Birds of paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae): regional levels of biodiversity and terrane tectonics in New Guinea

Michael Heads*
Science Faculty, University of Goroka, PO Box 1078 Goroka, Papua New Guinea
(Accepted 28 November 2000)

Abstract
Most species of birds of paradise (Paradisaeidae) are endemic in the rainforests of New Guinea. There are also a few species in the northern Moluccas and in northern Australia. Bowerbirds (Ptilonorhynchidae) are centred in New Guinea but are more widespread in Australia. The two families have often been regarded as sister groups, but in recent studies Paradisaeidae appear as sister to Corvidae, a worldwide family which is notably depauperate in New Guinea and Australia. This indicates vicariance of a worldwide ancestor, rather than invasion of New Guinea. Other families in the superfamily Corvoidea include Ptilonorhynchidae (basal), Campephagidae (Africa to New Guinea and Fiji), and Cracticidae (Australia to New Guinea). Biodiversity levels in Paradisaeidae and Ptilonorhynchidae were assessed from literature records by counting numbers of species in grid cells 1° latitude by 1° longitude. Birds of paradise are equally diverse in the Mendi square and the Mount Hagen–Wahgi Valley–Jimi Valley square. Bowerbirds are most diverse in the Mount Hagen–Wahgi Valley–Jimi Valley square. This area lies on one of the main tectonic boundaries in New Guinea, the former margin of the Australian craton, and is geologically distinctive in having several diverse accreted terranes juxtaposed there, including an ophiolite complex. It also includes the western slopes of Mount Wilhelm, one of the highest mountains in the New Guinea orogen. Paradisaeidae have secondary centres of diversity in the southern part of the New Guinea orogen (south of the former craton margin), while Ptilonorhynchidae have secondary centres north of the craton margin on the accreted terranes, and also in eastern Australia. Within New Guinea the two distributions correlate closely with the geological interpretation of the orogen as comprising southern (craton) and northern (accreted terrane) components. Within Australia, Paradisaeidae have two species per degree square in northern Cape York Peninsula (on the old Australian craton), and only one elsewhere in eastern Australia, whereas Ptilonorhynchidae have a clear Australian massing further south in Queensland, on the accreted terranes of the Tasman orogen.

Key words: vicariance, biogeography, rainforest, evolution, Pacific, tropics, conservation, Paradisaeidae, Ptilonorhynchidae

INTRODUCTION
The rainforests on the island of New Guinea are inhabited by the birds of paradise, whose surreal beauty, bordering on the bizarre, has fascinated the local people since time immemorial and Europe since 1522. In that year, Magellan’s men returned from the first trip around the world and presented the first specimens seen in the west to the King of Spain. By 1600, skins were appearing regularly on the international market, but it was not until 1824 that the first European, the French naturalist Lesson, saw the birds in the wild.

Birds of paradise are one of the most speciose bird groups in a region already known for its very high diversity, and the family has served as a critical case-study in global syntheses of evolution, ecology and biogeography (Wallace, 1869; Mayr, 1942; Croizat, 1958). Frith & Beehler’s (1998) magnificent monograph provides the information needed to reassess many aspects of the birds’ ecology and evolution.

The birds of paradise have 42 species, with 38 in New Guinea, two of these plus two endemics in Australia, and two endemics in the Moluccas. The bowerbirds (Ptilonorhynchidae) are another New Guinea-centred group; there are 18 species, with nine in New Guinea, seven in Australia, and two in both. The two families have often been regarded as sister taxa, but not in modern studies. They have very different anatomy, and
typical birds of paradise, but not bowerbirds, use their powerful, dextrous feet for feeding in a typically crow-like way and regurgitate food to their offspring.

The New Guinea avifauna is characterized by the near-endemic families Paradisaeidae and Casuarinidae (Ratites), a large number of striking endemic genera (Mayr, 1953) and a high species diversity (708 species, Beehler, Pratt & Zimmerman, 1986). Most of the species occur on both halves of the island: the Indonesian province of Irian Jaya in the west, and the mainland of Papua New Guinea (PNG) in the east. On the PNG mainland, there are 15 endemic bird species, and of these more than half are either birds of paradise (seven species) or bowerbirds (two species) (Beehler, 1993). Together these families form the most distinctive group of the mainland fauna, although they are absent from the northern PNG islands. Virtually any forested site on mainland New Guinea supports no fewer than five birds of paradise and a study site on Mount Misim, above Bulolo, had nine resident species and one vagrant. As Frith & Beehler (1998) concluded, New Guinea ‘appears to be an evolutionary engine for biological diversity’.

