

What is not a bird of paradise? Molecular and morphological evidence places *Macgregoria* in the Meliphagidae and the Cnemophilinae near the base of the corvid tree

Joel Cracraft* and Julie Feinstein

Department of Ornithology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024, USA

The cnemophiline 'birds of paradise' (Cnemophilinae) and Macgregor's 'bird of paradise' (*Macgregoria*) have traditionally been included in the Paradisaeidae although their relationships within the group have been enigmatic and subject to repeated discussion in the literature. Here we use sequences from two mitochondrial genes, cytochrome *b* and cytochrome oxidase I, along with a suite of morphological characters, to investigate their relationships to paradisaeids and other members of the passerine Parvorder Corvida. The combined data strongly support the removal of both groups from the birds of paradise: the cnemophilines are basal members of the Corvoidea and *Macgregoria* is a member of the Meliphagoidea and embedded in the honeyeaters (Meliphagidae) close to the genus *Melipotés*. The amount of sequence divergence among basal passeriforms and members of the Corvida, as well as available fossil evidence for Australian corvidans, suggest that cnemophilines represent an ancient lineage within the corvid radiation. Because cnemophilines and *Macgregoria* have been placed at the base of the paradisaeid tree, hypotheses of morphological, behavioural and ecological character-state transformations within the family will require reanalysis.

Keywords: Paradisaeidae; Corvida; Meliphagoidea; molecular systematics; *Macgregoria*; Cnemophilinae

1. INTRODUCTION

The birds of paradise (Corvida: Corvoidea: Paradisaeidae) encompass one of the more spectacular evolutionary radiations within the vertebrates. About 90 diagnosable phylogenetic species have diversified across New Guinea, nearby islands including the Northern Moluccas, and the eastern rainforests of Australia (Cracraft 1992; recognized as 42 biological species by Frith & Beehler (1998)). In the process, paradisaeids have evolved a stunning array of male plumage patterns and behavioural repertoires—classically explained by various models of sexual selection (Diamond 1986; Beehler 1987, 1989)—as well as diverse patterns of body size and bill morphology.

Because of this morphological and behavioural complexity, relationships among birds of paradise have long been uncertain, and most hypotheses have not been tested using modern phylogenetic methods. As a consequence, a variety of opinion about intergeneric relationships has arisen (Stonor 1936, 1938; Mayr 1945; Gilliard 1969; Diamond 1972; Schodde 1976; Nunn & Cracraft 1996; Frith & Beehler 1998), with much of the controversy centred around the systematic position of the manucodes (subfamily Manucodinae), the subfamily Cnemophilinae, and Macgregor's bird of paradise (*Macgregoria pulchra*). Previous molecular and morphological data have confirmed that the manucodines are indeed the sister group of the core birds of paradise, the Paradisaeinae (Helm-Bychowski & Cracraft 1993; Nunn & Cracraft 1996; Frith & Beehler 1998), and this is supported by new data in this paper.

Virtually all workers over the last 50 years have assumed the cnemophilines and *Macgregoria* to be members, albeit aberrant members, of the birds of paradise. This assumption has major implications for interpreting the evolutionary diversification of paradisaeids because both groups have typically been placed at the base of the family tree (e.g. Bock 1963; Frith & Beehler 1998), which creates a potential historical bias when reconstructing the evolutionary pathways of behaviour, plumage change, ecology and biogeography. That features of *Macgregoria* might be critical for interpreting paradisaeid evolution and behaviour has even found its way into the popular media (Attenborough 1996). Here we eliminate this bias by presenting molecular and morphological evidence that the cnemophilines and *Macgregoria* are not paradisaeids but instead are distantly related members of the corvidan assemblage.

2. METHODS

We sequenced the complete mitochondrial cytochrome *b* gene as well as the first 1020 bp (positions 6645–7661 in the *Gallus gallus* sequence; Desjardins & Morais 1990) of cytochrome oxidase I (COI) for all taxa, following methods previously described for fresh tissue (Nunn & Cracraft 1996; Lee *et al.* 1997) and for tissue taken from museum skins (Mundy *et al.* 1997). Some cytochrome *b* sequences were taken from previous studies (Helm-Bychowski & Cracraft 1993; Nunn & Cracraft 1996) and COI was sequenced for these taxa as well (in parentheses: GenBank accession numbers for cytochrome *b* and COI, respectively, and source of tissue (abbreviations: AM, Australian Museum; AMNH/PRS and AMNH/JC, Department of Ornithology frozen tissue collection, American Museum of Natural History; ANSP, Academy of Natural Sciences,

* Author for correspondence (jlc@amnh.org).

