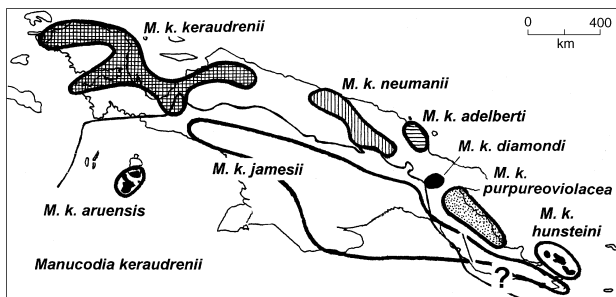


Figure 14 The distribution of *Manucodia keraudrenii*. There is also an endemic subspecies, *M. k. gouldii*, in northern Queensland.

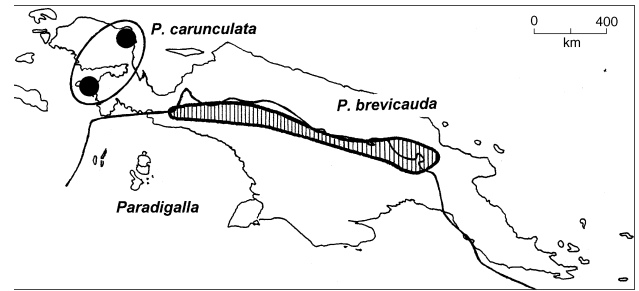


Figure 15 The distribution of *Paradigalla*.

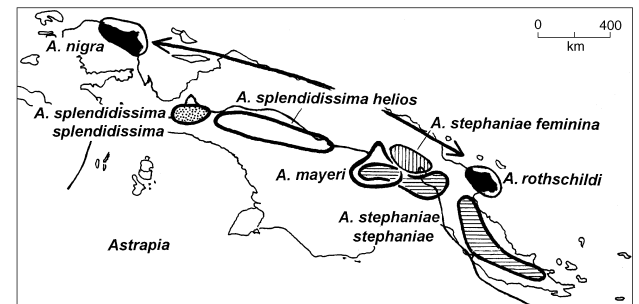


Figure 16 The distribution of *Astrapia*.

Huon and Papuan Peninsulas, like *Pteridophora*, *Epimachus fastuosus* and others. The two species are separated by the craton margin.

Paradigalla carunculata Lesson. Vogelkop (Arfak and Fakfak Mountains).

Paradigalla brevicauda Rothschild and Hartert (incl. *P. carunculata intermedia* Ogilvie-Grant, recently shown to be a juvenile form). Weyland Mountains east to about Goroka (like *C. l. amethystina* and *Epimachus mayeri bloodi*). Apart from records along the Bismarck Range (Sepik-Wahgi Divide, Mount Wilhelm, Goroka) the species is restricted to the craton.

The species of *Astrapia* Vieillot (Fig. 16) divide up the island amongst themselves.

Astrapia nigra (Gmelin). Vogelkop: Arfak and Tamrau Mountains (cf. *Paradigalla carunculata* and *Parotia sefilata*).

Astrapia rothschildi Foerster. Huon Peninsula (mainly in the east). As Gilliard (1969) wrote, 'It is perhaps significant that in *Astrapia* the most widely separated species, *A. nigra* of the Vogelkop in the west and *A. rothschildi* of the Huon Peninsula in the east, are morphologically the most similar'. This clear resemblance involves the long, broad, straight, blunt tail and the ventral coloration in the males, which is black or dark blue below the bill, copper in a narrow pectoral band, and oil-green on the abdomen. The females of *A. nigra* and *A. rothschildi* are darker birds than females of the other species, with only faint ventral marking. Further, only in *A. nigra* and *A. rothschildi* do all the rectrices grow longer with age – in the other species only the central pair do

so and in *A. splendidissima* the central rectrices grow shorter (Frith & Beehler, 1998).

Iredale (1956) wrote that *A. nigra* and *A. rothschildi* are 'certainly' nearest relatives, and Gilliard (1969) felt that the similarity is the result of 'true relationship and not character convergence.' On the other hand, Frith & Beehler (1998) surmised (on geographical grounds) that the predecessor of *A. rothschildi* 'budded-off' from the predecessor of *A. stephaniae*, although they admitted that the similarities between *A. nigra* and *A. rothschildi* are 'curious'. They suggested that these similarities may represent an ancestral state lost by the cordilleran species, but no evidence was given for this. Whether the similarities are symplesiomorphies or synapomorphies, the distribution of *A. nigra* plus *A. rothschildi* makes little sense on geographical grounds but is a standard biogeographical pattern (cf. *Paradisaea*, below).

Astrapia splendidissima Rothschild. The central pair of rectrices grow progressively shorter in the males of *A. splendidissima*, unlike all the other species (Frith & Beehler, 1998). This Snow Mountains species is thus set apart from, and sandwiched between, its long-tailed congeners in the Vogelkop and PNG in exactly the same way as *Parotia carolae* (next genus) is sandwiched between the black parotias of the Vogelkop and PNG.

Astrapia s. splendidissima Weyland Mountains and Wissel Lakes. The main summits of the Weyland Mountains lie in the SE corner of the accreted Weyland terrane, but are close to the craton margin, with the Wissel Lakes and the main cordillera on the other side. The two areas are connected by land above 2000 m, and while most records from the 'Weyland Mountains' presumably come from Weyland terrane, it is possible that some come from land on the craton – for example, Wissel Lakes are sometimes treated as lying in the Weyland Mountains.

Astrapia s. helios Mayr. From east of Wissel Lakes to at least Telefomin. The eastern limit of the race is unclear, but it probably contacts *A. mayeri*, next, in the vicinity of the Strickland Gorge.

Astrapia mayeri Stonor. Karius Range and the Doma Peaks by Tari, mountains by Laiagam, Mount Hagen and Mount Giluwe (this last, important locality is not located correctly on the otherwise very useful map in Rand & Gilliard, 1967). The western limit lies close to that of *Paradisaea rudolphi*, discussed below. On and west of Giluwe-Hagen there is overlap between *A. mayeri* and *A. stephaniae*, with the latter having a lower mean altitude.

Astrapia s. stephaniae (Finsch and Meyer). Doma Peaks (cf. *A. mayeri*, *Paradisaea rudolphi*, etc.) southeast to the Owen Stanley Mountains and Mount Dayman. This apparently crosses the craton margin into the Papuan Peninsula without differentiation, but does not cross it into the Bismarck Range, which is occupied by the next subspecies.

Astrapia s. feminina Neuman. Sepik-Wahgi Divide, Schrader Range, Bismarck Range. This and the nominate subspecies illustrate a standard break between birds of the Bismarck Range, north of the craton margin (here represented by the Wahgi Valley and the Bismarck Fault Zone), and those of the Kubor Range, south of the margin (cf.

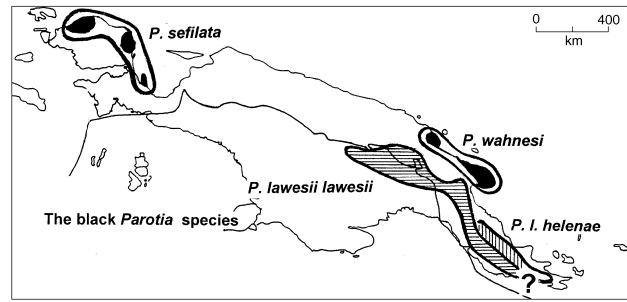


Figure 17 The distribution of *Parotia lawesii*, *P. sefilata* and *P. wahnesi*.

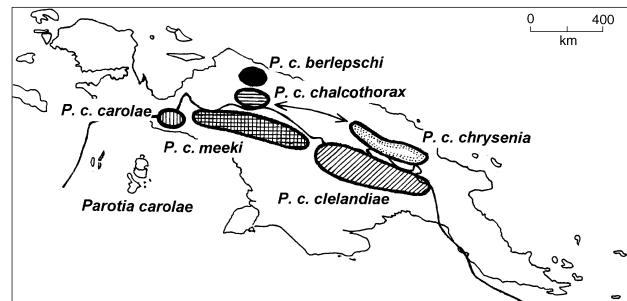


Figure 18 The distribution of *Parotia carolae*.

Manucodia keraudrenii, *Parotia carolae*, *Loboparadisaea*, possibly *Pteridophora alberti* if *P. a. hallstromi* is distinct).

Parotia Viellot. (Figs 17 & 18). The first three species (Fig. 17) are mainly black with blue eyes, and are 'unambiguous sister forms' (Frith & Beehler, 1998).

Parotia sefilata (Pennant). Vogelkop.

Parotia wahnesi Rothschild. Adelbert Mountains and Huon Peninsula.

Parotia lawesii lawesii Ramsay. Upper Strickland valley (about Oksapmin) east to the southern watershed of the Papuan Peninsula. *Parotia l. fuscior* Greenway (type from Mount Missim), and *P. l. exhibitata* Iredale (type from Mount Hagen) are both accepted by several authors, but not by Frith & Beehler (1998).