**Taxonomy of Paradisaeidae**

The ornamental feathers of adult male birds of paradise are more diverse than in any other family, and a large number of genera have been described – at first glance these birds suggest different families.

The enigmatic alpine *Macgregoria* De Vis was included in Cnemophilinae by Bock (1963), but in Paradisaeinae by Mayr (1962) and most subsequent authors. However, Frith & Beehler (1998) noted that it is ‘very much the odd genus’ in subfamily Paradisaeinae. Iredale (1956) observed live birds of *Macgregoria* and wrote that it is ‘even more out of place [in Paradisaeidae] than *Paradigalla* Lesson’ and ‘suggests a Honey-sucker as its nearest relation’. Cracraft & Feinstein (2000) supported this idea (without citing Iredale, 1956) and placed *Macgregoria* next to *Melipotes*, unusual in the Meliphagidae as it is frugivorous, like *Macgregoria*.

*Melampitta lugubris* Schlegel of the New Guinea mountains (Arfak Mountains to at least the Huon Peninsula and Wharton Range) has been proposed as the basal member (Sibley & Ahlquist, 1987) or a ‘closely-related sister form’ (Frith & Beehler, 1998) of the Paradisaeidae. It has usually been treated in Timaliidae or Orthonychidae, and is not discussed here further.

The Paradisaeidae comprised two subfamilies in Mayr’s (1962) treatment: Paradisaeinae, including most of the genera, and Cnemophilinae Mayr for *Cnemophilus* De Vis (incl. *Loria* Salvadori) and *Lohoparasidae* Rothschild. There is no dispute about the taxonomic cohesion of the Cnemophilinae, but the species are not closely allied to the other Paradisaeidae (Frith & Beehler, 1998). They differ strongly from the Paradisaeinae through their small, weak bills, wide gapes, weak, non-dextrous feet, sluggish behaviour, exclusive frugivory and domed nests. They have often been allied with bowerbirds but are treated here as a separate, unnamed family.

**Affinities of the Paradisaeidae and Ptilonorhynchidae**

Sibley & Ahlquist’s (1990) Corvidae subfamily Corvinae comprised six families in the usual sense, as follows (distributions from Howard & Moore, 1984):

- *Corvidae* (in the usual sense, comprising crows and jays) is the basal group. It has 26 genera and is worldwide, especially in America and Eurasia. There are seven genera in Malaysia/Indonesia but east of here diversity drops off markedly; there are only three species of *Corvus* in New Guinea, and only four species of *Corvus* in Australia. New Caledonia and Fiji have no extant Corvinae and New Zealand has one fossil genus only (Oliver, 1974).
- *Paradisaeidae* is sister to the remaining four families.
- *Artamidae* (wood swallows) comprises *Artamus* with 10 species: India (one), Indonesia (two), Australia (five), New Guinea (four), New Caledonia (one), and Fiji (one).
- *Cracticidae* (butcherbirds) has nine species, six in Australia and five in New Guinea (two shared).
- *Oriolidae* (orioles) comprises *Oriolus* from Africa (seven) and Eurasia (four) to Malesia (14) and Australia (two), and *Sphecotheres*: northern Australia and New Guinea.
- *Campephagidae* (cuckoo-shrikes) has nine genera. Africa has two, Madagascar, Mauritius and Réunion one, India to South-East Asia four, Malaysia to Polynesia five (including endemic species east to Samoa), and Australia three. New Guinea has three genera (one endemic) and 11 species, from the mangrove to upper montane forest.

Frith & Beehler (1998) noted that Cracticidae have a distribution ‘concordant’ with birds of paradise, and the group of families listed above (Corvinae) illustrate a standard Gondwanan (circum-Indian Ocean) distribution, Africa – southern Asia – Australasia, with relatively minor representation in Eurasia and the Americas (Corvidae only).