Philadelphia; ANSP/AM, field number of Andy Mack (specimens from ANSP); FMNH, Field Museum of Natural History, Chicago; NHMLAC, Natural History Museum Los Angeles County; NYZP, New York Zoological Park (Wildlife Conservation Society); QM, Queensland Museum, Brisbane; MOV, Museum of Victoria, Melbourne; SP-J, field number of Stephen G. Pruett-Jones; SVE, field number of S. V. Edwards; ZSSD, Zoological Society San Diego): trumpet manucode, *Phonygammmus keraudrenii* (X74252, AF197826, NHMLAC LAK2010); curl-crested manucode, *Manucodia comrii* (U15207, AF197827, AM no number, from S. V. Edwards); raggiana bird of paradise, *Paradisaea (raggiana) augustaevictoriae* (U25738, AF197828, ZSSD A0489241); red bird of paradise, *Paradisaea rubra* (U25736, AF197829, NYZP, AMNH no number); Wilson's bird of paradise, *Diphyllodes respublica* (U15200, AF197830, AMNH 0053 from NYZP); king bird of paradise, *Cicinnurus regius* (U15201, AF197831, ZSSD A0489242); blue jay, *Cyanocitta cristata* (X74258, AF197832, AMNH/JC); satin bowerbird, *Ptilonorhynchus violaceus* (X74256, AF197833, QM 3119); and hermit thrush, *Catharus guttatus* (X74261, AF197834, FMNH 89–285). In addition, sequences of the following taxa are reported here for the first time: American robin, *Turdus migratorius* (AF197835, AF197836, FMNH 88–670 (cytochrome *b*), AMNH/PRS 1189 (COI); Australian raven, *Corvus coronoides* (AF197837, AF197838, AMNH/PRS 2285); Australian magpie, *Gymnorhina tibicen leucnotus* (AF197867, AF197868, AMNH/JC); lesser cuckoo-shrike, *Coracina fimbriata* (AF197839, AF197840, ANSP 1306); crested cnemophilus, *Cnemophilus macgregorii* (AF197841, AF197842, AMNH 816487); yellow-breasted cnemophilus, *Loboparadisaea sericea sericea* (AF197843, AF197844, AMNH 809348); superb blue wren, *Malurus cyaneus* (AF197845, AF197846, AM FB625); straited pardalote, *Pardalotus striatus* (AF197847, AF197848, AM FBI062); white-browed scrubwren, *Sericornis frontalis* (AF197849, AF197850, SVE 1100); yellow-rumped thornbill, *Acanthiza chrysorrhoa* (AF197851, AF197852, AM FB780); white-naped honeyeater, *Melithreptus lunatus* (AF197853, AF197854, MOV 294); noisy friarbird, *Philemon corniculatus* (AF197855, AF197856, AM FB528); Lewin's honeyeater, *Meliphaga lewini* (AF197857, AF197858, AM FB226); noisy miner, *Manorina melanocephala* (AF197859, AF197860, AM FB1582); Macgregor's honeyeater, *Macgregoria pulchra* (AF197861, AF197862, AMNH 342052); common smoky honeyeater, *Melipotes fumigatus* (AF197863, AF197864, ANSP/AM 853); and red-throated myzomela, *Myzomela eques* (AF197865, AF197866, ANSP/AM 1023). Primers were those used in Nunn & Cracraft (1996), as well as many genus-specific primers designed from the sequences reported in that paper (available from authors).