Parotia l. helenae De Vis. (sometimes treated as a full species, *P. helenae*). Northern watershed of the Papuan Peninsula from the Waria River to Milne Bay, largely on the ultramafic Bowutu terrane.

This group of three species shows a disjunction between the Vogelkop (*P. sefilata*) and the upper Strickland Valley (*P. lawesii*)/Adelbert Mountains-Huon Peninsula (*P. wahnesi*). *Parotia sefilata* may well be the sister species of *P. wahnesi* as both have a longer tail than the other species and there are also behavioural similarities (E. Scholes, pers. comm.). In any case, the vast gap in the range of these black birds is largely filled by the only other parotia, *P. carolae*, with pale flank plumes, supra-narial tufts, eye-ring and yellow iris. Frith & Beehler (1998) wrote that the mode of

differentiation that would produce such a geographical pattern, with the less related *carolae* sandwiched between *sefilata* and *lawesii*, is 'unclear.

Nevertheless, a similar pattern occurs in *Astrapia*, with the short-tailed *A. splendidissima* of Irian Jaya sandwiched between the long-tailed species in the Vogelkop and PNG. The pattern would be explained by a separate, eastern origin of Vogelkop terranes (references below). Similar patterns are also seen in other birds: *Myzomela adolphinae* (Salvadori) (Meliphagidae) is disjunct between the Vogelkop (Arfak Mountains) and PNG: Mount Hagen, Kubor Mountains and the Bismarck Range eastwards (Rand & Gilliard, 1967). This species shows 'remarkable' (Rand & Gilliard, 1967) similarity with the mangrove species *M. erythrocephala* Gould of southern New Guinea, which partly fills the gap in the range of *M. adolphinae* (cf. *P. carolae*).

Erythrura papuana (Hartert) (Estrildidae) is a rare bird only known from western Irian Jaya (Arfak and Tamrau Mountains, Wissel Lakes) and disjunct in SE PNG (Okapa and further east – Aroa River, Mount Tafa and Mount Albert Edward) (Diamond, 1972). It is generally allopatric with the related *E. trichroa* Kittlitz which is widespread through the New Guinea mountains, although the two are notably sympatric at the Arfak Mountains and Mount Albert Edward.

Parotia carolae Meyer. (Fig. 18). Weyland Mountains to Crater Mountain, absent on the Vogelkop, Huon and Papuan Peninsulas (like *Loboparadisaea* and *Pteridophora*). The first three subspecies are on the craton, the last three occur north of the craton margin, with the six aligned in three parallel strips.

Parotia c. carolae. Weyland Mountains to Wissel Lakes, like *Astrapia s. splendidissima*.

Parotia c. meeki Rothschild. Irian Jayan cordillera (Snow Mountains, but not the Doorman Mountains), east to the Irian Jaya/PNG border (Star Mountains), where it meets the following subspecies.

Parotia c. clelandiae Gilliard. Telefomin to Crater Mountain. (The latter population has not been identified to subspecies, and is treated here for convenience only.)

Parotia c. chalthorax Stresemann. Doorman Mountains. This range lies on the northern part of the central cordillera in the Rouffaer terrane, separated from the main peaks (Mount Carstensz, Mount Wilhelmina, etc.) by the craton margin. The Rouffaer terrane is an ophiolite complex and also a major centre of endemism for plants with, for example, five species of *Rhododendron* L. endemic there (van Royen, 1979–83) and six species of *Grammitis* Swartz endemic or nearly endemic (Parris, 1983).

Parotia c. chrysenia Stresemann. There are four localities: Lordberg and Hunstein Range are both in the composite Sepik terrane, including rocks of oceanic, island arc and continental origin, Schrader Mountains comprise an ophiolite complex, and the fourth population, on the northern scarp of the Bismarck Range (Marum terrane), occurs on another ophiolite. This and the last subspecies have the longest occipital plumes in the species and the

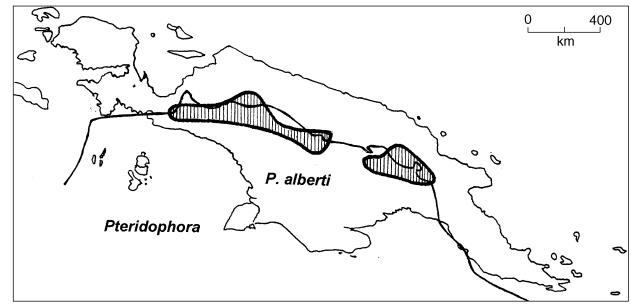


Figure 19 The distribution of *Pteridophora alberti*.

possible affinity between these ophiolite taxa is indicated in Fig. 18.

Parotia c. berlepschi Kleinschmidt. Locality unknown; the Van Rees and Foya Mountains have both been suggested. The Foya Mountains (mapped in Fig. 18) are the only known locality of the bowerbird *Amblyornis flavifrons* Rothschild (Beehler *et al.*, 1986) and comprise the Gauttier terrane. This is probably a dismembered portion of the Torricelli terrane, which lies further east and has endemics like *Epimachus fastuosus ultimus*.

Pteridophora alberti Meyer. (Fig. 19). Weyland Mountains east to Okapa (Frith & Beehler, 1998 noted that it 'possibly' occurs in the Kratke Mountains (cf. Mayr, 1962), and recorded that local informants apparently knew it from Kaintiba and Menyama). The genus is absent from the Vogelkop, Huon and Papuan Peninsulas, like *Loboparadisaea*, *P. brevicauda*, *P. carolae*, and *Epimachus fastuosus*, and with a similar eastern boundary to the last three of these. If distribution is brought about by migration (rather than evolution) it would seem unlikely that birds such as *Cnemophilus* and *E. meyeri* would fly to the Papuan Peninsula, but *Pteridophora*, *Paradigalla* and the others would not, but instead all stop at the same point.

Frith & Beehler (1998) accepted *Pteridophora alberti* as monotypic, but Mayr (1962) and Gilliard (1969) recognized three subspecies:

Pteridophora a. alberti. Irian Jaya,

Pteridophora a. bürgersi Rothschild. Schrader Mountains,

Pteridophora a. hallstromi Mayr and Gilliard. Giluwe, Hagen, Kubor, Karimui and Bismarck Range, with all but the last of these localities lying on the craton.

None of these subspecies are accepted by Frith & Beehler (1998), although the possibility that populations lying north of the craton margin (*bürgersi*) may differ from southern ones (*hallstromi*) is of special biogeographical interest, whatever the degree of differentiation. In fact, Frith & Beehler (1998) recorded that *hallstromi* has slightly longer wings and tail than *alberti* and *bürgersi*, which are almost identical in size.

Variation in the montane tree *Drimys piperita* Hook.f. shows a very similar pattern. 'Entity *reducta*' (Diels) Vink, at Wissel Lakes, Mount Wilhelmina, Mount Giluwe and the Kubor Mountains, and 'entity *subalpina*' Vink, only at Mount Wilhelm, are a pair of 'replacing taxa' (Vink, 1970).

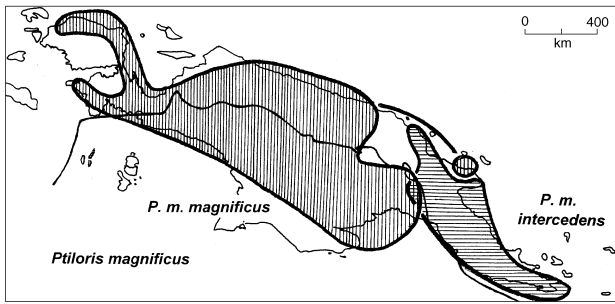


Figure 20 The distribution of *Ptiloris magnificentus* in New Guinea. The other members of the genus, *P. m. alberti*, *P. m. victoriae* and *P. m. paradiseus*, all in Australia, are not mapped.

Vink reported the 'unexplained circumstance' that the form of *reducta* most distinct from *subalpina* is found at the Kubor Mountains – the locality closest to Mount Wilhelm, while the form which connects the two morphologically, 'entity *subpittosporoides*' Vink, is restricted to Mount Wilhelmina. This Irian Jaya – Schrader/Wilhelm disjunction in both the birds and the plants could be explained by (right-) lateral movement of terranes.

Ptiloris magnificentus (Vieillot). (Fig. 20). *Ptiloris m. magnificentus*. Irian Jaya east to Crater Mountain in the south and Wewak in the north, with a disjunct population 500 km further east on Huon Peninsula (Yalumet). This disjunction is possibly related to the others involving the Huon Peninsula.

Ptiloris m. intercedens Sharpe. From Hall Sound and northern Madang Province to Milne Bay.

The two different subspecies are vocally distinct. All records from Crater Mountain are of the nominate race, except for a single record (heard only) of *P. m. intercedens*. Apart from this, *P. m. intercedens* is only recorded from areas north and east of the craton.

Ptiloris m. alberti Elliot. Cape York Peninsula, Queensland. This is an outlier of a widespread New Guinea species, like *M. keraudrenii gouldii*. The following two monotypes are the only bird of paradise species restricted to Australia:

Ptiloris victoriae Gould. Cairns district, Queensland.

