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Relicts from Tertiary Australasia: undescribed families and subfamilies of songbirds (Passeriformes) and their zoogeographic signal

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Abstract

A number of hitherto unrecognized, deeply divergent taxa of Australasian songbirds have been revealed by DNA sequence studies in the last decade. Differentiation among them is at levels equivalent to family and subfamily rank among songbirds generally. Accordingly, the purpose of this paper is to name and describe eleven of them formally under Articles 13.1, 13.2, 16.1 and 16.2 of the International Code of Zoological Nomenclature so that they are made available for use in zoology. The taxa are: families Oreoicidae, Eulacestomatidae, Rhagologidae, Ifritidae and Melampittidae, and subfamilies Pachycareinae, Oreoscopinae, Toxorhamphinae, Oedistomatinae, Peltopsinae and Lamproliinae. The families to which the subfamilies belong are documented. Morphological and behavioural traits of the new family-group taxa are discussed; reasons for taxonomic rankings are summarized; and grounds for the geographic origin of corvoid songbirds, to which all the new families belong, are briefly addressed. One new genus, *Megalampitta* in Melampittidae, is also described.

Key words: taxonomy, nomenclature, songbirds, family-group taxa, New Guinea, Australia, zoogeography

Introduction

Over the last decade, DNA sequence technology has realigned much of the phylogeny and classification of Class Aves (birds). Advances in our understanding of avian relationships have been most marked in the suborder Passeri (songbirds), which comprise almost half the world's species of birds. Impact has perhaps been greatest in the Australasian avifauna, the sequencing identifying Australasia (eastern Gondwana) as the source of the songbird radiation globally (Barker *et al.* 2002, 2004; Ericson *et al.* 2002; Jønsson *et al.* 2011; Aggerbeck *et al.* 2014).

These studies and others (*e.g.* Jønsson & Fjeldså 2006; Driskell *et al.* 2007; Jønsson *et al.* 2007; Irestedt *et al.* 2008; Norman *et al.* 2009a,b; Zuccon & Ericson 2012) reveal the primary songbird lineages endemic to Australasia as deeply diverged, at levels ranked as families and subfamilies elsewhere among songbirds. Many have been recognized (Schodde 1975; Coates 1990; Christidis & Boles 1994, 2008; Schodde & Mason 1999; Dickinson 2003; del Hoyo *et al.* 2002–2011) and have been validly named and described under the International Code of Zoological Nomenclature, hereafter the Code (ICZN 1999); see listings in Bock (1994). Yet several of the smaller groups either lack names or have been given names that are invalid because they have not been introduced in accord with the Code. Thus our purpose here is to name and describe them formally so that they can be brought into use in zoology. There are eleven such groups, all of which are sister to other Australasian-centered family-group taxa. They comprise: (1) two subfamilies in the family Acanthizidae (Australasian scrubwrens and thornbills), a member of the Australo-Papuan superfamily Meliphagoidea; (2) two subfamilies in the New Guinean family Melanocharitidae (berrypeckers), of uncertain phylogenetic position; (3) five families in the corvoid assemblage, a large group of mostly Old World families (over 700 species) that has its greatest diversity of root taxa in Australasia (Jønsson *et al.* 2011; Aggerbeck *et al.* 2014); and (4) two subfamilies respectively in the corvoid families Artamidae and Rhipiduridae.

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Methods and materials

Descriptions of the new family-group taxa are formulated as summaries of critical morphological and behavioural traits sufficient to diagnose the taxa (Article 13.1.1 of the Code). Morphological and behavioural features recorded are shape of body; structure and pattern of plumage; form of bill, skull, sternum, wing, tail and foot; structure and position of nest; shape, color and marking of eggs; and ecological niche. Primaries are numbered in ascendant sequence, with p10 outermost. Osteological features described—palate, orbital region of the skull, sternum and fossorial configuration of the head of the humerus—are those used conventionally for higher rank characterization in Aves (Bock 1962; Sibley & Ahlquist 1990; Livezey & Zusi 2006). The source for their terms is Baumel *et al.* (1979). New family-group names are formed and described in accord with Articles 13.1, 13.2, 29.1 and 64 of the Code, and are explicitly indicated as new and designated with a type genus (Articles 16.1 and 16.2 of the Code). Article 29.1 specifies that family-group names may be formed from the stem of the name of an included genus or its full generic name. Both options are used here to form names that are euphonious.

Sources of material from which the descriptions were drawn are:

1. Plumages, bills and feet—Australian National Wildlife Collection, CSIRO, Canberra (ANWC) for all taxa except *Melampitta gigantea*; American Museum of Natural History, New York (AMNH) for *Melampitta gigantea* and, in part, *M. lugubris*. Series measured for tail/wing ratios ranged from a minimum of four (*Ornorectes*) to six or more of each sex in other taxa.
2. Palate, skull, sternum and humerus—ANWC for *Pachycare*, *Oreoscopus*, *Toxorhamphus*, *Oedistoma*, *Eulacestoma*, *Ifrita*, *Melampitta* (*lugubris*), *Chaetorhynchus*, *Peltops*, *Rhagologus*, *Oreoica* and *Aleadryas*. A minimum of two skeletons per genus was examined of all taxa except *Pachycare*, *Eulacestoma*, *Melampitta* (*lugubris*) and *Aleadryas* (for which one each was available). No skeletal material of *Lamprolia* and *Ornorectes* was accessed.
3. Nests and eggs—ANWC (*Pachycare*, *Oreoscopus*, *Toxorhamphus*, *Ifrita*, *Rhagologus*, *Oreoica*); Natural History Museum, Tring (NHM) (*Oedistoma*); published information for most taxa in Coates (1990), for *Toxorhamphus* and *Aleadryas* in Mayr & Gilliard (1954), for *Lamprolia* in Cottrell (1967) and Coates *et al.* (2006), for *Ifrita* in Frith (1971a), for *Pachycare* in Frith (1971b) and Mack & Oppel (2006), and for *Melampitta* and *Megalampitta* in Frith & Frith (1990) and Diamond (1983).
4. Niche and behaviour—Coates (1990); personal observations (R. Schodde).

Descriptions and diagnoses of new taxa

I. Acanthizidae (superfamily Meliphagoidea)

Pachycare and *Oreoscopus*

New Guinean *Pachycare* was formerly placed in the corvoid family Pachycephalidae (Australasian whistlers), presumably because of bright yellow and grey plumage, form of bill, and "loud, melodious, whistled and explosive" vocalizations (*e.g.* Mayr 1941, 1967; Rand & Gilliard 1967; Sibley & Monroe 1990; Dickinson 2003; Boles 2007a). Coates (1990: 206) nevertheless expressed reservations about an exclusively whistler-like voice. Mack & Opel (2006), corroborated by data in ANWC, also showed that *Pachycare* builds a domed nest near the ground and lays white, reddish-spotted eggs, characteristic of many acanthizids (Acanthizidae) but unlike any pachycephalid. It has a dusky subterminal tail band in the outer rectrices as well, a trait that appears repeatedly in one form or another throughout the Acanthizidae, but is otherwise absent in Pachycephalidae. The position of *Pachycare* in the meliphagoid Acanthizidae has since been established by Norman *et al.* (2009a). Using 2644 base pairs of multi-locus nDNA and mtDNA sequence and osteological data, their study compared *Pachycare* with a comprehensive range of acanthizid genera including *Oreoscopus*, two genera of Pachycephalidae, and genera of three and five further meliphagoid and corvoid families respectively. *Pachycare* was recovered as sister to the northeast Australian Fernwren *Oreoscopus* in Acanthizidae, in a clade sister in turn to all other acanthizids. Support for pairing *Pachycare* and *Oreoscopus* was strong, and the node placing them sister to the rest of Acanthizidae was fully resolved. Similarly, Gardner *et al*. (2010) recovered *Oreoscopus* as sister to all other primary acanthizid lineages at some depth, although they did not examine *Pachycare*.

Distinctive osteological features of *Oreoscopus*—narrowly-winged ectethmoids, clavoid maxillo-palatines and completely perforate anterior synsacral foramina (Schodde & Mason 1999: 134)—also identify that genus as a deeply-diverged lineage in the Acanthizidae. Concerning the sister relationship between *Oreoscopus* and *Pachycare*, moreover, DNA divergence between them is almost as deep as between them and the rest of Acanthizidae (Norman *et al*. 2009a). This divergence is matched by marked differences in form, behaviour and niche. *Oreoscopus* is a quiet, dun-colored, troglodyte-like litter-forager of the forest floor; and it has completely operculate nostrils adapted to its mode of foraging. In contrast, *Pachycare* is a noisy, active, and brilliantly yellow and grey gleaner of foliage in the forest canopy; and its skull structure, especially the temporal region, is markedly different (see subfamily diagnoses), indicating that *Pachycare* uses its bill in a different manner.

The combined DNA sequence and morphological data thus lead us to separate *Pachycare* and *Oreoscopus* in two monogeneric subfamilies of Acanthizidae. All other genera of Acanthizidae are circumscribed within the subfamily Acanthizinae Bonaparte, 1854.