Anatomical characters have long played an important role in paradisaeid systematic studies (e.g. Stonor 1938; Bock 1963; Frith & Beehler 1998) and therefore were included here. Osteological characters were scored for the cranium and humerus for each genus in the study and added to the molecular data set (see table 1 for list and description). Skeletons examined in collections of the American Museum of Natural History include (catalogue numbers in parentheses): glossy-mantled manucode, *Manucodia atra* (AMNH 3967, 3968); crinkle-collared manucode, *M. chalybata* (2832, 6785); *Phonygammmus keraudrenii* (7690); *Paradisaea rubra* (21600); lesser bird of paradise, *P. minor* (4927, 7652); *Cicinnurus regius* (2505); *Diphyllodes magnificus* (7510); *Cnemophilus macgregorii* (16517), *Loboparadisaea sericea* (6467, 6783); variegated fairy wren, *Malurus assimilis* (9371); blue-and-white fairy wren, *M. leucnotus* (9370); brown thornbill, *Acanthiza pusilla* (9450); red-browed pardalote, *Pardalotus rubricatus* (9596),

P. striatus (9461, 9480); large scrubwren, *Sericornis nouhuysi* (6794); perplexing scrubwren, *S. virgatus* (7350), *S. frontalis* (9415); white-plumed honeyeater, *Meliphaga penicillata* (9414); black-and-red honeyeater, *Myzomela rosenbergii* (7528); Papuan black honeyeater, *M. nigrita* (7624); black-headed honeyeater, *M. melanocephala* (23447); New Guinea friarbird, *Philemon novae-guineae* (7433); *P. corniculatus* (1410); white-rumped miner, *Manorina flavigula* (9659); *Melipotes fumigatus* (16073); *Macgregoria pulchra* (6465); brown-headed honeyeater, *Melithreptus brevirostris* (9654); *Ptilonorhynchus violaceus* (4188); *Turdus migratorius* (16067, 18803); *Catharus guttatus* (10569); *Cyanocitta cristata* (10283, 17939); house crow, *Corvus splendens* (22977); black-faced cuckoo-shrike, *Coracina novae-hollandiae* (9304); and Australian magpie, *Gymnorhina tibicen* (11492).

χ^2 -tests of base frequency homogeneity and character partition analyses (incongruence length difference test (ILD) of Farris *et al.* (1994)) were conducted on both the cytochrome *b* and COI sequences and on character partitions using PAUP* 4.0b2 (Swofford 1999) with 1000 replicates and heuristic searches on data with invariant characters removed to avoid problems with this test reported in the literature (Cunningham 1997; Allard *et al.* 1999). PAUP* was also used to generate all sequence distance measures (uncorrected *p*-distance and transversion distance), which were exported to JMP 3.2 (SAS Institute, Inc.) for analysis and plotting.

Global parsimony analyses of all the data were undertaken using PAUP* 4.0b2 (Swofford 1999). Based on previous molecular studies and palaeontological data (Sibley & Ahlquist 1990; Helm-Bychowski & Cracraft 1993; Boles 1995a,b, 1997), it was expected that the majority of the taxa investigated in this study would be relatively divergent from one another, with some representing lineages that presumably had originations early in the Tertiary. Many investigators have long believed this situation can lead to a severe transition bias at third positions and thus have the potential to confound phylogenetic resolution of deeper divergences (e.g. Irwin *et al.* 1991; Meyer 1994; although see Källersjö *et al.* 1999; Broughton *et al.* 1999). In order to explore this possible effect on phylogenetic structure, a parsimony analysis of first and second positions using all changes, along with third positions using transversional changes only (hereafter termed '3Tv parsimony analysis') was undertaken and then compared with the global parsimony analysis. This strategy takes advantage of transitional changes at first and second positions that, compared with third positions, are more conservative and typically result in amino-acid replacements. At the same time, this approach preserves character-state variation at third positions by sampling transversional change; other workers have emphasized the potential phylogenetic informativeness of transversional change in general, and third position transversions in particular (Miyamoto & Boyle 1989; Irwin *et al.* 1991; Yoder *et al.* 1996; Groth 1998; Matthee & Robinson 1999). Two genera of thrushes, *Turdus* and *Catharus* (Turdidae), were used as outgroups; turdids are members of the Parvorder Passerida (Sibley & Ahlquist 1990), which is the sister group to the Corvida. Phylogenetic signal was assessed by use of bootstrap (BS) resampling (500 replicates) using PAUP*'s heuristic-search algorithm (jackknife resampling produced similar results).