Ptiloris paradiseus Swainson. Central Queensland (Rockhampton) to New South Wales (Hunter River, 100 km north of Sydney). The last locality, the southern limit of Paradisaecidae, is also the southern limit of an important centre of endemism for plants, the MacPherson Range–Macleay River Overlap (Ladiges, 1998). (Note that this distribution is not shown accurately in Frith & Beehler, 1998, Fig. 1.1., although it is in their map on p. 329).

Lophorina Vieillot. (Fig. 21). Present on the New Guinea mainland from the Vogelkop to Milne Bay, but not on the Western Papuan or D'Entrecasteaux Islands, like *Astrapia*, *Parotia*, *Epimachus*, *Drepanornis* and *Seleucidis*.

Lophorina s. superba (Pennant). Arfak and Tamrau Mountains.

Lophorina s. niedda Mayr. Wandammen Peninsula. These two subspecies form a related pair.

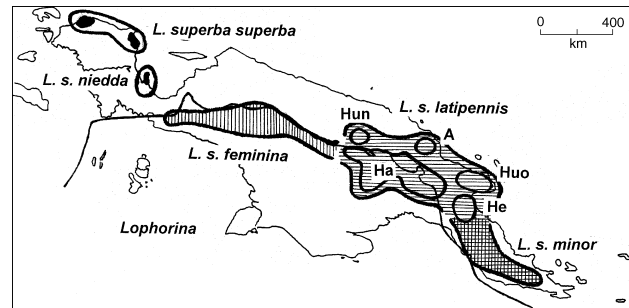


Figure 21 The distribution of *Lophorina superba*. Localities of critical populations as follows: Hun = Hunstein Mountains, Ha = Mount Hagen, A = Adelbert Mountains, Huo = Huon Peninsula, He = Herzog Mountains.

Lophorina s. feminina Ogilvie Grant. Weyland Mountains eastwards to approximately the Victor Emanuel Mountains.

Lophorina s. latipennis Rothschild. Frith & Beehler (1998) interpreted this subspecies (type from the Huon Peninsula) in a broad sense to include birds from the Doma Peaks east to about the Herzog Mountains (cf. Fig. 21). This includes *L. s. connectens* Mayr from the Herzog Mountains, *L. s. addenda* Iredale from Mount Hagen, birds from the Adelbert Mountains, and an unidentified, geographically isolated race from the Hunstein Mountains (*L. s. pseudoparotia* Stresemann, from there, is a hybrid of *L. superba* and *P. carolae*). Differentiation in this subspecies is not well resolved but biogeographically critical as it involves populations on the craton as well as several accreted terranes; Diamond (1972) noted that Eastern Highlands birds were slightly darker than Huon Peninsula birds.

Lophorina s. minor Ramsay. Papuan Peninsula, from Wau southeast.

Lophorina s. sphinx (Neumann). Locality unknown.

Epimachus Cuvier. (Figs 22 & 23). From the Vogelkop to Milne Bay, but absent from Western Papuan Islands, Huon Peninsula and the D'Entrecasteaux Archipelago.

Epimachus meyeri Finsch. (Fig. 22). Central ranges and the Papuan Peninsula, but absent from the Vogelkop and Huon Peninsulas. The distribution is almost identical to that of *C. loriae* and similar to that of *C. macgregorii* (Figs 6 & 7).

Epimachus m. albicans (van Oort). Weyland Mountains to Victor Emanuel Mountains.

Epimachus m. bloodi Mayr and Gilliard. Tari/Doma Peaks east to the Schrader Mountains and the Bismarck Range (Goroka).

Epimachus m. meyeri. Southeast from Mount Missim (above the towns of Wau and Bulolo). As well as being a boundary, this mountain and the nearby Mount Shungol (Herzog Mountains) comprise a centre of endemism for many bird subspecies (Rand & Gilliard, 1967).

Epimachus fastuosus (Hermann) (Fig. 23). Central ranges and the Vogelkop, but absent from Huon and Papuan Peninsulas.

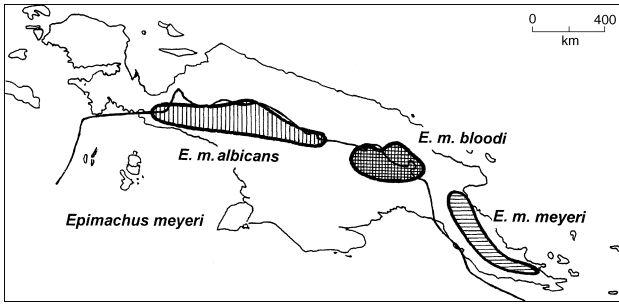


Figure 22 The distribution of *Epimachus meyeri*.

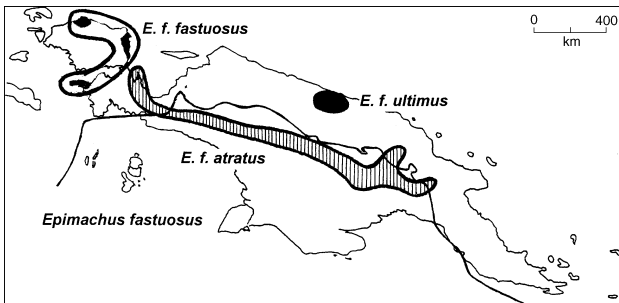


Figure 23 The distribution of *Epimachus fastuosus*.

Epimachus f. fastuosus. Tamrau, Arfak and Fakfak Mountains.

Epimachus f. atratus Rothschild and Hartert. Wandammen Peninsula and Weyland Mountains east to Okapa. As Frith & Beehler (1998) noted, the population from the Wandammen Peninsula (where *Pteridophora a. niedda* is endemic), might be expected to be intermediate between *atratus* and *fastuosus*. (Cracraft, 1992, noted that the differences between these two are not great and mainly concern darker underparts in *atratus*.) It would be good to re-examine the Wandammen population, as it is located on an interesting sliver terrane (Wandammen terrane) which includes a metamorphic core complex.

E. f. ultimus Diamond. Bewani and Torricelli Mountains, both on the Torricelli terrane.

The range of the red-eyed *E. fastuosus* overlaps with that of the blue-eyed *E. meyeri* on the main sector of distribution: Weyland Mountains – Goroka/Okapa. However, *E. fastuosus* has the additional localities: Vogelkop-Wandammen Peninsula, and Bewani-Torricelli Mountains (each with subspecies), whereas *E. meyeri* holds in addition the Papuan Peninsula with an endemic subspecies. *Epimachus fastuosus* thus masses in the north and west, *E. meyeri* in the southeast. These differences seem fundamental and are repeated in other groups. Where the *Epimachus* species are sympatric there is usually a narrow altitudinal difference with *E. meyeri* above *E. fastuosus*, but display stations have sometimes been recorded 'within throwing distance' of each other. It seems unlikely that minor differences in ecology or

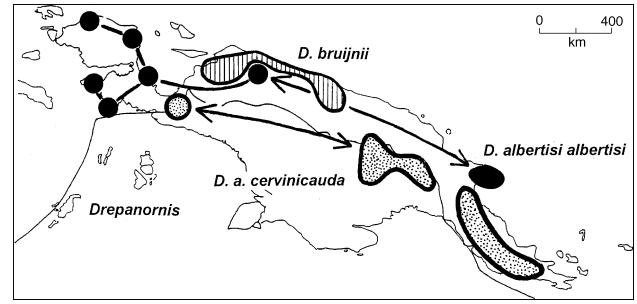


Figure 24 The distribution of *Drepanornis*.

means of dispersal could have caused the significant differences in biogeography.

Drepanornis Sclater. (Fig. 24). *Drepanornis a. albertisi* Sclater. Disjunct among the Vogelkop, the Foya Mountains and the Huon Peninsula. Frith & Beehler (1998) wrote that this range is 'peculiar, in the extreme' and 'distributionally odd'. Although they accepted the subspecies they suggested that it may be a taxonomic 'artefact' and that 'a future reviser may determine that *D. albertisi* is monotypic, with minor regional variation'. The degree of differentiation is less important in biogeographical studies than the spatial pattern of any variation. Whether the variations in *D. albertisi* represent subspecies or minor genetic entities below subspecies, the disjunct distributions of *D. a. albertisi* and *D. a. cervinicauda* form a simple pattern of parallel arcs with *D. bruijnii* (cf. *Parotia carolae*, Fig. 18) and there is no biogeographical reason to consider the range 'peculiar'. It is unusual in the Paradisaeidae, but even here similar disjunctions are seen in the 'curious' link between *Astrapia nigra* and *A. rothschildi* (above), the disjunctions in *Parotia* and *Paradisaea* (below), and the 500 km Wewak–Huon disjunction in *Ptiloris*.

Drepanornis a. cervinicauda (Sclater). Also disjunct, with a localized population at the Weyland Mountains (not at the Wissel Lakes) and the rest in PNG from Tari (cf. *Paradisaea rudolphi*, etc.) to the Wahgi Valley and Crater Mountain, both by the craton margin. The bird also occurs under the same subspecies name through the Papuan Peninsula. However, it is possibly significant that the Karimui population of *D. a. cervinicauda* is slightly darker on the back than the SE New Guinea birds (Diamond, 1972) and these populations are shown separately on the map (Fig. 24), with the craton margin running between them.