Subfamily Pachycareinae, *subfamilia nova*—goldenfaces

Type genus: *Pachycare* Gould, 1876

Diagnosis. Small, short-tailed, slender-bodied and brightly-colored songbirds with rich grey dorsum and golden-yellow face and ventrum; *sexes* similar except for grey cheek patch in females; *head* rather narrow, the *bill Gerygone*-like, uncompressed, tomia smooth except for terminal maxillary notch, and narial depression round-elliptic, with semi-operculate, holorhinal and internally fully pervious nostrils opening externally in distal elliptic apertures under operculum, rictal bristles fine and sparse; *skull* with fully perforate interorbital septum, narrowly-winged ectethmoids slightly flattened with club-like tips against the jugal bar, broadly linguate maxillo-palatines rather expanded towards the tips, linguate vomer with vestigial horns, rather narrow palatine shelf with acute transpalatine processes, and upright-oblong, well-defined temporal fossae with terete, ventrally-projecting postorbital processes that are longer than the short, acute anteriorly-projecting zygomatic processes; *sternum* with lateral trabeculae short, broadly-flattened and expanded moderately at tips, *c*. ⅓ x length of sternum, no other data; *wings* short and rounded, primaries 10 with p10 short, p7 and p6 longest, and p8=p5; *humeral fossae* pseudo-double, the outer fossa an untrabeculated cup, the *incisura capitis* deep, extending into a shallow inner tricipital fossa, ventral tubercle protuberant, and pectoral crest short, hardly decurrent below fossae; *tail* short and round-tipped with dull, narrow black subterminal bar through outer rectrices, tail/wing ratio (0.58–)0.60–0.63(–0.65), the rectrices 12, straight-sided without terminal flaring, shallowly acute at tips; *feet* short but stout, with booted tarsi, basal toe pads slightly enlarged. *Nest* a bulky dome with hooded side-entrance, of twigs (base) and grass fibers (body), lined with finer grass fiber and fern rootlets, and placed on the ground in the shelter of rocks or small tree buttresses; *eggs* 2–3 per clutch, broadly ovoid, matt- to satin-white with a sparse sprinkling of fine red-brown speckles concentrated in a zone or cap at the larger end. Arboreal, forest-living insectivores, gleaning actively among foliage and branchlets; posture horizontal (Coates 1990: 206); apparently monogamous.

Range and composition. Lower montane rainforests of New Guinea; one genus: *Pachycare* Gould, 1876, of one species: *P. flavogriseum* (A.B. Meyer, 1874).

Subfamily Oreoscopinae, *subfamilia nova*—fernwrens

Type genus: *Oreoscopus* North, 1905

Diagnosis. Small, short-tailed, long-legged songbirds densely-plumaged in olive-brown with white brow and throat, and black upper chest patch; *sexes* monomorphic; *head* slender, the *bill* slender and straight, tomia smooth except for slight terminal maxillary notch, and narial depression attenuately elliptic and completely operculate, with internally fully pervious nostrils opening externally as attenuately elliptic slits under the operculum, rictal bristles vestigial; *skull* with interorbital septum fully perforate with fine medial bar, small, weakly-winged ectethmoids not reaching jugal bar, long, terete maxillo-palatines clubbed at tips, linguate vomer with vestigial horns, narrow palatine shelf with truncated trans-palatine processes, and very small, rounded and ill-defined temporal fossae, flanked by reduced, pimple-like postorbital processes and short, acute anteriorly-projecting zygomatic processes; *sternum* rather narrow and narrowed distally, with shallow keel *c.* ⅓–½ x sternum width, lateral trabeculae slender, *c.* ⅓–½ x length of sternum, abruptly flared at tips, sternal rostrum moderately developed; *wings* short and broadly rounded, primaries 10 with p10 moderately developed, p5 and p6 longest, p7=p4 > p3=p8; *humeral fossae* pseudo-double, the outer fossa an untrabeculated cup, the *incisura capitis* deep, extending into a shallow inner tricipital fossa, ventral tubercle very protuberant, and pectoral crest moderately lengthened and decurrent below fossae; *tail* plain, rather short and round-tipped, tail/wing ratio (0.69–)0.70–0.72(–0.74), the rectrices 12, straight-sided without terminal flaring, shallowly acute at tips; *feet* moderately long and slender, with booted tarsi. *Nest* a bulky dome with side entrance, of loosely interwoven fern rootlets, fiber, bryophytes and leaves, lined with dry moss, plant down and fur, and placed on the ground hidden among ferns on banks and under logs; *eggs* 2 per clutch, broadly ellipsoid, satin-white, sometimes faintly, sparsely and finely speckled with red-brown at the larger end. Terrestrial, forest-living insectivores, hop-searching in and under leaf-litter on rainforest floor; apparently monogamous.

Range and composition. Montane rainforests of northeast Queensland; one genus: *Oreoscopus* North, 1905, of one species: *O. gutturalis* (De Vis, 1889).

II. Melanocharitidae (superfamily *incertae sedis*)

Toxorhamphus and *Oedistoma*

Historically, New Guinean *Toxorhamphus* has been linked with the paleotropic sunbirds (Nectariniidae) because of superficial similarities to the spiderhunters, *Arachnothera* (Gadow 1884; Dorst 1952), and to the Australasian honeyeaters (Meliphagidae) with which it shares a quadrifid, brush-tipped tongue, slit-like nostrils and long bill (Stresemann 1914; Scharnke 1931, 1932; Salomonsen 1967; Wolters 1979; Bock 1985). Similarly, for most of the 20th century, New Guinean *Oedistoma* was placed among the Australasian honeyeaters and, following Salomonsen (*l.c.*), treated as a sister genus of *Toxorhamphus*, which it resembles in form and plumage (Rand & Gilliard 1967; Beehler *et al*. 1986; Coates 1990).

DNA-DNA hybridization studies (Sibley & Ahlquist 1985, 1990) associated both genera with the New Guinean berrypeckers (Melanocharitidae) instead, in a cluster placed sister to the sunbirds and flowerpeckers (Dicaeidae). Since then, DNA sequencing studies (Barker *et al*. 2002, 2004; Driskell *et al.* 2007; Jønsson *et al.* 2011; Aggerbeck *et al*. 2014) have confirmed a close link between *Toxorhamphus*, *Oedistoma* and the Melanocharitidae, but nevertheless have found the complex to form a monophyletic group that is basal among corvoid and passeridan birds. Sibley & Monroe (1990) placed *Toxorhamphus* and *Oedistoma* in the tribe Toxorhamphini, and *Melanocharis* and *Rhamphocharis* in the tribe Melanocharitini. In contrast, Christidis *et al.* (1993) recovered *Oedistoma* sister to *Melanocharis-Rhamphocharis* from allozyme variation at 18 presumptive protein loci, with *Toxorhamphus* basal to both lineages. Furthermore, the branches between *Oedistoma* and *Toxorhamphus* in DNA sequence phylogenies (e.g. Barker *et al*. 2004; Jønsson *et al. l.c.*) are almost as deep as those between them and *Melanocharis*.

Morphological and behavioural features reinforce the distinctness of *Toxorhamphus* and *Oedistoma* and their links with Melanocharitidae. Although both genera have long, decurved bills and quadrifid, brush-tipped tongues for harvesting nectar, the fine structure of these organs differs markedly, indicative of different mechanisms for nectar uptake. Uniquely modified for capillary action, the tongue in *Toxorhamphus* is a slender tube, with a bowl at the base (presumably for holding nectar) and has a shallowly quadrifid tip in which the medial furcation is shallower than the two lateral. The four lobes of the tip, moreover, are terminally truncate and serrately toothed on the outer margins only (see subfamily diagnosis). In contrast, the tongue of *Oedistoma* is deeply brush-tipped and honeyeater-like and fitted for nectar-mopping instead. It differs from the basic form of the honeyeater tongue only in its more in-rolled sides and reduced laciniations on the medial lobes of a deeply quadrifid tip. The tongues of *Melanocharis* and *Rhamphocharis* are short and open in comparison, and barely fibriate at the tip. The shorter bills of *Melanocharis* and *Rhamphocharis* also bear a unique series of broad, evenly-spaced notches along the maxillary tomia; mandibular tomia are almost smooth. *Oedistoma* instead has the same pattern of fine tomial toothing on both maxilla and mandible as do sunbirds, except that the tubercles are aculeate, coarser and more widely spaced. *Toxorhamphus* differs in having both maxillary and mandibular tomia set with the same fine, close-packed tuberculate teeth as in sunbirds, but on the maxilla the teeth are laid out on stepped notches. The notches are more spaced out and shallower than those in short-billed *Melanocharis*, but their intermediate state on longer-billed *Rhamphocharis* suggests that all may be homologous. Such geometrically exact integumentary structures are missing from the coarsely and irregularly serrate bills of honeyeaters.

Although in *Toxorhamphus* the configuration of the fossa at the head of the humerus is essentially single, the decurrent *incisura capitis* is developed into an incipient inner fossa, trending toward the double condition. In *Oedistoma* (n = 1), the inner fossa is even deeper and the outer shallower, still closer to the double condition. *Melanocharis* and *Rhamphocharis* all have fully double humeral fossae. *Toxorhamphus*, *Oedistoma* and *Melanocharis* also build distinctive nests of similar form (Mayr & Gilliard 1954; Parker 1963; Coates 1990; data in ANWC). Their nests are neat, smoothly-bound cups thickly lined with a felt of plant down and structurally different from the rough twig nests of honeyeaters or coarse, pendant, variably hooded nests of sunbirds. Yet whereas those of *Toxorhamphus* and *Melanocharis* are perched on branchlets and decorated with spider egg sacs, the only reliably recorded and preserved nest of *Oedistoma* was hung from the rim and decorated with small leaves (Rothschild & Hartert 1896). There are also basic differences in egg pigmentation between *Toxorhamphus* and *Oedistoma* (see subfamily diagnoses). The "unmarked white" eggs of *Toxorhamphus poliopterus* recorded in Mayr & Gilliard (1954) and Coates (1990: 312) appear to be misdescribed; their description is here emended from material in ANWC.

Differences in structural morphology and nest-building described above, considered collectively with DNA sequence data, indicate that *Toxorhamphus* and *Oedistoma* are sister to the berrypeckers yet still deeply divergent from them and one another. Accordingly, we place them here in separate subfamilies within the Melanocharitidae, noting that their depths of DNA, morphological and behavioural divergence may be found to qualify them for family ranking in the future. Although Sibley & Ahlquist (1990: 669) and Sibley & Monroe (1990: 669) earlier used the name Toxorhamphini, they provided no description, publishing it as a *nomen nudum* (Articles 13.1 and 13.2.1 of the Code). The berrypecker genera *Melanocharis* and *Rhamphocharis* are here placed in the nominate subfamily, Melanocharitinae Coates, 1990.