3. RESULTS

(a) Sequence comparisons

Both genes had proportional base frequencies typical of avian mitochondrial DNA (e.g. Nunn & Cracraft 1996):

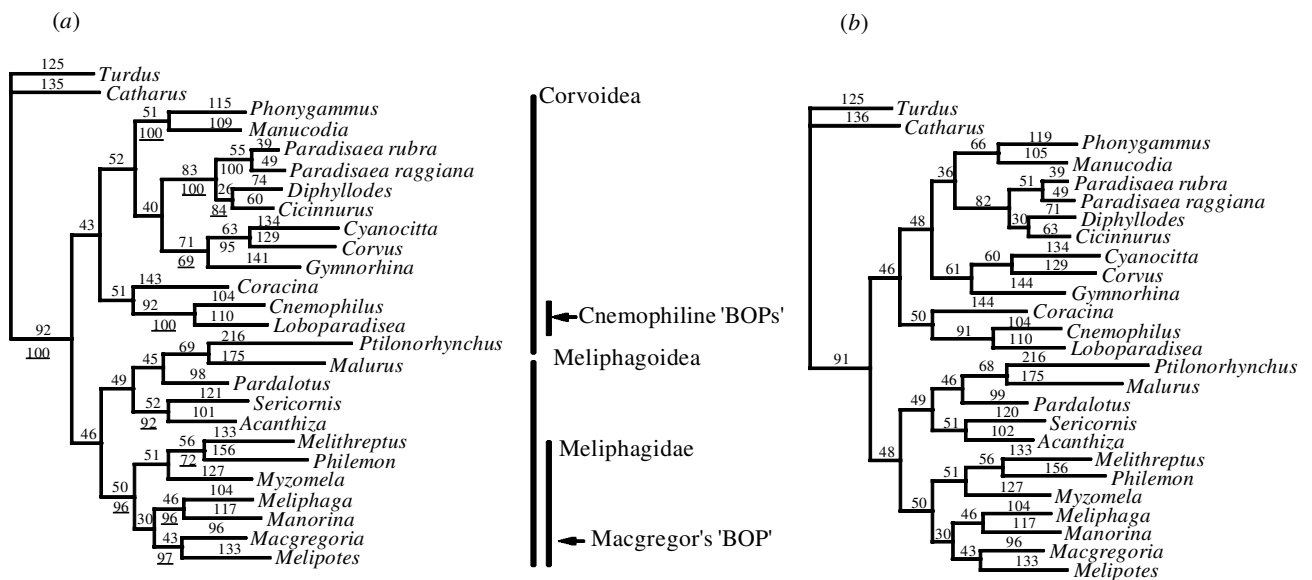


Figure 1. Two equally most parsimonious trees (4300 steps) of a global parsimony analysis (combined molecular and morphological data; morphological transformations treated as discussed in table 1) of corvidan ingroup taxa using two thrushes (Passerida) as outgroups. Numbers above branches are branch lengths; underlined numbers below branches are bootstrap values (500 replicates with heuristic search; only values > 50% shown). In both trees, the cnemophiline 'birds of paradise' and Macgregor's 'bird of paradise' are found to be distant relatives of paradisaeids.

cytochrome *b* (A, 28.7%; C, 33.1%; G, 13.1%; T, 25.1%), COI (A, 27.8%; C, 29.4%; G, 17.5%; T, 25.3%). Base frequencies were also found to be homogeneous across all taxa (cytochrome *b*, $\chi^2 = 42.092$, d.f. = 69, $p = 0.996$; COI, $\chi^2 = 46.107$, d.f. = 69, $p = 0.985$). These observations, the absence of any stop codons in the sequences, and the results from the phylogenetic comparisons are consistent with the amplified fragments being mitochondrial and not nuclear.

Pairwise *p*-distances and transversion distances were examined for each codon position as compared with overall divergence (data not shown). Because of the nature of the questions being asked in this study, relatively few closely related taxa were included; instead, the taxon sample spans the breadth of the corvidan passerines, many of which are distantly related (Sibley & Ahlquist 1990; Helm-Bychowski & Cracraft 1993). As a consequence, all pairwise comparisons—except for six within the Paradisaeinae—exhibit greater than 10.0% sequence divergence, and the majority are greater than 14.0%. These patterns are also seen in pairwise comparisons of transversion distances, only 11 comparisons exhibit transversion distances of less than 3.0%. Thus, as expected, third position transitions begin to show saturation near 10.0% *p*-distance (only six pairwise comparisons being below 10.0% *p*-distance).

(b) Phylogenetic analysis

Partition homogeneity tests on the two genes using the global and 3Tv parsimony strategies revealed that neither represented a significantly different partition (global analysis, $p = 0.387$; 3Tv analysis, $p = 0.597$). The data thus fit the criterion some workers have proposed that different data sets can be combined when they do not show evidence of biased phylogenetic signal (Bull *et al.* 1993). More interesting, however, is the observation that the 3Tv

analysis increased the congruence between the two genes (see below).