The disjunction in *D. a. cervinicauda* is very similar to that of the tree *Nothofagus grandis* Steen., known from the Vogelkop/Wissel Lakes, and disjunct in the PNG Highlands (Read & Hope, 1996) where it is one of the commonest species of *Nothofagus*. As van Steenis (1972) commented, its scarcity in west New Guinea is 'remarkable'.

Pachycephalopsis poliosoma (Sharpe) (Eopsaltriidae) also shows a very similar disjunction; Diamond (1972) wrote that 'It was initially surprising' (Rand & Gilliard, 1967) when Telefomin birds of *P. poliosoma*, separated from the Weyland Mountains by 500 km and the populations of

P. p. idenburgi Rand, *P. p. balim* Rand, and *P. p. approximans* Ogilvie-Grant, had to be assigned to *P. p. albigularis* (type from Weyland Mountains). It was 'even more surprising' to find that birds of the southern slopes of the Eastern Highlands, 800 km east of the Weyland mountains and on the opposite watershed, are also *P. p. albigularis*.

Drepanornis bruijnii Oustalet. (Fig. 24). Near the north coast, from Geelvink Bay to Vanimo. Lowland forest by rivers and on limestone hills, sea-level to 180 m. This species always occurs at lower altitudes than *D. albertsi* (600–2250 m) and the two are also geographically allopatric.

Cicinnurus respublica (Bonaparte) (*Diphyllodes respublica*) (Fig. 25). Western Papuan Islands: Waigeo and Batanta Islands but absent on nearby Salawati Island, like *Paradisaea rubra* (below). The first two islands make up an ophiolite terrane bearing strongly differentiated endemic flora and fauna.

Cicinnurus magnificus (Pennant) (*Diphyllodes magnificus*) (Fig. 25). *Cicinnurus m. magnificus*. Salawati Island, the Vogelkop and Wandammen Peninsula.

Cicinnurus m. chrysopterus (Elliot). Northern New Guinea, Japen Island. This appears to straddle the craton margin, with a distribution like that of *M. jobiensis* (above). However, populations from 'Weyland Mountains' and the southern slopes of the Oranje and Nassau Mountains, south of the craton margin, comprise *C. m. intermedius* Hartert, also recognized by Mayr (1962). As Cracraft (1992) noted, the two forms are apparently allopatric and genetic analysis may show that two distinct entities do exist.

Cicinnurus m. hunsteini (Meyer). PNG Highlands, Huon Peninsula, Papuan Peninsula (type from here: Astrolabe Mountains). Populations south of the Sepik-Wahgi divide are *C. m. hunsteini*, populations north of here are *C. m. chrysopterus* (cf. *Paradisaea minor* and *P. raggiana*), and there is a further possible break at the craton margin: although *C. m. extra* Iredale (type from Mount Hagen) has generally not been recognized, Diamond (1972) observed that Karimui birds are brighter and lighter red on the back than SE New Guinea birds (cf. *D. a. cervinicauda*). The two massings are shown in Fig. 25 separated by the craton margin.

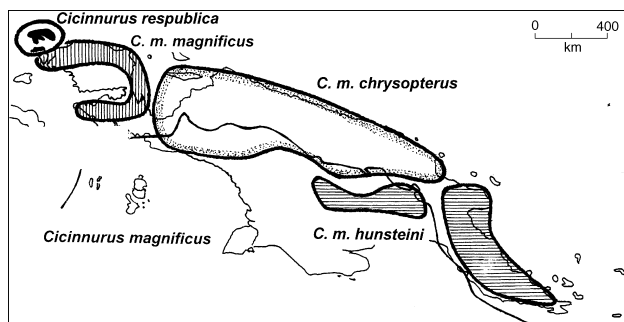


Figure 25 The distribution of *Cicinnurus respublica* and *C. magnificus*.

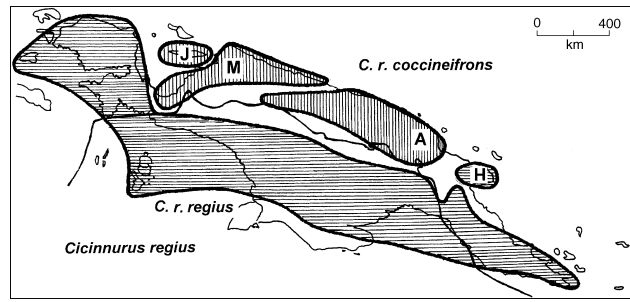


Figure 26 The distribution of *Cicinnurus regius*. Type localities of subspecies synonymized in Frith & Beehler (1998) as follows: J = Japen Island, M = Mamberamo River, A = Adelbert Mountains, H = Huon Peninsula.

Cicinnurus regius (Linnaeus) (Fig. 26). Widespread through New Guinea, and on Aru, Misool and Salawati Islands, but not on Waigeo, Batanta, Biak or the D'Entrecasteaux Islands. The subspecies have been the subject of debate with earlier authors recognizing six or more. Frith & Beehler (1998) (cf. Iredale, 1956) only accepted two, as mapped here.

Cicinnurus r. regius ranges widely through southern New Guinea, and also north of the craton boundary in the Vogelkop region and the Papuan Peninsula. The pattern is compatible with a proposed eastern origin of the Vogelkop (see below). *Cicinnurus r. gymnorhynchus* Stresemann from the Huon Peninsula was accepted by Mayr (1962) and Gilliard (1969) as distinct. Although Cracraft (1992) felt it was 'nearly 100% diagnosably distinct' from *C. r. regius*, he nevertheless placed it in synonymy under *C. r. regius* because of some overlap of characters, and was followed in this by Frith & Beehler (1998).

Cicinnurus r. coccineifrons Rothschild. All populations of *C. regius* on the accreted terranes of northern New Guinea, from Geelvink Bay to Madang, are placed with *coccineifrons* (type from Japen Island) by Frith & Beehler (1998). However, *coccineifrons*, *cryptorhynchus* Stresemann (lower Mamberamo R.) and *similis* Stresemann (Astrolabe Bay, etc.) were accepted as distinct by Mayr (1962), Gilliard (1969) and Cracraft (1992), with the last author noting the geographical replacement among the three.

A similar pattern to that of the *C. regius* subspecies is seen in the plant *Deplanchea* Vieill. (Bignoniaceae) (Avé, 1984) which has two New Guinea species, one on the Vogelkop, Aru Islands, southern and eastern New Guinea, and the other on the north coast at Jayapura and Wewak. Similarly, in *Lepidopetalum* Blume (Sapindaceae), *L. xylocarpum* Radlk. ranges in southern New Guinea from the Vogelkop to northern Milne Bay, surrounding the three other New Guinea species of the genus which all occur along the north coast (van Welzen *et al.*, 1992).

Semioptera wallacii Gray (Fig. 27). Northern Moluccas. This and *Lycocorax* are the only birds of paradise in the Moluccas. *Semioptera* (low hills to 1100 m) is not on Morotai or Obi and so its range is geographically and altitudinally enclosed by that of *Lycocorax*

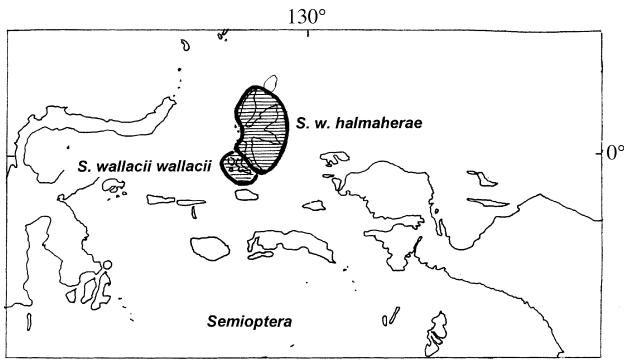


Figure 27 The distribution of *Semioptera*.

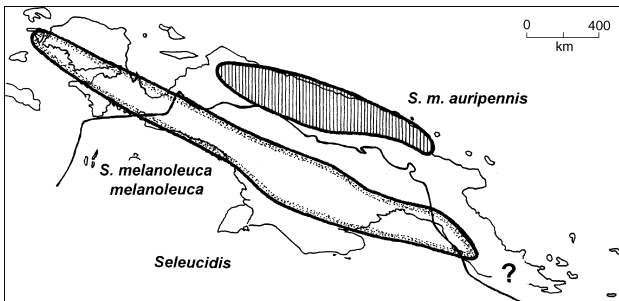


Figure 28 The distribution of *Seleucidis*.

(sea-level – 1600 m). *Lycocorax* is related by most authors to *Manucodia*, whereas *Semioptera* is usually placed with *Seleucidis*.

Semioptera w. wallacii. Bacan and Kasiruta Islands.

Semioptera w. halmaherae Salvadori. Halmahera.

Seleucidis melanoleuca (Daudin) (Fig. 28). Absent from the Huon Peninsula and most of the Papuan Peninsula, including much suitable habitat in the Ramu and Markham valleys. The genus favours periodically or permanently flooded swamp forest by rivers and may have been named for the inhabitants of Seleucia, the ancient city on the banks of the river Tigris (Frith & Beehler, 1998, give an alternative etymology).