Subfamily Toxorhamphinae, *subfamilia nova*—tube-tongued longbills

Type genus: *Toxorhamphus* Stresemann, 1914

Diagnosis. Small, plain citrine-yellow and grey songbirds with extremely long curved bills, broad wings, short white-tipped tails and indistinct, finely-feathered periorbital rings; *sexes* monomorphic except for smaller, shorter-tailed females; *head* slender with tight neck skin, the *bill* attenuated and decurved but straight-sided and narrowing only towards tip, uniformly black, tomia microscopically dentate distally with fine, even tuberculate teeth that, on the maxilla, are formed compoundly on broader shallow serrations, narial depression elongate elliptic, with inoperculate, holorhinal and internally fully pervious nostrils opening externally in a long, meliphagid-like slit along ventral margin of narial depression, rictal bristles undeveloped; *corneous tongue* a long slender tube, with a lipped bowl at the base and a shallowly and serrately quadrifid tip in which the medial furcation is much shallower than the two lateral furcations and their four lobes are terminally truncate and serrately toothed on the outer margins only—the teeth overlap one another and interlock immediately behind the tips of the lobes to form the distal section of the tongue tube which can then open and close progressively at the tip under controlled pressure from behind; *skull* with fully perforate interorbital septum except for vestigial medial bar, thickened, well-winged ectethmoids that reach the jugal bar, an aperturate palate with truncated, multi-tipped vomer, filamentous, spathuloid-tipped maxillo-palatines, slender palatines with shelf expanded distally through extension of trans-palatine processes, and small, shallow and moderately-defined temporal fossae flanked by short, ellipsoid postorbital processes projecting ventrally and long, spine-like zygomatic processes projecting anteriorly; *sternum* rectangular and moderately narrow, with deep keel *c.* 1 x sternum width, lateral trabeculae slender, *c.* ⅓–½ x length of sternum, hardly flared at tips, sternal rostrum short and deeply bilaterally compressed; *wings* broad and moderately rounded, primaries 10 with p10 well-developed and rather broad, p7–p6 longest, and p8=p5; *humeral fossae* near single, with deep, trabeculated outer fossa and distinct, if shallow, tricipital fossa, the *incisura capitis* rather deep, ventral tubercle much protuberant, and pectoral crest long and decurrent below fossae; *tail* short and square-tipped, tail/wing ratio *c.* (0.47–)0.50–0.54(–0.58), the rectrices 12, straight-sided with rounded tips; *feet* short, with rather slender toes and scutellate-laminiplantar tarsi, the scutes angled obliquely across the acrotarsus. *Nest* a neat, closely and smoothly woven perched cup of fine plant fiber, lined with a dense felt of white plant down, finely and smoothly walled over the outside with camouflaging green bryophytes, algae, cobweb and sometimes white spider egg sacs, and bound at the base to the top of a narrow horizontal twig or fork in shrubbery *c.* 2–3 m above ground; *eggs* 1 per clutch, ovoid, matt pale greyish blue sprinkled sparsely with fine pale red to purplish-red spots concentrated at the larger end. Versatile, forest-living nectarivores and insectivores of forest lower stages, probing and gleaning actively, nervously and acrobatically up to forest mid-stages, flying swiftly and directly between sites and calling with repeated tweeting in flight; apparently monogamous.

Range and composition. Lowland to montane rainforests of New Guinea; one genus: *Toxorhamphus* Stresemann, 1914, of two species: *T. novaeguineae* (Lesson, 1827), lowland New Guinea, and *T. poliopterus* (Sharpe, 1882), montane New Guinea.

Group name. The term "tube-tongued longbill" expresses an obvious and easily identified family-group difference from the plumed longbills, Oedisomatinae.

Subfamily Oedistomatinae, *subfamilia nova*—plumed longbills

Type genus: *Oedistoma* Salvadori, 1876

Diagnosis. Small to very small plain creamy olive songbirds with long decurved bills, rounded wings, short plain tails, bare and lemon-colored periorbital rings, plumed flanks and discolorous yellowish-white pectoral tufts at the sides of the breast under the wings; *sexes* monomorphic except for smaller, shorter-tailed females; *head* slender with tight neck skin, the *bill* attenuated and decurved, evenly tapered throughout length, dark grey with whitish mandibular unguis, tomia microscopically dentate distally with fine, evenly spaced tuberculate teeth on both maxilla and mandible, narial depression elongate elliptic, with inoperculate, holorhinal and internally fully pervious nostrils opening externally in a long, meliphagid-like slit along ventral margin of narial depression, rictal bristles present, fine and sparse; *corneous tongue* a semi-closed canal extensively open at each end, with an extensively laciniate, meliphagid-like quadrifid tip in which the medial furcation is much deeper than the two lateral furcations, and their four lobes are laciniate only at the tips; *skull* with fully perforate interorbital septum except for narrow medial bar, swollen, broadly winged ectethmoids that reach the jugal bar, a fully aperturate palate with atrophied vomer and maxillo-palatines and slender palatines with narrow, raked shelf, and large, shallow and ill-defined temporal fossae flanked by short, ellipsoid postorbital processes projecting ventrally and long, spine-like zygomatic processes projecting anteriorly; *sternum* rectangular and moderately narrow, proportionally larger than in *Toxorhamphus*, with deep keel as deep as width of sternum, lateral trabeculae slender, *c.* ⅓–½ x length of sternum, hardly flared at tips, sternal rostrum short and deeply bilaterally compressed; *wings* moderately rounded, primaries 10 with p10 short and narrow, p7–p6 longest, and p8=p5; *humeral fossae* semi-double, with deep, trabeculated outer fossa and distinct, moderately deep tricipital fossa, the *incisura capitis* deep, ventral tubercle much protuberant, and pectoral crest short, not decurrent below fossae; *tail* short and square-tipped, tail/wing ratio *c.* (0.46–)0.47–0.52(–0.56), the rectrices 12, straight-sided with rounded tips; *feet* short, with stout toes and scutellate-laminiplantar tarsi, the scutes angled obliquely across the acrotarsus. *Nest* a small, deep closely woven hanging cup of plant fiber, lined with a loose felt of white plant down, camouflaged with a neat covering of small leaves bound in with cobweb, and slung from the rim in a horizontal fork; *eggs c.* 1 per clutch, ovoid, matt creamy white, sparsely sprinkled with fine specks of pale rust-red concentrated in a zone at the larger end around which are also scrawled several transverse lines of blackish-brown. Versatile, forest-living nectarivores and insectivores of forest midstages, probing and gleaning actively, nervously and acrobatically from forest lower to upper stages, flying swiftly and directly between sites and calling with repeated tweeting in flight; apparently monogamous.

Range and composition. Lowland to lower montane rainforests of New Guinea; one genus: *Oedistoma* Salvadori, 1876, of two species: *Oedistoma pygmaeum* Salvadori, 1876 and *O. iliolophum* (Salvadori, 1876).

Comment. We use the name Oedistomatinae for this subfamily on the presumption that *O. iliolophum* (Salvadori, 1876) is the sister species of *O. pygmaeum* Salvadori, 1876, type species of *Oedistoma*. All molecular analyses comparing "*Oedistoma*" with *Toxorhamphus* and other groups of songbirds to date [?] have employed *O. iliolophum* solely as its representative. That species was previously included in the honeyeater genus *Melilestes* or tube-tongued longbill genus *Toxorhamphus* until Salomonsen (1967) moved it to *Oedistoma* without explanation. No substantive justification for this move has yet been published. DNA sequence data (Christidis *et al*., unpublished) confirm that *O. pygmaeum* and *O. iliolophum* are indeed sister species relative to other members of the Melanocharitidae; and morphology is consistent with this hypothesis. With respect to *Toxorhamphus*, *Oedistoma iliolophum* (n = 40) and *O. pygmaeum* (n = 4) share exclusively: olive-grey dorsa and pale grey ventra yellowing on bellies and crissa; yellowish white pectoral tufts at the side of the breast; plain-tipped tails; bare, yellowish periorbital rings (although those of *O. pygmaeum* have vestigial white feathering as in *Toxorhamphus novaeguineae*); evenly tapered bills with whitish unguinal stripe on the mandible; and, significantly, fine even toothing on distal sectors of both maxillary and mandibular tomia, without microscopic tuberculate teeth or compound toothing on the maxilla as found in *Toxorhamphus*. In sum, *O. iliolophum* and *O. pygmaeum* differ in little else than size and more plumose flanks in *O. iliolophum*. Accordingly we treat them as congeneric.

Group name. The term "plumed longbill" expresses an obvious and easily identified family-group difference from the tube-tongued longbills, Toxorhamphinae.

III. New families (corvoid assemblage)

1. *Aleadryas*, *Ornorectes* and *Oreoica*

Based on morphology, New Guinean *Aleadryas* and *Ornorectes* and Australian *Oreoica* have been placed separately or together in three different families—Pachycephalidae (Australasian whistlers), Falcunculidae (Australian shrike-tits) and Colluricinclidae (Australo-Papuan shrike-thrushes)—at one time or another over the last half century (Mayr 1967; Wolters 1980a,b; Sibley & Monroe 1990; Dickinson 2003; Boles 2007a). Recent multi-locus DNA sequence studies screening two or all three genera together consistently recovered them as a strongly supported monophyletic lineage (Jønsson & Fjeldså 2006; Driskell *et al.* 2007; Jønsson *et al.* 2007, 2010, 2011; Norman *et al*. 2009b). Shared morphological and behavioural traits are less obvious but do exist: rather stout bodies, crests of variable form, ventriloquial territorial songs in at least two genera (*Oreoica*, *Ornorectes*) and remarkably long, terete postorbital processes directed ventrally over the temporal fossae in the only two genera available for study (*Oreoica*, *Aleadryas*).

DNA sequence evidence for the relationships of this group (Australo-Papuan bellbirds) is less conclusive. In those studies sampling a broad range of corvoid families that include diverse members of Pachycephalidae, Falcunculidae and Colluricinclidae, the bellbirds have been linked to: (1) Old World orioles (Oriolidae) and New Guinean crested berrypeckers (Paramythiidae) (Barker *et al*. 2004; Jønsson & Fjeldså 2006; Driskell *et al.* 2007); (2) Old World cuckoo-shrikes (Campephagidae) and New Guinean false whistlers (Rhagologidae) (Jønsson *et al.* 2007); and (3) Campephagidae and the artamid-malanocotid (Australasian butcherbirds and woodswallows and African bush shrikes) cluster of families (Norman *et al*. 2009b). Jønsson *et al*. (2011) placed the group sister to all primary core corvoid lineages. Only Aggerbeck *et al*. (2014) recovered the bellbirds among the pachycephaloids, but at a depth deeper than that between the Cinclosomatidae (Australo-Papuan quail-thrushes) and Falcunculidae (Australian shrike-tits). In sum, the Australo-Papuan bellbirds clearly form a family-rank lineage among corvoid birds, as concluded by Norman *et al*. (2009b). Norman *et al*. (*l.c*.), like Sibley & Ahlquist (1985) earlier, used the name Oreoicidae for them but provided no description, leaving it a *nomen nudum* (Articles 13.1 and 13.2.1 of the Code). Consequently, we make the name available by diagnosing the family below.