Phylogenetic analyses were undertaken on 2163 bp of mitochondrial sequence and 17 morphological characters, for a total of 2180 characters. The results of a global parsimony analysis, giving all characters equal weight, yielded two equally parsimonious trees of 4300 steps (figure 1). Under each reconstruction both the cnemophilines and *Macgregoria* are removed from the birds of paradise. The cnemophilines have a surprising association with the campephagid *Coracina*, whereas *Macgregoria* is placed in the distantly related honeyeaters (Meliphagidae) near the genus *Melipotés*. The result for the cnemophilines is more ambiguous than for *Macgregoria* in that bootstrap values supporting the branch points between the cnemophilines and paradisaeids are below 50%. Those for *Macgregoria*, on the other hand, strongly support its placement within the meliphagids.

The global parsimony trees exhibit several highly unexpected results. First, in both trees the Meliphagoidea are not monophyletic because the bowerbird *Ptilonorhynchus* is clustered with the fairy wren *Malurus*, a relationship that is not supported by protein evidence (Christidis & Schodde 1991) or by DNA hybridization (Sibley & Ahlquist 1990). Furthermore, in one tree (figure 1a) the two lineages of the birds of paradise are not monophyletic despite a substantial amount of molecular and morphological evidence to the contrary (Sibley & Ahlquist 1990; Helm-Bychowski & Cracraft 1993; Frith & Beehler 1998). Other relationships are equally unexpected, including the cracticid *Gymnorhina* with the corvids, and *Pardalotus* with *Malurus* plus *Ptilonorhynchus* rather than with meliphagids and the acanthizids *Sericornis* and *Acanthiza* (Sibley & Ahlquist 1990; Christidis & Schodde 1991).

These results raise the conjecture that global parsimony is giving us a misleading signal; if so, what factors might

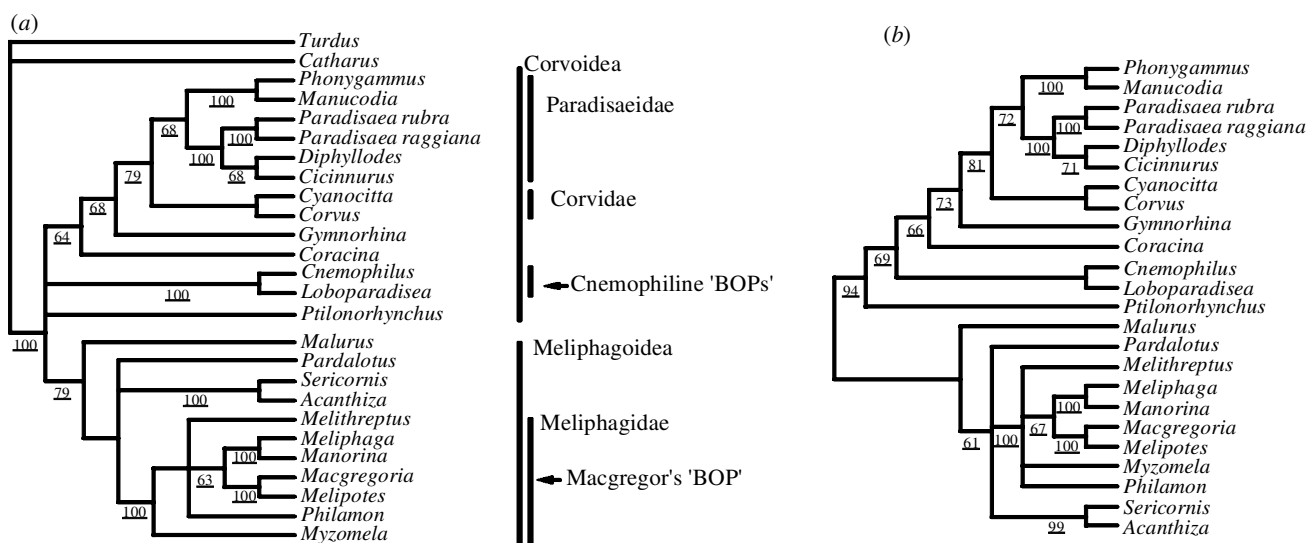


Figure 2. (a) A strict consensus tree produced by 3Tv parsimony analysis (morphological data treated as in the analysis of figure 1) of corvidan ingroup taxa using two thrushes (Passerida) as outgroups. Three equally parsimonious trees of 1845 steps were found. (b) Analysis of the corvidan ingroup using 3Tv parsimony analysis, with the thrush outgroups deleted and midpoint rooting used to place the root, produced two equally most parsimonious trees of 1682 steps. Underlined numbers below branches are bootstrap values (only values > 50% shown). In both analyses, the cnemophilines and *Macgregoria* are far removed from the paradisaeids.