Seleucidis m. melanoleuca. Vogelkop and southern New Guinea. Only two populations are mapped by Frith & Beehler (1998) outboard of the craton margin in the southeast (Lakekamu and lower Laloki Rivers), but the boundary is unclear and the species possibly extends to Milne Bay.

Seleucidis m. auripennis Schlüter. Central northern New Guinea: Mamberamo River to Madang, on the Gauttier and Torricelli terranes (cf. other central north coast taxa such as *Cicinnurus magnificus chrysopterus* and *C. r. coccineifrons*). Common in hill forest on uplifted karst at 180 m in Sandaun (West Sepik) Province.

Paradisaea Linnaeus (Figs 29–31). The species and subspecies divide up New Guinea amongst themselves, with three subspecies mainly south of the craton margin and ten in the north. This pattern of diversity in the north is

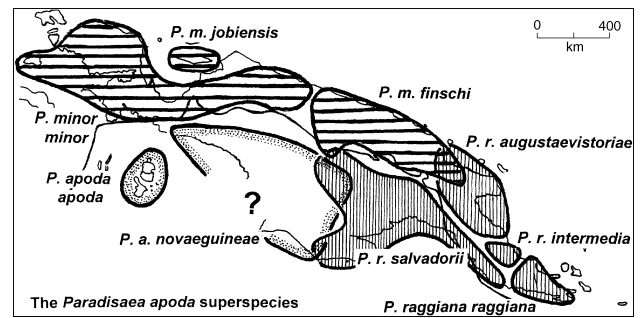


Figure 29 The distribution of the *Paradisaea apoda* superspecies.

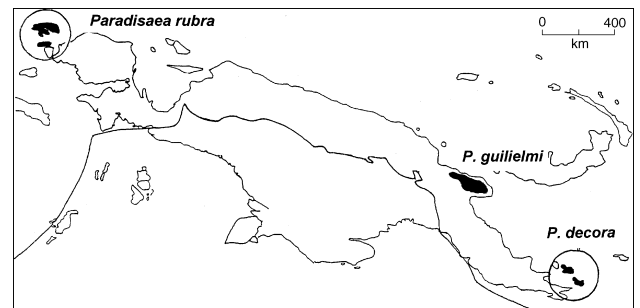


Figure 30 The distribution of the green-crowned, red-eyed members of *Paradisaea* subgen. *Paradisaea* (*P. rubra* and *P. guilielmi*), and also *P. decora*.

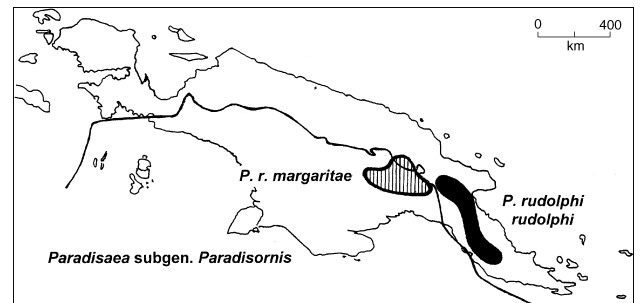


Figure 31 The distribution of *Paradisaea* subgen. *Paradisornis* (*P. rudolphi*).

accentuated if *P. raggiana* is included under the very similar *P. apoda*, as proposed by Mayr (1962). *Paradisaea minor* is also similar and in these three species the rectrices all become longer with age; in the other species only the central pair do. The three species occur more or less throughout New Guinea up to about 1550 m.

Paradisaea apoda Linnaeus. (Fig. 29). Irian Jaya south of the craton margin.

Paradisaea a. apoda. Aru Islands.

Paradisaea a. novaeguineae D'Albertis and Salvadori. Mimika River to Strickland River.

Paradisaea raggiana Sclater. PNG south of the craton margin, plus Huon and Papuan Peninsulas. Notably absent west of Madang, being replaced there by *P. minor*.

Paradisaea r. salvadorii Mayr and Rand. Southern PNG from the Irian Jaya border possibly to Cloudy Bay.

Paradisaea r. raggiana. Milne Bay, west to Cloudy Bay, but the boundary with *salvadorii*, if any, is unclear.

Paradisaea r. intermedia De Vis. Collingwood Bay to Mambare River (i.e. the lowlands of Oro Province, where other notable endemics include *Ornithoptera alexandrae* Rothschild, the world's largest butterfly).

Paradisaea r. augustaevictoriae Cabanis. Mambare River northwest to Madang, including the Watut and Huon regions.

Paradisaea minor Shaw. Northern New Guinea from Misool Island to Madang, absent from the Huon and Papuan Peninsulas. Records are all from north of the craton margin except around the Wissel Lakes.

Paradisaea m. minor. Misool Island to Jayapura. Apparently contacts *P. apoda* between Etna Bay and Mimika River.

Paradisaea m. jobiensis Rothschild. Japen (Jobi) Island.

Paradisaea m. finschi Meyer. East of the Irian Jaya/PNG border, to the upper Ramu River.

Paradisaea decora Salvin and Godman (Fig. 30). D'Entrecasteaux Archipelago (Fergusson and Normanby Islands only; notably absent from Goodenough). This was included with the last three species by Frith & Beehler (1998), although they admitted it was 'anomalous' here. It shares 'decomposed' flank plumes with the next two species, giving an outer arc of distribution: Vogelkop – Huon Peninsula – D'Entrecasteaux Archipelago.

The following two species range in the Western Papuan Islands and on the Huon Peninsula mountains, respectively, and are of special interest as they form a monophyletic pair in Frith & Beehler's (1998) strict consensus tree.

Paradisaea rubra Daudin. (Fig. 30). Waigeo and Batanta Islands, duplicating the distribution of *Cicinnurus respublica* on the ophiolite terrane. *Paradisaea rubra* is precisely vicariant with *P. minor*, which is on Misool and the mainland but not on Waigeo or Batanta.

Paradisaea guilielmi Cabanis. (Fig. 30). Huon Peninsula mountains. Geographically sympatric with *P. minor* in the west of its range and *P. raggiana* in the east, but occurring at higher altitude than both.

Frith & Beehler (1998) had *P. rubra* and *P. guilielmi* as 'inferred sister species', but neither they nor Gilliard (1969) give any characters linking them. Nevertheless, the two do seem related. In the males of both, but in no other species, the oil-green throat coloration extends above the eye to cover the front of the crown, and the iris is reddish-brown, not yellow. This last character also occurs in the females (Frith & Beehler, 1998, confirmed by C. Frith, pers. comm.; Gilliard, 1969 and Cooper & Forshaw, 1977, incorrectly illustrated and described the iris of *P. guilielmi* females as yellow). Frith (pers. comm.) added that *P. rubra* and *P. guilielmi* share a solid yellow wing marking similar in extent. In addition, from figures given in Frith and Beehler the tail wires (central rectrices) seem longer relative to body size in these two species. Gilliard (1969) also observed that in both species the flank plumes are 'decomposed', referring

to the 'wispy' effect (cf. Gilliard, 1969, Pl. 17) caused by the long, distant barbs being held at an angle greater than 45° or so to the rachis. This character also occurs in *P. decora* (above), from the D'Entrecasteaux Archipelago. (Gilliard also referred, tantalizingly, to 'similarities of structure' and display between *P. decora* and *P. rubra*, but did not elaborate). Finally, the outermost primaries in *P. rubra* and *P. guilielmi* have no emargination on the inner vane, unlike the other species. Whatever rank it warrants, the grouping of *P. rubra* and *P. guilielmi*, possibly related to *P. decora*, gives an interesting biogeographical affinity: Vogelkop – Huon (–?D'Entrecasteaux).

Frith & Beehler's (1998) only comment on the *P. rubra*–*P. guilielmi* pairing is that the two species are 'aberrant' (along with the quite different *P. rudolphi*). In fact Frith & Beehler (1998) do not really seem to accept the pairing as shown in their cladogram: they do not recognize *P. rudolphi* as a separate genus 'mainly because this would force us to treat the less aberrant *P. rubra* and *P. guilielmi* as distinct genera', but in fact they would only need a single genus for these two as they are sister species. Likewise, in the species treatments under *P. guilielmi* Frith & Beehler (1998) wrote only that this is, 'like *P. rubra*, an aberrant sister form to the main *Paradisaea* clade'. This interpretation fits with their theory of invasion of the offshore islands and coastal ranges from the central ranges (cf. Diamond, 1972), but it is not quite correct according to their cladogram, in which *P. rubra* and *P. guilielmi* together form the sister group to the rest of *Paradisaea* subgen. *Paradisaea*. Their dispersal theory would predict the two outlying species to be separately related to the central group of species, as implied in their comments. The affinity of the two species is inexplicable under the dispersal theory, which is probably why it has been neglected. However, the distribution is easily compatible with an accreted terrane model of New Guinea biogeography, or indeed any model that accepts geological change such as large-scale lateral and vertical movements as relevant to biological distribution.