The family Paradisaeidae has also been related by other authors to the following groups, which do not change the biogeography of Sibley & Ahlquist’s (1990) group as described, apart from adding to its Indian Ocean main massing:

- *Dicruridae* (drongos) comprises *Dicrurus* Vieillot: Africa three species, Madagascar four, Asia seven, Philippines – Indonesia nine, New Guinea two, Australia one; and *Chaetorchynchus* Meyer: mountains throughout mainland New Guinea.
- *Callaeidae* (wattlebirds): two New Zealand genera.
- *Grallinidae* (magpie larks) is in Australia (three species) and New Guinea (two species) (one shared).

The Ptilonorhynchidae have traditionally been placed with the Paradisaeidae (but not by Sibley & Ahlquist,
They have also been regarded as closely related to the Turnagravidae, with two probably extinct species in New Zealand (North and South Islands) (Finsch, 1875, cited but not referenced by Oliver, 1974; Falla, Sibson & Turbott, 1979; Christidis, Leeton & Westerman, 1996). Oliver (1974) also pointed out similarities of Turnagra with Cracticidae and Manucodia.

There was a ‘serious [zoogeographic] objection’ (Frith & Beehler, 1998) to a possible affinity between Paradisaeidae and the New Zealand Callaeidae until it was realized that bowerbirds were related to Turnagravidae, also of New Zealand. This latter affinity was itself regarded as ‘surprising on biogeographic grounds’ by Christidis et al. (1996), although biogeographic connections between New Guinea and New Zealand are common in other taxa, either via Australia, or as a direct link (e.g. the Raoulia Hook. f. group of genera (Compositae, Breitwieser et al. 1999), a clade in Rytidosperma Steud. (Gramineae, Linder, 1999)).

Main massings for the related families in Corvinae are as follows:

- Tropical Asia: Corvidae;
- New Guinea: Paradisaeidae, Ptilononthychidae, ‘cнемоophilines’;
- New Guinea – Malesia: Dicruridae;
- Malesia: Oriolidae;
- Malesia-Polynesia: Campephagidae;
- Australia – New Guinea: Grallinidae, Cracticidae, Artamidae;
- New Zealand: Callaeidae, Turnagravidae.

The Australian families of superfamily Corvoidea are all small and the group is probably replaced there by Meliphagoidea such as Meliphagidae (12 genera in Australia, 11 in New Guinea, 3 in New Zealand, one in other areas from Malesia to the Pacific).

Cracraft & Feinstein (2000) carried out molecular analysis of a sample of Corvoidea and its putative sister group Meliphagoidea. They did not include Artamidae or Oriolidae but gave the following clades for Corvoidea: Ptilononthychidae (‘cнемоophilines’ (Campephagidae, Cracticidae, Paradisaeidae + Corvidae)). Thus the ‘cнемоophilines’ represent a family, or alternatively all the families could be treated in Corvidae (as done by Sibley & Ahlquist, 1990).

The basal position of bowerbirds (New Guinea centred) and ‘cнемоophilines’ (New Guinea endemic) in this cosmopolitan group emphasizes the importance of New Guinea as a primary biogeographic centre (in the sense of Craw, Grehan & Heads, 1999), it is not merely a receptacle for taxa dispersed from elsewhere. However, neither should the massing of basal families in New Guinea be used as evidence for New Guinea as a ‘centre of origin’ for Corvoidea, with ‘dispersal flights’ leaving from here. This would not explain the standard, global pattern of differentiation in the group. For example, Corvidae are worldwide, with most diversity in tropical Asia. Although seven genera are present in Malaysia/Indonesia, the family is represented in New Guinea by only three species of Corvus, indicating vicariance with Paradisaeidae and fragmentation of an already global common ancestor.

In another cladogram, Cracraft & Feinstein (2000) had cнемоophilines sister to Campephagidae, indicating vicariance between a New Guinea orogen endemic and a Gondwanic group. This is a standard pattern seen, for example, in the two genera of Dicruridae, Chaetorhynchus and Dicrurus, mentioned above.