Family Oreoicidae, *familia nova*—Australo-Papuan bellbirds

Type genus: *Oreoica* Gould, 1838

Diagnosis. Small-medium to medium-sized, stout-bodied songbirds with short, rounded to slender, semi-erectile crests that are discolorous or concolorous with the head, and grey to red-brown plumage that lacks spotting or streaking; *iris* contrastingly erythristic in two of three genera; sexes slightly dimorphic or similar; *head* rather broad, the *bill* shrike-like with strong bilateral compression, tomia smooth except for terminal maxillary notch, and narial depression elliptic, with internally semi-perforate to impervious nostrils opening externally in small, round apertures distally in narial depression, rictal bristles coarse but sparse to vestigial; *skull* with near-imperforate interorbital septum, broadly winged ectethmoids that reach the jugal bar in a broadened foot, a palate with truncated vomerine horns, broad, square-tipped maxillo-palatine processes and broad palatine plate shallowly notched on distal margin, and small, shallow and ill-defined temporal fossae flanked by short simple zygomatic processes projecting anteriorly and distinctively long terete postorbital processes that project ventrally over the zygomatic; *sternum* short and broad (*Aleadryas*) to rather long and narrow (*Oreoica*), with shallow (*Aleadryas*) to deep (*Oreoica*) keel *c.* ½–1 x sternum width, lateral trabeculae rather long, *c.* ⅓–½ x length of sternum, abruptly and moderately flared at tips, sternal rostrum short (*Aleadryas*) to rather long (*Oreoica*); *wings* rounded to moderately pointed, primaries 10, with p10 short and p7–5 subequal > p4 > p8 in *Aleadryas* and *Ornorectes*, and p10 longer and p7 > p8=p6 > p5 in *Oreoica*; *humeral fossae* single with deep trabeculated outer fossa and rather shallow *incisura capitis* in *Aleadryas* and semi-double with deep *incisura capitis* in *Oreoica*, ventral tubercle moderately protuberant, pectoral crest short, hardly decurrent below fossae; *tail* medium-long, narrow and rounded with 12 acute-tipped rectrices and tail/wing ratio (0.73–)0.75–0.79(–0.81) in *Aleadryas* and *Ornorectes*, shorter and squarer with 12 flared, round-tipped rectrices and tail/wing ratio (0.70–)0.72–0.75(–0.77) in *Oreoica*; *feet* stout, with scutellate tarsi. *Nest* a deep, roughly but compactly interwoven cup of dry fiber, bark strips and rootlets, lined with finer fiber and rootlets, in *Aleadryas* camouflaged on the outside by draped and interwoven green moss and leafy liverworts (Coates 1990), and inserted or suspended in upright forks and crotches in small trees *c.* 1–3 m above the ground. Eggs 2–3 per clutch, broadly ovoid, satin-white, in *Aleadryas* thinly sprinkled with fine black and some grey spots (Mayr & Gilliard 1954), in *Oreoica* thinly sprinkled with coarse spots and small blotches of black and sepia. Forest- and woodland-living insectivores, foraging by hop-searching in litter and bushes; apparently monogamous. All three living species have piping or whistled territorial songs which are distinctively ventriloquial in at least two.

Range and composition. Foothill to mid-montane rainforests of New Guinea, and arid-zone scrubs of Australia; three genera: *Aleadryas* Iredale, 1956, of one species: *A. rufinucha* (Sclater, 1874), mid montane New Guinea; *Ornorectes* Iredale, 1956, of one species: *O. cristatus* (Salvadori, 1876), foothill to lower montane New Guinea; *Oreoica* Gould, 1838, of one species: *O. gutturalis* (Vigors & Horsfield, 1827), arid Australia.

Group name. Despite the use of "bellbird" as a species name for the New Zealand Bellbird *Anthornis melanura*, a meliphagid, and for birds outside the Australo-Papuan region (*e.g.* tropical American *Procnias*), we suggest it as a simple and appropriate group name for the members of Oreoicidae. It will maintain the name Crested Bellbird for the most widely known of them, *Oreoica gutturalis* in Australia. The two New Guinean species could then become Piping, Russet or Brown Bellbird (*Ornorectes cristatus*), after plumage or territorial song, and Rufous-naped Bellbird (*Aleadryas rufinucha*).

2. *Eulacestoma*

Because of its remarkable bilaterally compressed bill, New Guinean *Eulacestoma* was grouped traditionally with the Australasian shrike-tits (Falcunculidae) and whistlers (Pachycephalidae) (Mayr 1941, 1967; Rand & Gilliard 1967; Beehler & Finch 1985; Beehler *et al.* 1986; Coates 1990; Sibley & Monroe 1990; Dickinson 2003; Boles 2007a). Multi-locus DNA sequence studies since have corroborated a sister relationship between the shrike-tits and whistlers (Barker *et al.* 2004; Jønsson & Fjeldså 2006; Driskell *et al.* 2007; Norman *et al.* 2009b; Jønsson *et al.* 2011; Aggerbeck *et al.* 2014), but not with *Eulacestoma*. Norman *et al.* (*l.c.*) did recover exclusive links between them, but support was weak. Other studies (Jønsson *et al.* 2007, 2011) found *Eulacestoma* sister instead to a large cluster of corvoid families that includes the crows (Corvidae), shrikes (Laniidae), birds-of-paradise (Paradisaeidae), fantails (Rhipiduridae), monarchs (Monarchidae) and, in the first study, whistlers. Since then, Aggerbeck *et al.* (2014), using sequences from 22 loci and with robust support, recovered *Eulacestoma* as sister to the Australo-Papuan sittellas (Neosittidae). These, in turn, were sister to a group of corvoid families that included the Old World orioles (Oriolidae), vireos (Vireonidae) and Australo-Papuan whipbirds (Psophodidae). Whatever the inter-familial relationships of *Eulacestoma*, they are clearly distant from other corvoid families.

Morphological traits support these findings. Although the bills of *Eulacestoma* and *Falcunculus* are similar in appearance, the structure of the temporal area of the skull, where jaw muscles attach, differs markedly. Unlike its form in *Eulacestoma* (see diagnosis), the temporal fossa is smaller, deeper and clearly defined in *Falcunculus*, with both postorbital and zygomatic processes short but clearly developed; the latter is distinctively thickened at the base. Thus the bills of the two genera are evidently used in different ways, and convergent in gross form. Moreover, the ectethmoids are short and narrow in *Falcunculus*, and its lachrymals appear to be free. Based on the combined molecular and morphological data now available, *Eulacestoma* is separated here in its own family.

Family Eulacestomatidae, *familia nova*—ploughbills

Type genus: *Eulacestoma* De Vis, 1894

Diagnosis. Small, short-tailed, bull-headed songbirds with olive-citrine plumage; *sexes* dimorphic, males black-breasted and -winged with large, flat, circular gape wattles, females plain-plumaged, intrinsically dimorphic in rufous- and olive-winged plumages (possibly age-related) and unwattled; juveniles flushed rufous on wings and sides of breast; *head* broad, the *bill* much compressed bilaterally and as deep as long, tomia smooth except for terminal maxillary notch, and narial depression rounded, with inoperculate, holorhinal and internally pervious nostrils opening externally in large rounded apertures, rictal bristles short and inconspicuous; *skull* with near-imperforate interorbital septum, moderately-winged and -flared ectethmoids that are fused with the lachrymals and flattened with club-like tips against the jugal bar, a narrowed and vertically twisted palatine shelf to conform with bill compression, and broad, shallow and ill-defined temporal fossae that extend over the occiput and are flanked by short, fine postorbital and vestigial zygomatic processes; *sternum* broad with shallow keel *c.* ¼–⅓ x sternum width, lateral trabeculae short, *c.* ⅓ x length of sternum, hardly flared at tips, sternal rostrum reduced; *wings* short and rounded, primaries 10, with p10 moderately developed, p7–p5 longest, and p8=p4 or p3; *humeral fossae* single, very deep and trabeculated, the *incisura capitis* shallow, hardly developed into a tricipital groove, ventral tubercle short and rounded, and pectoral crest lengthened and decurrent below fossae; *tail* rather short and square-tipped, tail/wing ratio (0.62–)0.65–0.70(–0.72), the rectrices 12, straight-sided without terminal flaring, shallowly acute at tips; *feet* short but stout, with booted tarsi. *Nest* and *eggs* unrecorded. Arboreal, forest-living, weak-flying insectivores, gleaning by prying, digging and pounding actively with bill along tops and undersides of moss- and liverwort-draped branches and limbs; apparently monogamous.

Range and composition. Montane rainforests of New Guinea; one genus: *Eulacestoma* De Vis, 1894, of one species: *E. nigropectus* De Vis, 1894.

3. *Rhagologus*

Despite its streak-plumaged females, New Guinean *Rhagologus* has traditionally been included in the family Pachycephalidae (Australasian whistlers) because of its whistler-like appearance (*e.g.* Salvadori 1876; Mayr 1941, 1967; Rand & Gilliard 1967; Sibley & Monroe 1990; Dickinson 2003; Boles 2007a). Early DNA-DNA hybridization work (Sibley & Ahlquist 1982, 1985, 1990) lent support to that presumption. Nevertheless, all five multi-locus DNA sequence studies that have screened *Rhagologus* (Jønsson *et al*. 2007, 2010, 2011; Norman *et al.* 2009b; Aggerbeck *et al.* 2014) place it firmly elsewhere, among a complex of corvoid songbirds that includes the Australasian butcherbirds and woodswallows (Artamidae), African bush-shrikes, wattle-eyes and vangids (Malaconotidae, Platysteiridae, Vangidae), southeast Asian ioras (Aegithinidae) and Old World cuckoo-shrikes (Campephagidae). Nearest relatives within that complex are still unclear. The ioras (Jønsson *et al.* 2011) or the cracticid-artamid group (Aggerbeck *et al*. 2014) have been indicated, but support values are weak, and depth of divergence considerable.