It is especially noteworthy that practically the same disjunction (Western Papuan Islands–Huon Peninsula) seen in *Paradisaea* also occurs in *A. nigra* (Vogelkop) – *A. rothschildi* (Huon Peninsula). For these two species Frith & Beehler (1998) suggested that the 'curious' plumage similarities may represent symplesiomorphies. In addition, *P. sefilata* of the Vogelkop may be sister to *P. wabnesi* of the Huon (see above).

In a similar example, *Melipotés* (Meliphagidae) comprises three species: the black-breasted *M. gymnops* Sclater (Arfak, Tamrau and Wandammen Mountains) and *M. ater* Rothschild & Hartert (Huon Peninsula mountains), separated by *M. fumigatus* Meyer with a slaty lower breast (Rand & Gilliard, 1967). Likewise in the three subspecies of *Amalocichla incerta* Salvadori (Eopsaltriidae), the Arfak Mountains race (nominat) and *A. i. brevicauda* ('eastern New Guinea – Sepik, Sarawaged, etc.:', Rand & Gilliard, 1967) are 'doubtfully distinct', while *A. i. olivascentior* Hartert of Wandammen, Weyland and Snow Mountains is quite different.

A similar disjunction is also seen in *Drepanornis a. albertisi*: Vogelkop, Foya Mountains, and Huon Peninsula (Fig. 24). As noted above, the distribution has been seen as 'peculiar in the extreme... it may be an [taxonomic] artefact' (Frith & Beehler, 1998). Similarly, in the black parotias: Vogelkop–Huon or Vogelkop–Strickland, the disjunct forms are 'certainly' sister taxa, but the mode of their differentiation is 'unclear' (Frith & Beehler, 1998). The long-tailed astrapias have a very similar pattern. All these disjunctions would be accounted for by the proposed eastern origin of the Vogelkop (Pigram & Panggabean, 1984; de Boer, 1995a, b; de Boer & Duffels, 1996a, b).

Many other animal and plant taxa also show the Vogelkop–Huon disjunction (Heads, 2001b, listed fourteen supraspecific plant taxa, six plant species, and two spider species).

Van Welzen (1997) analysed 961 endemic New Guinea plant species with respect to the accretion history of the terranes and concluded that most plant distribution patterns can be correlated with the geological history of the island. However, he felt that two cannot: species that are widespread on both the craton and the accreted terranes (although these may have already been widespread before terrane accretion), and the disjunct east–west distributions found in fifteen species. Van Welzen (1997) illustrated this pattern with a map of *Dimorphanthera amblyornidis* (Becc.) F.v.M. (Ericaceae), disjunct between the Vogelkop, and the Huon and Papuan Peninsulas, very like the disjunctions in *Astrapia* and *Paradisaea*. Van Welzen concluded that 'Perhaps the species delimitation has to be re-evaluated' for the disjunct plants, but as indicated, it is a common pattern in different groups and is also compatible with geology as the terranes have all moved, some great distances.

Paradisaea rudolphi (Finsch) (Fig. 31). This species, the blue bird of paradise, is usually treated either as a taxonomically isolated subgenus of *Paradisaea* (as in Frith & Beehler, 1998) or as a genus (*Paradisornis* Meyer). It occurs only in inland areas, at higher altitude than the other *Paradisaea* species.

Paradisaea r. margaritae Mayr and Gilliard. Doma Peaks, Giluwe, Wabag mountains, Sepik-Wahgi Divide, Bismarck Range (middle Jimi Valley only), Kubor Mountains, south-east to Karimui.

Paradisaea r. rudolphi. Kainantu and Okapa south-eastwards to Mount Kenive. Diamond (1972) recognized Karimui specimens as *margaritae*, while populations east of here at Awande (near Okapa) were *rudolphi*. This break corresponds precisely with the craton margin, and similar distributions are known in many plant and animal taxa (Heads, 2001b). For example, populations of *Coracina caeruleogrisea* Gray, Campephagidae, from Awande-Okasa (near Okapa) are nearer *C. c. adamsoni* Mayr and Rand of eastern PNG (Astrolabe Bay and Hall Sound east), while birds from Karimui belong with the western *C. c. strenua* (Schlegel) from further west (Diamond, 1972).

In the Papuan Peninsula *P. r. rudolphi* is present on the southern slopes of the mountains, but rare or absent on the

northern slopes (Bowutu terrane), resembling a similar pattern in the subspecies of *Parotia lawesii*.

Cnemophilus macgregorii and *P. rudolphi* are 'equally anomalous' (Frith & Beehler, 1998) in that both are widespread on the cordillera but do not extend to its western limit at the Weyland Mountains. Frith and Beehler wrote that 'An explanation for these truncated ranges is not readily forthcoming...' For birds of paradise and other fauna the Weyland Mountains/Wissel Lakes region is also a centre of endemism (*A. s. splendidissima*, *P. c. carolae*) and wide disjunction (*D. albertisi cervinicauda*) – such correlated presence, absence and disjunction is a normal aspect of biogeographical nodes (Craw *et al.*, 1999).

Frith & Beehler (1998) wrote that the western limit of *P. rudolphi* at the Doma Peaks by Tari is 'strangely truncated', and 'an anomaly – its absence from Irian Jaya is a 'biogeographical mystery'. Conversely, Flannery (1995) observed that several mammal taxa ranging from the west (Wissel Lakes) into PNG are 'mysteriously truncated' at the Strickland River, close to Doma Peaks where *P. rudolphi* is 'strangely truncated' coming from the east. In fact, highlands taxa often break off range near Tari, either at the Doma Peaks (Mounts Ambua, Ne and Kerewa) or the Karius Range. Examples include:

Fishes (from Allen, 1991)

Craterocephalus nouhuysi (Weber): east to the upper Strickland/Karius Range,

Hephaestus habbemai (Weber): east to the upper Strickland/Karius Range,

Glossamia trifasciata (Weber): east to the upper Strickland/Karius Range,

Mogurnda cingulata Allen and Hoese: east to the upper Strickland/Karius Range,

Glossogobius concavifrons (Ramsay and Ogilby): east to the upper Strickland/Karius Range,

Glossogobius sp. 6: west to the Tari Valley.

Birds of paradise:

Astrapia mayeri: west to the Karius Range and Doma Peaks,

Drepanornis albertisi cervinicauda: west to the Karius range; disjunct at the Weyland Mountains,

Epimachus meyeri bloodi: west to Tari and Doma Peaks.

Mammals (from Flannery, 1995):

Xenuromys Tate and Archbold: east to the Doma Peaks; also disjunct at Milne Bay,

Pogonomelomys bruijni (Peters and Doria): east to the Doma Peaks,

Crossomys Thomas: west to the Karius Range,

Leptomys Thomas: west to Doma Peaks and lowermost Fly river; also disjunct in the Vogelkop and 'inexplicably absent' from most of Irian Jaya,

Melomys gracilis Thomas: west to the Karius Range.

Ferns (from Parris, 1983):

Grammitis tuberculata Parris: Mount Hagen and Doma Peaks only,

Grammitis hirtiformis (Rosenst.) Copel. west to Tari,

Grammitis clavipila Parris: west to Tari,

Grammitis intromissa Christ (Parris): west to Tari.

Gymnosperms:

Araucaria hunsteinii K. Schumann: west to Tagari valley, between Tari and the Karius Range (Gray, 1973).

Angiosperms:

Parsonsia sanguinea var. *vinkii* Middleton: Tari to Mount Giluwe (Middleton, 1997),

Olearia lanata Koster: Doma Peaks and Mount Hagen (van Royen, 1983),

Senecio kandambren van Royen: west to Doma Peaks (van Royen, 1983).

The western limit of *P. rudolphi* and its absence from Irian Jaya is striking in itself, but the break at Doma Peaks is no more unusual or mysterious than many of the other biogeographical nodes shown in many birds of paradise and other taxa, for example the Vogelkop, the Wissel Lakes/Weyland Mountains region, the Huon Peninsula, the Papuan Peninsula and the D'Entrecasteaux Archipelago. It is interesting that the Karius Range and Mount Bosavi also mark the western limit of Late Cenozoic volcanism in PNG, and travelling west this is not seen again until the Weyland Mountains (Milsom, 1985). Within New Guinea many Australian groups, such as Paradiisadidae and epacridoid Ericaceae, are more diverse in PNG than Irian Jaya, whereas Asian groups like *Rhododendron* (Ericaceae) are more diverse in Irian Jaya.

DISCUSSION

All the smaller islands on which birds of paradise occur lie within the New Guinea orogen. Islands that lie outside the orogen, such as New Britain and New Ireland, do not have birds of paradise (or bowerbirds), despite being close to New Guinea and having suitable habitat.