be invoked to explain these results? One possible explanation is homoplasy in third positions due to an excess of transitional change. *Ptilonorhynchus* and *Malurus*, for example, could be clustering together (but with bootstrap support of less than 50%) due to having very long branches. One test of this (Siddall & Whiting 1999) is to see whether the two suspect taxa maintain their relative positions when the other is deleted. When *Ptilonorhynchus* is deleted, *Malurus* remains grouped with the pardalotids and acanthizids in the Meliphagoidea, which is relatively consistent with the work of others (e.g. Sibley & Ahlquist 1990); when *Malurus* is deleted, however, *Ptilonorhynchus* moves to the base of the corvids. This suggests *Ptilonorhynchus* was attracted to *Malurus* for reasons other than a close relationship.

Second, compared with the relatively long terminal branches of the majority of taxa, internodal branch lengths are much shorter, thus making spurious associations among lineages more likely. Finally, when first and second positions, on the one hand, are compared with third positions using an ILD test, the two partitions are discovered to be weakly incongruent or very weakly congruent depending on the level of significance one is willing to accept ($p = 0.091$). The phylogenetic signal thus appears to be different in the two partitions. To test whether this weak incongruence might be related to an excess of third position transitions, an ILD test was performed on the 3Tv data set comparing all first and second position changes with that of third position transitions; congruence between the partitions now increases substantially ($p = 0.194$), thus implying that transitions in third positions are contributing to a different phylogenetic signal. Both ILD tests were undertaken to maximize their effectiveness (Cunningham 1997; Allard *et al.* 1999).

Because of a number of questionable phylogenetic associations produced under global parsimony and the

suggestion from the ILD test that these might be due, at least in part, to homoplasy within third position transitions, an analysis was undertaken in which transitional changes were eliminated from third positions. In the 3Tv parsimony analysis, an assessment of phylogenetically informative variation of all the molecular and morphological data yielded three equally parsimonious trees of 1845 steps (figure 2a). In the strict consensus the Paradisaeidae are monophyletic and the corvids are their sister group, followed by the cracticid *Gymnorhina*, the campephagid *Coracina*, and then an unresolved polytomy involving the cnemophilines, bowerbirds and the meliphagoids. Within the meliphagoids, *Malurus* is at the base, the meliphagids are monophyletic, and *Sericornis* and *Acanthiza* are united but unresolved with respect to *Pardalotus*. Once again, *Macgregoria* is clustered with *Melipotus* with high bootstrap support. Overall, the tree is much more congruent with relationships inferred from other data such as DNA hybridization (Sibley & Ahlquist 1990) than are the results of the global parsimony analysis (figure 1).

In this analysis both the cnemophilines and *Macgregoria* are far removed from the Paradisaeidae. The Meliphagoidea are strongly monophyletic (with 79% BS) and separated from the other corvidans. Using this data set, the base of the corvids and the placement of the root remain ambiguous, yet the data are consistent with the hypothesis that cnemophilines are basal corvids along with bowerbirds.

The potential influence of a distant outgroup on the ingroup reconstruction was also evaluated in a separate analysis (figure 2b; two trees of 1682 steps). Eliminating the two thrushes and using midpoint rooting produced a result nearly identical to that of figure 2a except that now the cnemophilines are seen as the sister group of all corvids except the bowerbirds. Moreover, eliminating the outgroup has resulted in strong support (94% BS) for

the separation of the meliphagoids and corvids (assuming the root is correctly placed). Support for the placement of the cnemophilines near the base of the corvid lineage and distant to the paradisaeids has increased over the results of figure 2a, as they are separated from paradisaeids by a series of nodes with moderate to high bootstrap values. *Macgregoria* is once again clustered with *Melipotés*.