Summarizing, although Gilliard (1969) commented that ‘Authorities agree that the ancestors of Australo-Papuan animals are of Asiatic origin’, and that Paradisaeidae were ‘derived from a single colonization of New Guinea’, it now seems more likely that they, ‘cнемоophilines’, and bowerbirds are autochthonous developments in the Australia–New Guinea region out of...
a corvoid ancestral complex which was globally distributed but had most of its diversity around the Indian Ocean and Australasia.

Within Corvoidea the vicariance between Paradisaeidae and Corvidae is straightforward, but the comparative distributions of the other corvoid families have not been analysed. It is shown below that Ptilorhynchidae and Paradisaeidae, at least, have rather different patterns despite considerable overlap.

**Previous work on bird of paradise biodiversity**

Gilliard (1969) mapped the birds of paradise and bowerbirds, and Cooper & Forshaw (1977) reproduced these, with minor corrections, in their lavishly illustrated companion volume. Frith & Beehler (1998) provided the first dot maps for the species with many new records. A compilation of these (Fig. 1) shows the known localities of birds of paradise in New Guinea. PNG has been better collected than Irian Jaya, and in New Guinea in general the coasts and mountain axis have been better collected than the intermediate areas. This pattern is also seen in plant collections (van Welzen, 1997).

Apart from species lists for different areas of different sizes there has been little analysis of regional variation in bird of paradise diversity. Beehler et al. (1986) observed that the New Guinea Central Highlands region (i.e. Victor Emanuel Mountains to Mount Giluwe and Mount Hagen) ‘is known for its diversity of birds of paradise’, and Michaux’s (1994) tabular summary showed the species distributions in geological provinces. Croizat (1958) calculated the number of races of birds of paradise (out of 90) at ‘nodes’ as follows:

- Mountains south of Upper Sepik/Ramu and Astrolabe Bay [PNG Highlands]: 25 races (28%);
- Weyland/Oranje node: 20 races (22%);
- Sepik/Ramu node: 15 races (16.5%);
- Vogelkop: 10 races (11%);

![Fig. 2. Numbers of species of Paradisaeidae (excluding subfam. Cnemophilinae and Macgregoria) in 1° x 1° grid cells.](image)
Western Papuan Islands: six races (6.7%);
Islands off southeastern New Guinea: five races (5.6%);
Japen Island: four races (4.5%);
Aru Islands: four races (4.5%).

The results below support and extend these observations.

METHODS

This study assesses regional levels of biodiversity in birds of paradise and bowerbirds by counting numbers of species in 1° latitude by 1° longitude grid cells. This method was first used in the 1960s to map species diversity in the very rich plant communities of southern Africa and Australia (references in Heads, 1997). Since then it has been applied around the world and groups analysed in this way include: reptiles, birds and mammals in northwestern Australia (Whitehead, Bowman & Wideman, 1992; Woinarski, 1992); Crassulaceae in North America, Mexico and southern Africa (Jürgens, 1995; Thiede, 1995); Banksia L.f. and Hakea Schrad. (Proteaceae) in southwestern Australia (Groom & Lamont, 1996; Lamont & Connell 1996); Huperzia Bernh. (Lycopodiaceae) in the Neotropics (Ollgaard, 1996); pteridophytes in Iberia (Moreno Saiz et al., 1996); several groups of plants and animals in New Zealand (Heads, 1997, 1998, 1999), and plants in New Guinea (Heads, 2001).

RESULTS

There are two equally diverse 1° squares for birds of paradise (Fig. 2): the Mount Hagen–Wahgi Valley–Jimi Valley square, and the Mendi square. The same result was found in an analysis (not shown here) of the earlier maps of Cooper & Forshaw (1977), and as these were based largely on the maps of Gilliard (1969) the main pattern has not changed much in 30 years of collecting. No new species have been described since 1939, with the exception of Cracraft’s (1992) two new species.
Cracraft’s phylogenetic species are equivalent to the subspecies of other authors.

Bowerbird biodiversity (Fig. 3) was calculated using data from PNG (Coates, 1990), Irian Jaya (Cooper & Forshaw, 1977) and Australia (Blakers, Davies & Reilly, 1985). The last species in this family was described in 1939, as in Paradisaeidae. The most diverse 1° square for bowerbirds – the Mount Hagen square – is one of the two most diverse for birds of paradise.