Another tectonic boundary, the craton margin, also serves as a boundary of some sort in most species of birds of paradise. It is also a generic boundary in *Pteridophora* which is restricted to the craton (except on the Bismarck Range) and absent from the Vogelkop, Huon and Papuan Peninsulas, just like the marsupial *Neophascogale* Stein (Flannery, 1995). The Bismarck Range (Jimi and Benabena terranes) just north of the craton margin has outlying populations of seven taxa otherwise found only on the craton (*Pteridophora*, *Cnemophilus lorae*, *C. macgregorii*, *Epimachus m. bloodi*, *E. fastuosus*, *Paradigalla brevicauda*, and *Paradisaea rudolphi margaritae*). This could be the result of local range expansion across the terrane suture, or there may be a purely tectonic explanation. Pigram & Davies (1987) indicated that the Jimi and Bena Bena terranes ('stitched' together by the batholith which forms Mount Wilhelm) are probably displaced portions of the northern edge of the craton. The amount of displacement, if any, has not been determined. The Mount Wilhelm batholith, whether or not regarded as a separate terrane (Pigram & Davies, 1987, map it as part of the Australian craton) is separated from the craton by the Bismarck Fault Zone and is biogeographically very distinctive. If the Jimi and Benabena terranes are included with the craton, many birds of paradise species show even closer correlation with the tectonic boundary. In addition, the

unresolved variation in *Cicinnurus m. chrysopterus*, *C. m. hunsteini*, and *Epimachus fastuosus atratus* noted above may also follow the craton margin.

Ophiolite endemism

Endemism on ophiolite terranes is a good example of biogeographical and tectonic correlation. Ultrabasic or ultramafic rocks, high in magnesium and iron, usually occur as part of ophiolite suites which are sections of oceanic crust and upper mantle that have been uplifted and obducted. This has occurred at plate margins during island-arc collision, and accreted arc terranes and orogenic belts frequently include ophiolites. The New Guinea orogen is characterized by abundant outcrops of ultramafic rocks. In the Western Papuan Islands, Waigeo and Batanta, with nearby Kofiau but not Salawati, comprise an ophiolite complex, the Waigeo terrane (Pigram & Davies, 1987). Waigeo and Batanta are also distinguished by the presence of striking local endemics such as *Cicinnurus respublica* (Fig. 25) and *Paradisaea rubra* (Fig. 29). Similarly, *Melidora* Lesson (Alcedinidae) is endemic to Waigeo, Misool, Batanta and Japen Islands, but is not on Salawati. In fact the straits between Salawati and Batanta Islands are less than 2 miles wide but 'have prevented the crossing' of seventeen species of Salawati birds to Batanta, and five from Batanta to Salawati (Mayr, 1940).

Another ophiolite is the Torricelli terrane with the strangely isolated endemic *Epimachus fastuosus ultimus* (Fig. 23).

Other ophiolite terranes in New Guinea include the Rouffaer terrane (Doorman Mountains) with *P. carolae chalcothorax* endemic, and the Schrader-Marum terranes (northern slopes of the Bismarck Range above the Ramu River) with the possibly related *P. c. chrysenia*.

The largest ultramafic outcrop in New Guinea is the Papuan Ultramafic Belt (Bowutu terrane) (400 × 40 km) which forms a series of lesser mountain ranges north of the main ranges of the Papuan Peninsula. Its emplacement must have been a major tectonic event. *Parotia lauesii helenae* is found largely on the Bowutu terrane and detailed mapping is needed.

Botanists have long recognized that ophiolites in northern New Guinea were strong foci of endemism but usually assumed that this was the result of edaphic rather than historical factors. In a very interesting paper, Polhemus (1996) pointed out that although many animals show similar patterns zoologists have been slow to realize that this correlation greatly weakens the edaphic hypothesis. Instead, Polhemus (1996) regarded the ophiolites as biogeographically significant because they are arc terrane markers. The most mature phase of arc collision is seen in old arc fragments now deeply embedded in modern 'mainlands', such as the mountains of New Guinea, New Zealand and the Philippines. The remnants of these Mesozoic arc systems have been crushed between even older arcs or continents but the disjunct distributions of living taxa are the biological legacy of the ancient arcs.

Means of dispersal

Initially it seemed unlikely that bird populations would remain more or less *in situ* for as long as indicated here. However, many ornithologists have questioned the apparent significance of birds' means of dispersal in establishing their distributions, as the following quotations indicate:

Birds offer us one of the best means of determining the law of distribution; for though at first sight it would appear that the watery boundaries which keep out the land quadrupeds could be easily passed over by birds, yet practically it is not so... (Wallace, 1869).

To the person who is impressed by the bird's potential mobility, the occurrence of the same or representative species at widely separated localities is simply a matter of flight from one station to the other... But the avian geographer is not so easily answered. He knows that most birds are closely confined to their own ranges... (Chapman, 1926).

Most species of birds, especially on tropical islands, are extraordinarily sedentary (Mayr, 1940).

That birds can fly across barriers is one of those apparently simple facts that are not simple (Darlington, 1957).

Despite powers of dispersal through the air, we have the paradox that ornithologists constantly stress the value of birds as objects of distributional and dispersal studies derived from the fact that known cases of such dispersal are so rare (Deignan, 1963).

It has been shown many times that apparent 'means of dispersal' invoked by some as an explanation of distribution do not correlate with actual distributions. For example, studying the eighty-three species of swifts (Apodidae), Brooke (1970) observed that these are among the strongest-flying land-birds and are usually gregarious. He concluded: 'One might suppose that such birds would be exempt from the standard zoogeographical patterns, but this is not borne out by an examination of their breeding distribution. In fact, standard zoogeographical patterns emerge...'

Chronology

Subspecies have often been regarded as the result of Pleistocene events much younger than the geological events discussed above. The Pleistocene ice ages are often invoked as a major determinant of diversity in tropical rain forest.

However, there are many problems with this scenario. For example, a long pollen record from the Amazon rain forest showed evidence of continuous rain forest for 40,000 years – it was not fragmented during the glacial maxima (Colinvaux *et al.*, 1996). DNA differences between sister species of North American birds indicate a speciation history over the last 5 Myr, implying a history ten times longer than that predicted by the Late Pleistocene origins model (Klicka & Zink, 1997). Similarly, in the *Pseudomyrmex viduus* (F. Smith) group of ants, centred in the Amazon basin, the

geographical ranges of most species do not coincide with the proposed Pleistocene forest refugia. Phylogeny, biogeography and host plant specificity indicates that much of the diversification took place in the Tertiary rather than during the Pleistocene ice ages (Ward, 1999).

Likewise, it now seems that many Andean birds and mammals differentiated well before the Pleistocene, and probably even before the uplift of the Andes. Most botanists and zoologists previously thought that species in the Andes evolved at most a few million years ago, but DNA evidence from tanagers, antbirds, brushfinches and others shows lineages dating back 4–10 Myr, again, an order of magnitude older than previous estimates (conference papers presented by J. Bates, J. Lundberg and S. Hackett, reported in Moffat, 1996).

These data are compatible with the terrane tectonics explanation correlations suggested here for the Paradisaeidae. Based on DNA hybridization, Sibley & Ahlquist (1985) calculated a date of 18–20 Ma for the split between *Manucodia* and the other members of subfam. Paradisaeinae, which is compatible with Mayr's (1953) proposal that the family was isolated in the New Guinea region in the early Tertiary. Christidis & Schodde (1992), using allozymes, found that conventional calibrations implied many genera of birds of paradise diverged within the last 2 Myr, much more recently than suggested in this paper. Using mitochondrial DNA and conventional calibrations Nunn & Cracraft (1996) dated divergences between congeneric paradisaeid species at 1–4 Ma. There is clearly considerable disagreement in the dates, mainly because of difficulties with calibration. Current methods of calibrating molecular clocks and applications of clocks in biogeography have been critically reviewed by Craw (in press). Cracraft & Feinstein (2000) emphasized the existence of variable evolutionary rates in the group, but suggested that the cnemophilines could be an Eocene group.

Hall (1998, 2001), Holloway (1998) and Holloway & Hall (1998) have recently contributed detailed accounts of biogeography and terrane tectonics in the SE Asia/SW Pacific region, along with general discussion on the synthesis of these subjects.

In Hall's (1998, 2001) model of New Guinea, the Papuan and Sepik ophiolites were emplaced in Palaeocene/early Eocene, and subsequently the north New Guinea arc terranes originated as the South Caroline Arc, about 4000 km north of New Guinea in the central Pacific. Hall's reconstruction for 30 Ma shows the east Philippines, northern Moluccas and north New Guinea terranes (with New Britain) forming a relatively continuous arc, running parallel with and 1–2000 km north of mainland New Guinea, before moving south and west to converge on New Guinea and eventually dock. After docking they continued to be translated west in the major left-lateral shear zone.

This reconstruction accounts for the close biogeographical connections among these regions, and the great differences between the northern and southern Moluccas, and between New Britain and mainland New Guinea.

Holloway & Hall (1998) noted that while de Boer (1995a) reviewed geological evidence for a more easterly position of the Vogelkop Peninsula, near the Solomons, other patterns (*Myrmephytum* Becc. – Rubiaceae, *Aporosa* Blume – Euphorbiaceae) are consistent with a westerly position for the Vogelkop (cf. Hall, 1998, 2001). Holloway and Hall concluded that ‘An alternative most parsimonious hypothesis might be that dispersal occurred...’ However, before bringing in dispersal, it should be acknowledged that the Vogelkop is a geological and biogeographical composite, and even within the northern Vogelkop, the Arfak–Nettoti terranes have biogeographical affinities quite different from those of the Tamrau–Tohkiri terranes (as, for example, in *Diplycosia* spp., Ericaceae, Sleumer, 1967).