As diagnosed, frugivorous *Rhagologus* has little in common with the insectivorous ioras, which are predominantly yellow-, green- and black-plumaged with silken-plumed flanks, display aerobatically and build perched cup-shaped nests bound smoothly with cobweb. Nor do its rather broad palate, open nares and unstructured temporal region of the skull resemble the narrowed palate, heavily ossified nasal cavity and compound zygomatic processes found in the Australasian butcherbirds and woodswallows (Schodde & Mason 1999: 533) and, in part, vangas. The insectivorous pachycephalids have a broad palate and internally perforate nasal cavity similar in form to those of *Rhagologus*, but the temporal region of the skull differs markedly: its fossa is much narrower, deeper and more clearly defined in pachycephalids, and both postorbital and simple zygomatic processes are well-developed and directed ventrally at an angle of *c*. 45°. Combined morphological, behavioural and DNA sequence evidence reveal *Rhagologus* as a deeply divergent corvoid lineage that cannot be placed in any other family. Accordingly, it is described at family rank here.

Family Rhagologidae, *familia nova*—false whistlers

Type genus: *Rhagologus* Stresemann & Paludan, 1934

Diagnosis. Medium-small, slim, nondescript grey-brown songbirds of pachycephalid form but with discolorous rufous crissa; *sexes* dimorphic: males dull grey or brownish with muted ventral mottling, and females and juveniles cinnamon-faced and brightly streaked and spotted white on dorsum and ventrum respectively; *head* and *bill Pachycephala*-like, the former more slender, the latter with smooth tomia except for terminal maxillary notch, and narial depression elliptic, with semi-operculate, holorhinal and internally pervious nostrils opening externally in an elliptic aperture distal in narial depression, rictal bristles coarse but sparse; *skull* with fully perforate interorbital septum except for narrow medial bar, short-winged ectethmoids that do not reach the jugal bar, small free lachrymals, a palate with bi-horned vomer with truncated tips, slender, round-tipped maxillo-palatine processes, and broad, shallow and ill-defined temporal fossae flanked by vestigial postorbital and zygomatic processes; *sternum* moderately narrow, with well-developed keel *c*. ⅔–¾ x sternum width, lateral trabeculae short, *c*. ⅓ x length of sternum, much flared at tips, sternal rostrum well-developed and deeply compressed bilaterally; *wings* narrowly rounded, primaries 10, with p10 moderately developed, p7 longest and p8=p6 > p5; *humeral fossae* semi-double with deep, trabeculated outer fossa and distinct, if shallow, tricipital fossa, the *incisura capitis* deep, ventral tubercle protuberant, and pectoral crest not decurrent below fossae; *tail* rather long and square-tipped, tail/wing ratio (0.70–)0.71–0.74(–0.76), the rectrices 12, slightly flared and broadly rounded at the tips; *feet* rather slender, with booted tarsi and distinctly broadened toe pads. *Nest* a thick, coarse cup of interwoven rootlets and tendrils, lined with finer rootlets and tendrils, camouflaged on the outside by loosely but thickly interwoven moss and leafy liverworts, and inserted in the upright fork of a small tree *c*. 2–3 m above the ground; *eggs* 1 per clutch, ellipsoid, matt pale to mid buff-cream, rather densely and coarsely freckled and flecked with purple-brown to red-brown, the markings often concentrated in a cap at the larger end. Sluggish, quiet, arboreal, forest-living frugivores (with some insectivory) of lower forest stages (Coates 1990: 204); apparently monogamous.

Range and composition. Mid montane rainforests of New Guinea; one genus: *Rhagologus* Stresemann & Paludan, 1934, of one species: *R. leucostigma* (Salvadori, 1876).

Comment. The description herein of the nest and eggs of *Rhagologus leucostigma* (n = 10 clutches in ANWC) appears to be the first published. The nests and eggs were collected by indigenous hunters under the direction and supervision of R. Schodde and I.J. Mason in Morobe Province, Papua New Guinea, in 1973 at Wagau in the Herzog Range, 12–18 October (clutches E02248, E02302, E02303, E02304, E02348, E02349 and E02375), and at Mindik in the Rawlinson Range, 30 October–1 November 1973 (clutches E02407, E02423 and E02447). Nests for five of the clutches were kept as well.

Group name. Although unrelated to members of Pachycephalidae, the single species of *Rhagologus* bears remarkable similarity to them in appearance. Accordingly we suggest False Whistler as the simplest and least disruptive English name for it.

4. *Ifrita*

The relationships of New Guinean *Ifrita* have long been perplexing. Mathews (1930) referred the genus to family Bowdleriidae in the Old World warbler complex, Mayr (1941) and Rand & Gilliard (1967) to the Old World babblers (Timaliidae), Deignan (1964), Beehler & Finch (1985) and Beehler *et al*. (1986) to an enlarged Australo-Papuan Orthonychidae (logrunners), and Boles (2007b) to Eupetidae, which included a mix of Afro-Asian rail-babblers and Australo-Papuan whipbirds and quail-thrushes. Cracraft *et al.* in Dickinson (2003) treated *Ifrita* as *incertae sedis*. Since then four multi-locus DNA sequence studies have clarified its position (Jønsson *et al*. 2007, 2011; Norman *et al.* 2009b; Aggerbeck *et al*. 2014). All found it embedded, without close relatives, among a cluster of Australasian and Old World corvoid families that includes the monarchs (Monarchidae), shrikes (Laniidae), crows (Corvidae), birds-of-paradise (Paradisaeidae) and Australian mudnesters (Corcoracidae). The two most comprehensive of these studies, moreover, recovered *Ifrita* respectively sister to the first three and last two of these families, with strong support (Jønsson *et al*. 2011; Aggerbeck *et al*. *l.c.*).

In morphology and behaviour, *Ifrita* is altogether unlike the mostly black, rufous or pied, hawking monarchs, pied or brown perch-pouncing shrikes or large, varicolored, omnivorous corvids, let alone the mostly brilliantly plumaged, polygynous birds-of-paradise and ground-feeding mudnesters. It is a rather small brown scansorial creeper on the branches of forest trees, for which its stout, powerfully clawed feet are evidently adapted. It nevertheless lacks syndactyly of the toes that restricts lateral flexibility of movement as in the Australo-Papuan treecreepers (Climacteridae). Flight is weak, as indicated by rounded wings and short, broad sternum with reduced keel, and is apparently used for little more than movements from tree to tree. Neither nest nor eggs (see family diagnosis) resemble those of monarchs, shrikes or crows; and the nest is constructed of plant fiber, not mud. Because it is sister to other lineages recognized as families, we rank *Ifrita* at family level as well.

Family Ifritidae, *familia nova*—ifrits

Type genus: *Ifrita* Rothschild, 1898

Diagnosis. Small-medium, stocky, tawny-brown songbirds with powerful feet and a black cap wreathed in iridescent mid blue; *sexes* dimorphic: ear streak white in males, tawny in females; juveniles as adults but duller; *head* rather broad, the *bill* thrush-like, tomia smooth except for terminal maxillary notch, and narial depression elliptic, with inoperculate, holorhinal and internally pervious nostrils opening externally in small circular apertures distal in narial depression, rictal bristles short and sparse; *skull* with fully perforate interorbital septum except for narrow medial bar, short, blunt-winged ectethmoids that do not reach the jugal bar, apparently fused lachrymals, a palate with broad, bifid-tipped vomer and broad, square-tipped maxillo-palatine processes, and narrow, deep, well-defined temporal fossae flanked by short, thick, ventrally projecting postorbital processes and longer, finer, anteriorly projecting zygomatic processes; *sternum* broad with shallow keel *c*. ⅓–½ x sternum width, lateral trabeculae short, *c*. ¼–⅓ x length of sternum, hardly flared at tips, sternal rostrum reduced; *wings* rounded, primaries 10, with p10 well-developed, p7 longest and p8=p4; *humeral fossae* single, very deep and trabeculated, the *incisura capitis* moderately deep and developed into a shallow tricipital depression, ventral tubercle squared and protuberant, and pectoral crest lengthened and decurrent below fossa; *tail* rather short and square-tipped, tail/wing ratio 0.62–0.70(–0.73), the rectrices 12, straight-sided without terminal flaring, shallowly acute at tips; *feet* stout with enlarged toes and claws, tarsi booted. *Nest* a bulky cup of fern tendrils and rootlets, lined with finer pieces of the same materials and occasional feathers and skeletonized leaves, camouflaged on the outside with thickly interwoven moss and leafy liverworts, and inserted in the upright fork of a small tree *c*. 1–3 m above the ground; *eggs* 1, rarely 2 per clutch, broadly ovoid, satin milk-white, sparsely sprinkled with discrete, round spots of purplish-black, concentrated towards the larger end and sometimes forming a sparse cap. Arboreal, scansorial, forest-living insectivores, gleaning by creeping and probing, nuthatch-like, up and down branches and limbs; breeding system unknown.

Range and composition. Montane rainforests of New Guinea; one genus: *Ifrita* Rothschild, 1898, of one species: *I. kowaldi* (De Vis, 1890).

5. *Melampitta*

After Mayr (1931) demonstrated that its syringeal morphology was oscine, the ground-living *Melampitta* group of montane New Guinea has been included among the Old World babblers (Timaliidae) or Australo-Papuan logrunners, quail-thrushes and whipbirds (Orthonychidae *sensu lato*) for much of the later 20th century (Mayr 1941; Deignan 1964; Rand & Gilliard 1967; Wolters 1980a; Beehler & Finch 1985; Beehler *et al.* 1986). DNA-DNA hybridization (Sibley & Ahlquist 1987; Sibley & Monroe 1990) then placed it sister to the birds-of-paradise (Paradisaeidae), to which Dickinson (2003) responded by treating it as *incertae sedis* and Boles (2007b) by returning it to the Australo-Papuan quail-thrushes and whipbirds. Subsequent multi-locus DNA sequence studies (Jønsson & Fjeldså 2006; Irestedt *et al.* 2008; Jønsson *et al.* 2011; Aggerbeck *et al.* 2014) have consistently recovered *Melampitta* sister to members of a cluster of families that include not only the birds-of-paradise, but also Afro-Asian drongos (Dicruridae), Australasian fantails and monarchs (Rhipiduridae, Monarchidae), and Australian mudnesters (Corcoracidae). Relationships to the birds-of-paradise and Australian mudnesters have the strongest support (Jønsson *et al. l.c.*: 1 mtDNA region and 4 nuclear loci, 72 corvoid taxa across all families; Aggerbeck *et al. l.c.*: 22 loci, 43 corvoid genera across all families).