The ‘cnemophilines’ (Fig. 4) are most diverse in two disjunct massings: a region in the Irian Jaya mountains between Mandala Peak and Mount Trikora (= Wilhelmina), and the Bismarck Mountains–Kubor Mountains–Wau area of PNG. Similar disjunctions are seen in many groups (e.g. affinities in the plants Dacrycarpus de Laubenf., Cotula L. and Nothofagus Bl. mapped in Heads, 1998). The ‘cnemophilines’ are notably absent from the Vogelkop and Huon Peninsulas despite suitable habitat there; these two areas are formed from separate, but possibly related, accreted terranes. The central distribution of the ‘cnemophilines’ and their main massing straddle the main geological boundary in New Guinea (between cratonic rock and accreted terranes), which is also the boundary between the main massings of Paradisaeidae and Ptilonorhynchidae.

Apart from the overlap at Mount Hagen, the different locations of the species massings of Paradisaeidae (south central New Guinea) and Ptilonorhynchidae (northern New Guinea, NE Queensland) are clear-cut. If the geographic affinities of the Paradisaeidae in the Hagen square are examined, it is found that the majority, 13, are southern, while five are northern, and three are widespread.

Within Australia Paradisaeidae have two species per degree square in northern Cape York Peninsula (on the old Australian craton, Scheibner, 1985), and only one elsewhere in eastern Australia, whereas Ptilonorhynchidae have a clear Australian massing further south in Queensland, from Cooktown to Townsville (Hodgkinson-Broken River terrane), and a secondary massing inland from Brisbane (Yarrol-Tamworth terrane). These are accreted terranes of the Tasman orogen (Scheibner, 1985).

DISCUSSION

Tectonics and biodiversity

Birds of paradise, ‘cnemophilines’ and bowerbirds are most diverse in the mountains of the New Guinea orogen (Fig. 5), and are totally absent north of here, for example on New Britain and New Ireland. The New Guinea orogen is composed of a southern, cratonic portion (related to rocks of the Australian craton), and a northern belt of accreted terranes (Fig. 5).

The five 1° squares with 17 species or more of Paradisaeidae (Fig. 2) all lie in the southern portion of the New Guinea orogen (south of the former craton margin) except the Hagen square which straddles the craton margin. In contrast, except, again, for the Hagen square, the 12 New Guinea squares with maximum diversity (five species) of Ptilonorhynchidae (Fig. 3) all lie north or east of the craton margin. Likewise, in a sample of 961 New Guinea endemic plants 876 were found to occur in the northern half of New Guinea (van Welzen, 1997). There is also a massing of Ptilonorhynchidae in Queensland on the accreted terranes of the Tasman orogen. This northern New Guinea – Cairns link is a common pattern, seen for example in a group of genera in the plant family Monimiaceae (Philipson, 1986) (Fig. 6), with Wilkiea linking Queensland south of Cape Melville with the accreted terranes of PNG. In northern Cape York Peninsula, Wilkiea is absent, but Tetrasynandra and Austromatthaea delimit the quite distinct biogeographic centre favoured by birds of paradise.

Species numbers of several other diverse montane taxa in New Guinea have also been counted in 1° squares (Heads, 2001). Only one of these, the fern genus Grammitis Swartz, showed the same centre of diversity (the Hagen square) as the birds of paradise and bowerbirds. In other groups, Schodde (1972) referred to the ‘extraordinary richness’ of Pittosporaceae in the Bismarck–Kubor Mountains, and Parsons (1999) cited...
the Mount Hagen/Sepik–Wahgi Divide as one of 10 centres of endemism for mainland New Guinea butter¬flies and wrote that the area is particularly noteworthy for its distinctive endemics.