Hall (2001) suggested that biogeographers could contribute to testing tectonic models ‘by, for example, mapping distributions of fossil plants and interpreting their environment.’ However, both of these approaches are probably of rather limited value; Hall himself noted that the fossil record is poor or non-existent for most plants and animals and this is actually true for the vast majority. Mapping the living organisms, especially the diverse groups, is a more important and much bigger project.

Holloway & Hall (1998) wrote that ‘The reluctance of some biogeographers to consider the palaeontological data is something that geologists find difficult to understand.’ Much palaeontology, unlike tectonics, is based on dispersalist assumptions, but panbiogeographical studies make a point of integrating data from fossils (when available) and extant taxa (e.g. Heads, 1989: Fig. 16d showing fossil and extant brachiopod taxa; Fig. 19 comparing Mesozoic molluscs and the plant *Coriaria* L., Heads, 1990: Fig. 34 showing living and fossil *Drapetes* Lam.). What riles palaeontologists is that panbiogeography does not privilege the fossil data to the great extent that the centre of origin theory does, with the oldest fossil being the ancestor of its taxon, at the place and time of origin of the taxon. In panbiogeography, fossil records are treated in the same way as living records. Fossil data can provide essential evidence for morphogenetic studies but are almost always too scattered to be of much use for biogeographical analysis. Fossil data on birds of paradise, or any birds for that matter, contribute practically nothing to analysing relationships among the regions of New Guinea. Despite this, Holloway & Hall (1998) claimed that ‘Hypotheses of strict terrane fidelity by biotas are not well-supported by fossil evidence...’, which is probably true, but only because there is hardly any fossil evidence of these groups to begin with.

Hall (1998) argued that ‘DNA studies offer one way of determining a time-scale for biological development’, but this is probably one of the few things it does not offer. Likewise, modern molecular phylogeography (Avice, 2000) often claims to be testing between dispersal and vicariance. However, the molecular divergences are nearly always calibrated using a literal reading of the fossil record, that is, a group whose oldest fossil is x years old, is assumed to actually be x years old. As indicated, this is a key procedure of the dispersalist school, so a study based on it can hardly be considered an unbiased test of dispersal vs. vicariance.

Occasionally authors have calibrated the sequence data using a simple equation of biogeography and geology. Trans-Tasman Sea disjuncts would be taken to be the same age as the opening of the Tasman. This approach is better but still simplistic, as trans-Tasman taxa could be much older than the formation of the ocean basin.

Cladistics was an important attempt to get away from basing analysis on a concept of absolute degree of difference between taxa. But now, as before cladistics, degree of difference (numbers of base pairs difference, etc.) is again assumed to be meaningful, especially with respect to time. It seems that the staggering technical advances made in molecular biology over the last 10 years have raced far ahead of conceptual developments in the subject.

The critique of ‘dispersal’ is, of course, counter-intuitive: organisms move – surely have they achieved their distribution by this movement? Holloway & Hall (1998) wrote that ‘To a geologist the dismissal of the role of dispersal seems bizarre’. It probably also seems bizarre to the layman (as do fields like quantum mechanics), but is based on the simple observation that distribution of taxa and their means of dispersal show no correlation. The same distribution is held by many taxa with many different means of dispersal, while taxa with similar means of dispersal have quite different distributions.

As in New Guinea, parallel arc distribution patterns in the endemic New Zealand biota can be related to tectonic arc structures in those islands (Craw, 1982; Heads, 1989). However, Holloway (1998) and Holloway & Hall (1998) suggested that the same parallel arc distributions occur in plants introduced by Europeans, in response to climate, and cited the maps in Wilson *et al.* (1992) as evidence for this. This supposed similarity between distributions of indigenous plant and introduced ones is used by Holloway & Hall (1998) as evidence to support their conclusion of ‘absence of widespread terrane fidelity’.

The distributions of the introduced species do indeed reflect the west–east decrease in rainfall in the South Island and the hot, sunny climate of the central regions, as indicated by Wilson *et al.* (1992). However, they do not, despite Holloway (1998) and Holloway & Hall’s (1998) claim, have similar distributions to the highly complex but repeated patterns of the local and regional endemics. The lack of correlation between the endemic distributions and present climate is precisely why these distributions (Heads & Patrick, in press) are so interesting. The lack of correlation is well-known to New Zealand ecologists (references in Heads, 1997) who for many years have invoked different kinds of historical factors to explain the distributions.

Although Holloway & Hall (1998) suggested that panbiogeographers ‘postulate a high degree of terrane fidelity by biota’, the correlations of a great number of New Zealand and New Guinea endemics with terranes is more of a matter of observation than hypothesis. Indeed, Holloway & Hall (1998) concluded: ‘Some degree of terrane fidelity is suggested... for groups such as cicadas (de Boer, 1995a), some plant taxa (Ridder-Numan, 1998; on Borneo) and water bugs (Polhemus & Polhemus, 1998), but it might be dangerous to extrapolate this to a generality.’ It would

certainly be dangerous for dispersal theory. Novotny & Missa (2000) ascribed high beta diversity in New Guinea insects to high topographic diversity and the island's complex geological history whereby 'several tectonic blocks that now compose the island of New Guinea remain distinct centres of endemism'. Birds of paradise and bowerbirds (Heads, 2001b, c) are two more groups which illustrate a high degree of geological control.

CONCLUSIONS

Integrations of biogeography and terrane tectonics in New Zealand (Craw, 1982; Heads, 1989, 1997, 1998) gave interesting results, and biologists have recently begun to use accreted terranes in explaining distributions of New Guinea plants (van Welzen *et al.*, 1992; Vermeulen, 1993; Turner, 1995; van Welzen, 1997; Heads, 1999) and invertebrates (de Boer, 1995a; de Boer & Duffels, 1996a, b; Polhemus, 1996). For higher vertebrates, Michaux (1994) analysed the distributions of mammals and birds of paradise with respect to the tectonic regions: Australia–New Guinea foreland, inner Melanesian rift and outer Melanesian rift, and indicated how the biological 'generalized tracks' correlate with these regions and accretion tectonics.

Discussing mammals, Flannery (1995) wrote that 'tectonic movements have been the prime cause of many of the zoogeographical patterns that we see in New Guinea today.' The northern coastal ranges include 'the most peculiar and inexplicable mammal distributions found anywhere in New Guinea.' The range of the marsupial *Pseudochirops albertisii* (Peters) (Arfak Mountains, Japen Island, Weyland, Cyclops, Bewani and Torricelli Mountains) is 'quite enigmatic... Without massive tectonic movements its distribution would be inexplicable, as its present distribution is disrupted by ocean (Geelvink Bay), massive rivers (e.g. the Mamberamo) and swamp (the Meervlakte). Not even the most extreme late Pleistocene climatic change could account for its present distribution. Yet the tectonic changes necessary to produce its distribution are so massive... as to be breathtaking...' This disjunction parallels the Vogelkop–Huon disjunctions in *Astrapia* and *Paradisaea*.

Disjunctions in Malesian vascular plants were discussed by Baker *et al.* (1998) who concluded that these 'probably require a tectonic explanation'. Likewise, Tan (1998) suggested that disjunctions in Malesian mosses 'can now be better explained by relating them to local plate tectonic movements than by the long-distance dispersal hypothesis.'

Recent ideas on the structure of the Andes are similar to those suggested here for the New Guinea orogen: the tectonic structure of the Andes is more complex than previously thought, and Flynn (J. Flynn, quoted in Moffat, 1996) cited the importance of lateral, as well as vertical, movement on faults. Flynn emphasized that 'The Andes are not homogeneous, biologically or geologically... There is no such thing as "the Andes"' (cf. Katinas *et al.*, 1999). In a similar way, neither New Guinea nor its avifauna are a single entity but are the result of many separate terranes being welded together and onto the Australian craton.

Birds of paradise are sedentary forest dwellers with small home ranges and many are fairly tolerant of disturbance, occurring in forest edge, secondary forest and around gardens. Given this ecology, it is suggested that many of the populations that have been caught in the dramatic geological movements (horizontal and vertical) of different parts of New Guinea have survived more or less *in situ*. This has led to fragmentation and juxtaposition of ranges and has also effected the altitudinal range of the taxa. Most of the accreted terranes, such as Arfak, Tamrau, Wandammen, Weyland, Finisterre (Huon Peninsula), D'Entrecasteaux and, especially, the ophiolite terranes, mark important nodes: mutual boundaries, and centres of endemism, absence and disjunction.

This reassessment of the relationship between tectonics and biology in New Guinea indicates the importance of autochthonous evolution in New Guinea, which appears to be an important biogeographical centre in its own right rather than a mere receptacle for colonists from Indonesia and Australia. This study shows that there is at least a *prima facie* case for the importance of terrane tectonics in bringing about biological distribution, and it is probably unrealistic to discuss New Guinea biogeography without referring to the relevant terranes and their individual histories.

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BIOSKETCH

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