Apart from the Australian mudnesters (Corcoracidae) and, subtly, the birds-of-paradise, the *Melampitta* group bears negligible similarity to any of these tree-living families in form or niche. Its two species, *lugubris* and *gigantea*, are litter-foragers of the forest floor. They have large feet and toes, very short rounded wings with uniquely recurved and emarginated primaries, and (*lugubris*) shortened sternum with much reduced keel—all consistent with terrestriality. Unlike the respective Australian mudnesters or birds-of-paradise, moreover, they appear to be neither communal nor polygynous (Coates 1990). Both species share a tuft of short plush feathering over frons and forehead that *could* be homologous to such tufts found in many genera of birds-of-paradise (*e.g. Semioptera*, *Paradisaea*, *Parotia*, *Astrapia*, *Cicinnurus*). Yet, although sharing a shallowly configured temporal region with *Manucodia*, *Melampitta lugubris* has a fully perforate nasal cavity, without any of the heavy ossification found in birds-of-paradise (Bock 1963). It also builds a bulky, bryophyte-draped domed nest near the ground (Frith & Frith 1990), unlike the coarse arboreal cups of twigs and leaves of birds-of-paradise or dish-shaped mud nests of the Corcoracidae. For *gigantea*, Diamond (1983) nevertheless recorded the nest as a "large suspended basket of vines"; no mention was made of a dome or side-entrance. Neonatal young of *M. lugubris* hatch downy, not naked as in birds-of-paradise, and are fed by direct feeding, not regurgitation (Frith & Frith 1990; Frith & Beehler 1998: 135, 138). Combined DNA sequence, morphological and behavioural evidence thus indicate that *Melampitta*, although apparently sister to the birds-of-paradise (Paradisaeidae) and perhaps the Australian mudnesters (Corcoracidae), is deeply divergent. Accordingly it is ranked at family level here.

Family Melampittidae, *familia nova*—melampittas

Type genus: *Melampitta* Schlegel, 1871

Diagnosis. Small-medium to medium-large, all-black songbirds with long, slender or stout legs, short or rather long tail, and a tuft of short, spike-like feathering with degenerated barbules across the frons; sexes apparently monomorphic except for iris color (*lugubris*), juveniles brown on lower body; *head* rather narrow, the *bill* thrush- or corvid-like, all black, maxilla moderately or well-hooked, tomia smooth except for terminal maxillary notch, narial depression elliptic, with inoperculate, holorhinal, internally fully pervious nostrils opening externally in rounded to elliptic apertures distal in narial depression, rictal bristles absent (*lugubris*) or sparse, fine and short (*gigantea*); *skull* (*lugubris*) with fully perforate interorbital septum except for narrow medial bar, narrow, short-winged ectethmoids that do not reach the jugal bar, ellipsoid maxillo-palatines, round-tipped vomer, long and narrow palatine shelf with shallowly attenuate transpalatine processes, and small, shallow and ill-defined temporal fossae flanked by atrophied, pimple-like postorbital processes and short, spiny, anteriorly projecting zygomatic processes; *sternum* (*lugubris*) short and broad, almost square and much broadened distally, with shallow keel ¼ x sternum width, lateral trabeculae medium-long, *c.* ⅓–½ x length of sternum, abruptly and slightly flared at tips, sternal rostrum very short; *wings* short and broadly rounded, with distinctively recurved and emarginated primaries with broader trailing vane, primaries 10, with p10 well-developed, p6=p5 > p4 > p3 > p7; *humeral fossae* (*lugubris*) single, very deep but hardly trabeculated, the *incisura capitis* moderately deep and developed into a shallow tricipital depression, ventral tubercle squared and protuberant, and pectoral crest atrophied; *tail* plain, round-tipped, short or moderately long, tail/wing ratio 0.58–0.70 (*lugubris*), 0.80–0.90 (*gigantea*), the rectrices 12 (perhaps 10 in some populations of *M. gigantea*), straight-sided without terminal flaring, shallowly acute or spiny at tips; *feet* large, the tarsi booted, long and slender (*lugubris*) or stout (*gigantea*). *Nest* a 'suspended basket of vines' (*gigantea*) or bulky dome with a side-entrance, of densely interwoven rootlets, tendrils and fronds, lined with a thick cup of fern hairs and scales, camouflaged externally with interwoven green bryophytes, and inserted in the side of a tree-fern trunk or bound among upright fern stems *c.* 1.5–3 m above the ground (*lugubris*); *eggs c.* 1 per clutch, chalky white, sparsely marked all over with spots and small blotches of black, grey and purplish-grey, usually concentrated at the larger end, sometimes forming a zone (*lugubris*). Terrestrial, forest-living omnivores, foraging by hopping and running, probing, litter-tossing and digging (Coates 1990: 418); apparently monogamous.

Range and composition. Hill to montane rainforests of New Guinea; two genera: *Melampitta* Schlegel, 1871, of one species: *M. lugubris* Schlegel, 1871; *Megalampitta* Schodde & Christidis, this work, of one species: *M. gigantea* (Rothschild, 1899).

Comment. Relationships between *Melampitta lugubris* and *Megalampitta gigantea* are unresolved. *M. gigantea* is over twice the bulk of *M. lugubris*, has a much longer tail, proportionally shorter and much stouter feet, and stiffened remiges and rectrices with spiny tips that are accentuated by abrasion; and on the alula is a small bony spur of unknown function (Diamond 1983). Likely immatures of *gigantea* (AMNH 5907637 ♂, and Bishop Museum BBM 101808 ♀) are black-hooded and reddish-brown to fuscous ventrally and over the lower back in a pattern reminiscent of adult plumage in the oriolid genus *Pitohui*. Material of *gigantea* is nevertheless so limited (6 specimens from different regions of New Guinea) that sexual, age and geographic characteristics of plumage are not yet fully understood. Yet despite this, differences in size, proportions and plumage structure between 'cinclid'-shaped *lugubris* and 'corvid'-like *gigantea* are sufficient to indicate deep divergence and exploitation of different adaptive zones, a conclusion reinforced by the habit of *gigantea* of roosting in sinkholes (Diamond *l.c.*). In syringeal musculature, moreover, the two species appear to differ as much from one another as they do from other corvoid families (Mayr 1931). Their territorial songs are dissimilar: a descending series of rapid, harsh 'buzzy' notes or single sharp chirped whistles repeated at intervals in *lugubris* (Beehler *et al.* 1986; xeno-canto website), and a clear slurred double- or triple-note whistle, rising and falling in pitch and monotonously repeated, in *gigantea* (Diamond *l.c.*; xeno-canto website). It leads us to place *gigantea* in its own genus and suggest that, when better known, it could justify family-group ranking.

Genus *Megalampitta*, *genus novum*

Type species: *Mellopitta gigantea* Rothschild, 1899

Mid-sized songbirds of crow-like appearance, all-black when adult and apparently with chestnut to fuscous-brown belly and lower back when immature, differing from their apparent sister genus *Melampitta* in *great bulk*, *long rounded tail* with tail/wing ratio 0.80–0.90, *thick corvid-like bill* with rictal bristles, *spiny tips* to remiges and rectrices, a *bony spur* on the alula, *proportionally short very stout feet* with coarse reticulate scaling over the back of the tibio-tarsal joint, and *syringeal musculature* with the following features: thin tracheal rostral muscle and *Musculus laryngo-syringeus ventralis*, vestigial cleft between left and right strands of the *M. laryngo-syringeus dorsalis*, long as well as powerful *M. syringeus ventro-lateralis*, and covering of the *M. syringeus ventralis* by the *M. laryngo-syringeus ventralis*.

Nomenclature. The generic name *Mellopitta* Stejneger, 1885, is a synonym of *Melampitta* Schlegel, 1871, of which the type species is *Melampitta lugubris* Schlegel. The name *Megalampitta*, although drawing on *Melampitta* and *megas*, Greek for large, is to be treated as an arbitrary combination of letters, not as a Latin or Greek word (Art. 30.1.4.1 of the Code); its gender is assigned here as feminine (Art. 30.2.2 of the Code).

IV. Artamidae (corvoid assemblage)

Peltops

The distinctively black, red and white species of New Guinean *Peltops* have been placed variously with Old World muscicapid flycatchers (Muscicapidae), Australasian monarchs (Monarchidae) or Australasian robins (Petroicidae) (Mayr 1941; Rand & Gilliard 1967; Wolters 1980b). Mayr (1986) treated the genus as *incertae sedis*. DNA-DNA hybridization (Sibley & Ahlquist 1984, 1985, 1990), nevertheless, grouped *Peltops* among the Australo-Papuan butcherbirds and woodswallows (Artamidae), a position widely accepted since (Beehler & Finch 1985; Sibley & Monroe 1990; Schodde & Mason 1999; Dickinson 2003; Russell & Rowley 2009). Its species are sallying insectivores with flycatcher habits, but both structural morphology and the consensus of multi-locus DNA sequencing (Norman *et al*. 2009b; Jønsson *et al*. 2010, 2011; Kearns *et al*. 2013; Aggerbeck *et al*. 2014) corroborate placement in the artamid complex. Like butcherbirds and woodswallows, they have spiny, doubled zygomatic processes, a heavily ossified nasal cavity and a narrow bony palate: nares are amphirhinal, the anterior palate pseudo-desmognathous and the palatine shelf constricted with elongated trans-palatine processes (Schodde & Mason 1999: 533). Monarchs also have well-ossified nasal cavities, but the palate does not reach the pseudo-desmognathous condition, and zygomatic processes are single.