Why is the Hagen–Wahgi square so diverse for both birds of paradise and bowerbirds, as well as other groups? Possible, trivial reasons include the fact that it is well-collected – but so are the Owen Stanley Mountains, and other montane taxa show centres in other areas. Another reason might be that Mount Wilhelm, the western slopes of which lie in the Hagen square, is the highest mountain in PNG – but the Irian Jaya peaks are higher, and in any case the top 1000 m or so of these mountains seem largely irrelevant, as the only alpine species in either family (Macgregoria pulchra De Vis) is now regarded as a honeyeater. However, the Hagen square is also the most conspicuous on a geological map of PNG (Bain et al., 1972) as several distinctive geological terranes are juxtaposed there, including the Kubor Mountains with Palaeozoic basement exposed since the Triassic, the granodiorite of the Mount Wilhelm region, the ophiolite complex of the Marum terrane, and several others (cf. Fig. 5). A similar crowding of taxa in areas of terrane juxtaposition occurs in New Zealand (Heads, 1997, 1998, 1999) and, to a spectacular extent, in New Caledonia.

The different secondary massings of birds of paradise and bowerbirds

In New Guinea the main massings of birds of paradise lie south of the main centres of diversity in bowerbirds. This could conceivably be correlated with more high land in this region and a higher altitude of birds of paradise compared with bowerbirds, but no author has indicated that this is the case. Beehler et al. (1986) wrote that most of the 11 Papuan species of bowerbirds inhabit mountain forest. Schodde & Calaby (1972) cited the relatively sharp change at 1200–1700 m elevation between the lowland bird faunas dominated by pigeons, large parrots, kingfishers and small honeyeaters, and montane faunas dominated by birds of paradise, bower¬birds, large honeyeaters, thickheads, malurid warblers and small lorikeets.

Table 1 gives an analysis of numbers of species at different altitudes. The two numbers given for Paradisaeidae indicate the total number of species at that altitude, and the number of species most common at that altitude (from data in Cooper & Forshaw, 1977 and Frith & Beehler, 1998).

There is no obvious difference in altitudinal distribution; both families are clearly most diverse in the 1000–2000 m band. This includes what is usually referred to as ‘lower montane’ forest although the trees here are still very tall and often with little moss cover, and the term ‘hill forest’ may give a better impression of the general scenery. The second most diverse altitudinal band for both families are the lowlands from 0–1000 m. Thus altitude cannot explain the different geographic massings of the two families.

However, there is a clear geological difference between the southern parts of the New Guinea orogen (south of the former craton margin) where Paradisaeidae have secondary centres of diversity, and the northern areas of the orogen where Ptilonorhynchidae have secondary centres. The respective distributions of the two families correlate well with the tectonic history of the orogen as an amalgamation of southern and northern components.

An important conclusion from biodiversity assessment studies for conservation strategies is that different taxa often have their most speciose regions in different areas. This generalization was confirmed recently in a

<table>
<thead>
<tr>
<th>Family</th>
<th>0–1000 m</th>
<th>1000–2000 m</th>
<th>2000–3000 m</th>
<th>3000–4000 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ptilonorhynchidae</td>
<td>8</td>
<td>14</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Paradisaeidae</td>
<td>20(9)</td>
<td>25(18)</td>
<td>15(7)</td>
<td>6(0)</td>
</tr>
</tbody>
</table>

Fig. 6. A ‘closely knit group’ of genera in Monimiaceae (Philipson, 1986): Tetrasynandra Perkins, Austromatthaea L. S. Smith, Wilkiea F. Muell., extending to New South Wales (keyed next to Faika – arrows), Kairoa Philipson, Lauterbachia Perkins, Faika Philipson, Parakibara Philipson, and Matthaea Blume, extending into the Philippines. The final two genera of the group, Steganthera Perkins and Kibara Endl. (not mapped) are widespread throughout NE Queensland, New Guinea, northern Moluccas, and Sulawesi.
massive survey of over 9000 species in South Africa using a grid of squares 25 km × 25 km, although plant diversity was often a good indicator of insect diversity (van Jaarsveld et al., 1998). Efforts to conserve birds of paradise and bowerbirds should take into account their apparent primary centre of diversity in the Mount Hagen–Jimi Valley–Wahgi Valley region, as well as their rather different secondary centres of diversity south and north of the craton margin.

Acknowledgements

Andy Mack and Deb Wright of the Wildlife Conservation Society helped my work in many ways. I am also grateful to Peter Linder, Steve Wagstaff and Peter van Welzen for reprints, Ed Scholes for literature and discussion, Joel Cracraft and Gary Nelson for helpful suggestions, and my students for checking the species counts, making useful suggestions and providing good company in the field.

REFERENCES