Less clear is the position of *Peltops* within the artamid complex. The multi-locus phylogenies of Norman *et al*. (2009b), Jønsson *et al*. (2010) and Jønsson *et al*. (2011), each based on a wide range of corvoid genera, all recovered woodswallows, butcherbirds and *Peltops* as three equidistant lineages in one monophyletic cluster. Divergence within the cluster is deep, dating to the late Oligocene according to Jønsson *et al*. (2011). Aggerbeck *et al.*'s (2014) review of the corvoid radiation using markers from 22 genes corroborated the monophyly of the cluster, but found *Peltops* to be sister to a woodswallow-butcherbird lineage, with comprehensive support. Kearns *et al.*'s (2013) more focused phylogeny of the artamid cluster instead found *Peltops* sister to the butcherbirds alone, and recovered the cluster as paraphyletic with respect to the Asian ioras (Aegithinidae) and African bush-shrikes, wattle-eyes, batises and vangas (Malaconotidae, Platysteiridae, Vangidae). Support for paraphyly and a sister relationship between the woodswallows (*Artamus*) and Asian ioras (Aegithinidae) was nevertheless weak and at variance with the more broadly based and better supported phylogeny of Aggerbeck *et al*. (*l.c*.). Irrespective of the relationships of *Artamus*, it is clear from all molecular phylogenies that *Peltops* is a deeply diverged lineage in the complex. That and the consensus of morphological, zoogeographic and DNA sequence data lead us to treat *Peltops* as one of three subfamilies in one family for which the senior name is Artamidae Vigors, 1825. The two other subfamilies are Artaminae and Cracticinae Chenu & des Murs 1853 (1836), the bracketed date indicating priority according to Article 40.2.1 and recommendation 40A of the Code. Because *Peltops* has not been assigned formal family-group status, we do so here, noting that its depth of divergence and position may be found to qualify it for family ranking in the future.

Subfamily Peltopsinae, *subfamilia nova*—peltopses

Type genus: *Peltops* Wagler, 1829

Diagnosis. Small, slender songbirds with bulky flycatching bills and black plumage boldly patterned with red on lower back and crissum and white on cheeks and mantle; *sexes* monomorphic; bill broadened with bulbous culmen, all-black, tomia smooth except for terminal maxillary notch, no narial depression, the nostril amphirhinal, externally elliptic and internally semi-pervious, rictal bristles present but sparse, x ½ length of bill; *skull* with semi-closed interorbital septum, short-winged ectethmoids that do not reach the jugal bar, heavily ossified palate with expanded maxillo-palatines fusing with an extended bony shelf from the maxillary to almost meet across the roof of the palate in a pseudo-desmognathous configuration, narrow palatine shelf with attenuate transpalatine processes, slender pterygoids fused to the palatine shelf, and small well-defined temporal fossae flanked by short, ventrally projecting postorbital processes and short, doubled, ventrally projecting zygomatic processes; *sternum* short, little longer than broad and narrowed distally, with shallow keel ⅓ x sternum width, lateral trabeculae medium-long, *c*. ⅓–½ x length of sternum, abruptly and slightly flared at tips, sternal rostrum reduced and short; *wings* narrowly rounded, primaries 10 with p10 moderately developed, p7 > p8 > p6 > p5=p9; *humeral fossae* single with deep, trabeculated outer fossa and rather shallow *incisura capitis*, ventral tubercle not protuberant, pectoral crest short, not decurrent below fossa; *tail* rather long, narrow and shallowly emarginate at the tip, tail/wing ratio (0.72–)0.74–0.78(–0.80), the 12 rectrices slightly flared and broadly acute at tips; *feet* short, with booted tarsi. *Nest* a small, compact cup of dry twigs, rootlets and vegetable fiber without green bryophyte camouflaging, inserted in a horizontal fork at the end of outer branches of trees at *c*. 6–35 m above the ground; *eggs c*. 1 per clutch, ovoid, pale satin-buff with sparse black-brown spots concentrated at the larger end. Arboreal, forest-living insectivores of mid and upper forest stages, sallying from exposed perches; apparently monogamous.

Range and composition. Lowland and montane rainforests of New Guinea; one genus: *Peltops* Wagler, 1829, of two species: *P. blainvillii* (Lesson & Garnot, 1827), lowland New Guinea, and *P. montanus* Stresemann, 1921, montane New Guinea.

Group name. The Linnaean name *Peltops* is so widely anglicized as the English group name for this genus (*e.g.* Beehler *et al.* 1986; Coates 1990; Dickinson 2003; Russell & Rowley 2009) that we support it over the English name "shieldbill" as used by Gill & Wright (2006) and Beehler *et al.* (2012).

V. Rhipiduridae (corvoid assemblage)

Lamprolia and *Chaetorhynchus*

Lower montane New Guinean *Chaetorhynchus* (Papuan Silktail) has conventionally been placed in the Old World family Dicruridae (drongos) and, with a square-tipped tail of 12, not 14 rectrices, considered "ancestral" in that family (Mayr 1941; Vaurie 1949, 1962; Rand & Gilliard 1967; Wolters 1979; Sibley & Monroe 1990; Dickinson 2003; Rocamora & Yeatman-Berthelot 2009). The enigmatic Fijian *Lamprolia* (Fiji Silktail) has usually been placed with Australasian monarchs (Monarchidae) in recent classifications (Pratt *et al.* 1987; Sibley & Monroe 1990; Dickinson 2003; Coates *et al.* 2006), following Olson (1980) and DNA-DNA hybridization data in Sibley & Ahlquist (1985). Beecher (1953) and Harrison & Parker (1965) referred *Lamprolia* to the Australo-Papuan malurid wrens (Maluridae) instead, whereas Cottrell (1967) and Heather (1977) even proposed affinities with the birds-of-paradise (Paradisaeidae). In response, Wolters (1977) placed it in its own family; and Mayr (1986) treated it as *incertae sedis*. In the two multilocus DNA sequence studies that have so far screened both, *Chaetorhynchus* and *Lamprolia* were recovered as sister genera with strong support (Irestedt *et al.* 2008; Jønsson *et al.* 2011). Moreover, both these studies and two more (Norman *et al.* 2009b; Nyári *et al.* 2009) found this lineage to be sister to the Indo-Australasian fantails (Rhipiduridae), also with strong support, distant from drongos, monarchs and birds-of-paradise.

Morphological information is limited and non-committal. No specimen material of *Lamprolia* was available to us other than as photographic images. Moreover, the nest and eggs of *Chaetorhynchus* appear to be undescribed. Even so, indicative traits of *Chaetorhynchus* are as much or more rhipidurid as dicrurid. Its unguinal ridge along a basally broadened mandible, dense long rictal bristling arising from below as well as above the commissure of the bill, broad palatine shelf, simple zygomatic processes, and 12 rectrices are all rhipidurid. The tarsi of *Chaetorhynchus*, nevertheless, are short and thick as in drongos, not long and slender as in all fantails; *Lamprolia* has similarly short, thick tarsi and 12 rectrices. *Chaetorhynchus* also differs from both drongos and fantails in its narrowed sternum; the form of the sternum in *Lamprolia* may thus be informative. Irestedt *et al.* (2008) record no shared derived morphological traits that would link *Lamprolia* to *Chaetorhynchus* or the fantails exclusive of the monarchs (*cf.* Olson 1980). Yet despite a dearth of indicative morphological information, the corroborated DNA phylogenies resolve the phylogenetic position of these genera with reasonable certainty: they are based on comprehensive taxon sampling of 23 to 72 corvoid genera, use markers from two mitochondrial regions and four nuclear genes, and have robust support. DNA distances from *Rhipidura* are deep, Jønsson *et al.* (2011) dating the divergence at around the middle Oligocene. This may justify family ranking in the future, but we prefer a conservative approach at this stage and treat the *Chaetorhynchus*-*Lamprolia* group as a subfamily, Lamproliinae, in the Rhipiduridae (fantails) to indicate its phylogenetic affinities. Although Wolters (1977) used the name, he provided no description, leaving it a *nomen nudum* (Article 13.1 of the Code). The other subfamily, Rhipidurinae Sundevall, 1872, comprises the single genus *Rhipidura*.

Subfamily Lamproliinae, *subfamilia nova*—silktails

Type genus: *Lamprolia* Finsch, 1874

Diagnosis. Medium-small, rather slender black songbirds with glossed or spangled plumage over the head, and patches of silky white exposed over rump and central tail feathers (*Lamprolia*) or hidden in base of inner wing coverts (*Chaetorhynchus*); *sexes* nearly monomorphic, females smaller and rather duller than males; *head* broad, the *bill* flycatcher-like, all black, maxilla well-hooked, mandible with unguinal ridge, tomia smooth except for terminal maxillary notch, narial depression elliptic, with inoperculate, holorhinal, internally pervious nostrils opening externally in round apertures distal in narial depression, rictal bristles coarse, extending to near tip of bill in *Chaetorhynchus*; *skull* (*Chaetorhynchus*) with near-imperforate interorbital septum, narrow, short-winged ectethmoids that reach the jugal bar, round-lobed maxillo-palatines, short-horned vomer, broad palatine shelf with shallowly attenuate transpalatine processes, slender pterygoids fused to the palatine shelf, and moderately large, oblate temporal fossae flanked by short, terete, ventrally projecting postorbital processes and short, simple, spiny, anteriorly projecting zygomatic processes; *sternum* (*Chaetorhynchus*) narrow, especially distally, with deep keel 1 x sternum width, lateral trabeculae medium-long, *c.* ⅓–½ x length of sternum, abruptly and slightly flared at tips, sternal rostrum moderately long and deeply bilaterally compressed; *wings* (*Chaetorhynchus*) broadly rounded, primaries 10 with p10 moderately developed, p6 > p5=p7 > p8 > p4; *humeral fossae* (*Chaetorhynchus*) single with deep trabeculated outer fossa, rather shallow *incisura capitis*, moderately protuberant ventral tubercle and short pectoral crest not decurrent below fossa; *tail* medium-long and slightly rounded in *Lamprolia*, longer, narrower and square-tipped in *Chaetorhynchus*, tail/wing ratio (0.83–)0.84–0.87(–0.91), the 12 rectrices slightly flared with broadly truncated outer to rounded inner tips (*Chaetorhynchus*); *feet* short, faintly scutellate to booted. *Nest* a bulky cup of closely interwoven tendrils, fiber, rootlets and shredded bark strips, lined with down and feathers, camouflaged loosely with green moss and leafy liverworts, and suspended at the rim from a horizontal fork in saplings *c.* 1–3 m above the ground, usually under a large protecting leaf (*Lamprolia*); eggs *c.* 1 per clutch, whitish-pink, blotched sparsely lilac and dull red-brown (*Lamprolia*). Arboreal, forest-living insectivores of lower forest stages, sallying and hawking from set perches and gleaning along branches, with bowing and tail flicking (Coates 1990: 142; Pratt *et al.* 1987: 248); apparently monogamous.

Range and composition. Lower montane rainforests of New Guinea, and rainforests of Fiji; two genera: *Chaetorhynchus* Meyer, 1874, of one species: *C. papuensis* Meyer, 1874, New Guinea; *Lamprolia* Finsch, 1874, of one species: *L. victoriae* Finsch, 1874, Fiji.

Nomenclature. Although the generic names of the two silktails were published in the same year, choice of the type genus, *Lamprolia*, for forming the subfamily name here was guided by Article 64 of the Code, not Article 24. Article 64 directs that any included nominal genus treated as valid in the new family-group is eligible; thus no first reviser action is required.

Group name. With the finding that *Chaetorhynchus* is not a drongo, it seems advisable to avoid its misleading English name, Pygmy Drongo. We suggest 'Silktail' as the least disturbing group name for the members of this subfamily, for which the distinguishing species names 'Papuan' (*C. papuensis*) and 'Fiji' (*L. victoriae*) would then be suitable.

Discussion

The discovery of these deep lineages of songbirds, all but two endemic to New Guinea, shines light on that great island as a reservoir of remarkable avian diversity. Along with other Australasian songbird families (Ptilonorhynchidae, Climacteridae, Acanthizidae, Orthonychidae, Petroicidae, Melanocharitidae, Cnemophilidae, Paramythiidae, Psophodidae, Neosittidae, Cinclosomatidae, Machaerirhynchidae, Paradisaeidae), the newly recognized groups are centred wholly or in significant part in montane New Guinea, in cool rainforests rich in floristic elements once widespread in mid Tertiary Australia (Truswell 1989). Of the eleven newly described taxa, moreover, seven are members of the corvoid assemblage. Although there is general agreement that other root lineages of songbirds arose on the Australian fragment of east Gondwana (Ericson *et al.* 2002; Barker *et al.* 2004; Jønsson *et al.* 2011), the source of the corvoid assemblage has become subject to conflicting interpretations of phylogeographic history and the role of New Guinea.

The now-traditional model, summarized by Schodde (2006) and implicit in Christidis & Schodde (1991), Christidis (1991), Schodde & Faith (1991), Schodde (1991), Ericson *et al.* (2002) and Barker *et al.* (2002, 2004), used direct correlation of palaeogeographic, phylogeographic and biocommunity data to hypothesize:

(1) corvoids arose and first radiated in the widespread rainforests of early–mid Tertiary Australia, along with other root songbird lineages;

(2) ancestral elements of some corvoid groups (Old World orioles, primarily New World vireos, African malaconotoids, Asian ioras, and drongos, shrikes and crows) dispersed out via southeast Asia to radiate in Afro-

Asia and reach North America after the Australian craton drifted far enough north by the mid Tertiary for the Sulawesi ophiolites and adjacent Sunda and South Caroline island arcs to serve as stepping stones (Jønsson *et al.* 2008; Hall 2009);

(3) some, but not all, indigenous corvoid elements diverged *in situ* in Australia as they adapted to sclerophyllous habitats that developed and spread over that continent as it desiccated progressively from later Tertiary into Quaternary times (Byrne *et al.* 2011); and

(4) the great majority of these corvoid elements, together with other root songbird lineages and their supporting rainforest-inhabiting flora and fauna—the substance of the mid Tertiary Australian biome—took refuge in montane New Guinea as its massive rain-catching cordillera rose on the north rim of a drying Australia through the later Tertiary. This fauna and flora is the Tumbunan biota of Schodde & Calaby (1972) and Schodde (2006); it is perceived as substantively relictual, and includes such old avian elements as *Alectura*, *Otidiphaps*, *Psittrichas* and *Cormobates*.

Using Bayesian and LAGRANGE analyses for reconstructing age of divergence and ancestral areas, Jønsson *et al.* (2011) and Aggerbeck *et al.* (2014) reached a different conclusion. They postulated that Australian proto-corvoids reached an emerging proto-Papuan archipelago immediately north of Australia in the early–mid Tertiary, and radiated there instead. From that source, some lineages dispersed episodically out through southeast Asia to radiate in Africa and North America, while others moved back secondarily to Australia or the rising mountains of mainland New Guinea in the later Tertiary. In this model the New Guinea region is interpreted as the powerhouse for the radiation of corvoids.

The second interpretation nevertheless faces difficulties of zoogeographic and palaeogeographic circumstance. One is the dearth of root avian lineages today on islands of the South Caroline-Melanesian island arcs, the presumed source of the corvoid radiation north of the Australian craton. Mayr (1940) pointed this out over half a century ago. Comparative figures for the occurrence of corvoid families in the Bismarck Archipelago and North Moluccas, island groups north of Australia that were mobile components of those arcs over the last 40 MY (Hall 2002, 2009), are given in Table 1. None of the families found there are “relictual”, niche-restricted endemics that might signal an old centre of radiation. On the contrary, most are widespread elsewhere in Australasia and are dispersive, many of their species migratory or nomadic today, and many of their elements reaching the Indonesian archipelagos and Afro-Asia in the past (Jønsson *et al.* 2008).

Another problem is an apparent lack of time-space coincidence in palaeogeographic and cladogenic events. Concerning time, combined estimates from Jønsson *et al.* (2011) and Aggerbeck *et al.* (2014) indicate that modern corvoid families branched from one another between 35 and 20 MYA, in the Oligocene. Concerning space, the stand-out biodiversity hotspot for these lineages is the huge central cordillera of New Guinea (see Table 1). Eighteen of the 29 corvoid families currently recognized occur there (data from Dickinson 2003; Jønsson *et al. l.c.*; Aggerbeck *et al. l.c.*), including the five newly published here; four are endemic. According to a consensus of tectonic reconstructions (Dow 1977; Pigram & Davies 1987; Pigram & Symonds 1991; Charlton 2000; Hall 2002; Schellart *et al.* 2006; and references therein), the New Guinean cordillera had its genesis in ophiolite emplacement along the north rim of the Australian craton in the early Tertiary, picked up on Australia’s northward drift. Increasing pressures on the “mobile belt” thus formed, generated by oblique collision with the westward-moving Pacific plate, resulted in mountain building. Orogenesis appears to have been embryonic from the late Oligocene into the Miocene, *c.* 25—20 MYA, and only accelerated later, culminating in massive, telescopic upthrusting within the last 10 MY. It raised the system into a cohesive cordillera of 3000–5000 m altitude, the highest ranges between the Himalayas and Andes. Over the same post-Oligocene period, New Guinea, as the north rim of the Australian craton, accreted oceanic and continental terranes in the west (Vogelkop), north (Mamberamo-Sepik basins and north coast ranges) and east (Papuan Peninsula), much of it from the South Caroline-Melanesian island arcs (Hall *l.c.*). New Guinea itself has only taken on its present form within the last 5 MY with the raising of the Mamberamo-Sepik basin and episodic flooding of the Arafura Plain.

These complex events, much simplified here and still incompletely resolved (Hall 2002), seem either too early or too late to account for the biogeographic history postulated for corvoids by Jønsson *et al.* (2011) and Aggerbeck *et al.* (2014). In particular, the island arcs north of the Australian craton, which Jønsson *et al.* (*l.c.*) and Aggerbeck *et al.* (*l.c.*) illustrate as the source of the corvoid radiation, appear to have been too far away in the critical late Eocene-early Oligocene period, around *c.* 35 MYA, to receive proto-corvoid stocks (Hall 2009). Clearly, further research is required to determine whether New Guinea was a launching pad or refuge for the corvoid radiation.

TABLE 1. Representation of core corvoid families (22) and subfamilies (5) in Australia, New Guinea, and the fringing North Moluccas and Bismarck Archipelago. Only taxa represented by locally breeding species are included. Circumscription of the corvoid assemblage follows Aggerbeck *et al.* (2014).

Family, subfamily	Australia		New Guinea		North Moluccas	Bismarck Archipelago
	rainforest	sclerophyll (hard-leafed vegetation)	montane (>800 m)	lowland (<800 m)		
Oriolidae	+	+	+	+	+	-
Paramythiidae	-	-	+	-	-	-
Psophodidae	+	+	+	-	-	-
Eulacestomatidae	-	-	+	-	-	-
Daphoenosittidae	-	+	+	-	-	-
Pachycephalidae	+	+	+	+	+	+
Oreoicidae	-	+	+	+	-	-
Falcunculidae	-	+	-	-	-	-
Cinclosomatidae	-	+	+	+	-	-
Campephagidae	+	+	+	+	+	+
Rhagologidae	-	-	+	-	-	-
Artamidae	+	+	+	+	+	+
Artaminae	+	+	+	+		+
Cracticinae	+	+	+	+		
Peltopsinae	-	-	+	+		
Machaerirhynchidae	+	-	+	+	-	-
Rhipiduridae	+	+	+	+	+	+
Lamproliinae	-	-	+	-	-	-
Rhipidurinae	+	+	+	+	+	+
Dicruridae	+	+	-	+	+	+
Ifritidae	-	-	+	-	-	-
Melampittidae	-	-	+	+	-	-
Paradisaeidae	+	-	+	+	+	-
Corcoracidae	-	+	-	-	-	-
Monarchidae	+	+	+	+	+	+
Laniidae	-	-	+	-	-	-
Corvidae	-	+	-	+	+	+
Totals	10 + 3	14 + 3	18 + 5	13 + 4	9 + 1	7 + 2

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