The removal of the cnemophilines and *Macgregoria* from the paradisaeids is not merely a consequence of combining the molecular and morphological data. A 3Tv analysis of each gene separately, or combined, results in the cnemophilines being placed at or near the base of the corvids (resulting multiple parsimonious trees preclude an exact placement), far removed from paradisaeids, and in having *Macgregoria* united with *Melipotés*.

(c) Morphological evidence

Corvidans exhibit a large amount of variation in skull morphology (Stonor 1938; Bock 1963), and some of that is relevant for understanding the phylogenetic position of the cnemophilines and *Macgregoria*. Following are new observations and interpretations relevant to the systematics of these two taxa based on 15 characters from the skull and two from the humerus (table 1).

Table 2 lists character-state changes optimized on, and common to, all three most parsimonious trees of figure 2a that are pertinent to the phylogenetic placement of the cnemophilines and *Macgregoria*. A total of ten morphological character-state changes exclude the cnemophilines from the paradisaeids and at the same time place them at the base of the corvidan tree. None of the changes are unique (i.e. have a consistency of 1.00) across the entire tree, but all but one (character 2) are unique within the corvids above the level of the cnemophilines. Cnemophilines possess many features that are primitive relative to the derived condition of paradisaeids and their close relatives: delicate vomers that are barely expanded distally, and thin dorsoventrally (Bock 1963), absence of ossification in the floor of the nasal cavity (when viewed ventrally; Bock 1963, figs 4 and 5), absence of a nasal septum, maxillopalatines that are club-shaped at their distal end and excavated laterally (Bock 1963, fig. 1). Thus, the morphological data, like the molecular data, support the hypothesis that cnemophilines are not closely related to paradisaeids but are primitive corvidans with a skull much like that of bowerbirds.

The morphological data indicate that *Macgregoria* is nested deeply within the Meliphagoidea and is the sister taxon of the meliphagid *Melipotés*. This relationship is supported by 12 character-state changes on the three most parsimonious trees, and two of those character-state transformations, 16(2) and 10(1), are unique on the entire tree. Like the cnemophilines, *Macgregoria* lacks the derived corvid characters mentioned above. Instead, it shares many characters of meliphagoids, and of meliphagids in particular, including long and narrow maxillopalatines that are club-shaped and highly excavated, a distinct and expanded foot of the ectethmoid that rests along the jugal bar (Bock 1963, fig. 9), very long transpalatine processes, and a derived condition of the pneumatic fossae of the humerus (see table 2 for others).

4. DISCUSSION

(a) Systematics of *Macgregoria*

Macgregoria was described as a paradisaeid without discussion (De Vis 1897), and Sharpe (1891–1898) soon thereafter suggested a close relationship between *Macgregoria* and the paradisaeid genus *Paradigalla*, presumably because both have nearly all black plumage. Since that time most workers have left *Macgregoria* within the paradisaeids, but with little supporting evidence; Iredale (1950), on the other hand, proposed removing *Macgregoria* from the Paradisaeidae, but again for no stated reason other than it was different from other paradisaeids. The only relevant data after that time were provided by Bock's (1963) discussion of cranial anatomy, and he proposed that *Macgregoria* was closer to the cnemophilines than to the paradisaeines. This conclusion was reached, however, largely because character variation was not examined across all corvidans, nor were character polarities understood within a cladistic framework. As demonstrated in this study, *Macgregoria* and the cnemophilines have a much more primitive skull than do paradisaeines, but this primitive resemblance cannot be used as evidence of their close relationship. Recently, Frith & Beehler (1998) examined 52 characters, mostly plumage, and placed *Macgregoria* as the sister group of the Paradisaeinae. Their sampling, however, was restricted to birds of paradise except for three outgroup taxa, none of them basal corvids. Their conclusions regarding *Macgregoria* were based on a single osteological character, the supposed presence of an ossified nasal septum in *Macgregoria* and paradisaeines, but in fact *Macgregoria* lacks a nasal septum (as discussed above), a condition typical of basal corvids and meliphagoids. Other characters noted by them are found elsewhere among the corvids and thus do not specify a *Macgregoria* and Paradisaeinae relationship.

The molecular and morphological data strongly support the placement of *Macgregoria* within the Meliphagidae, and taking into account the small sample of meliphagid genera included here, *Macgregoria* is the sister group of *Melipotés*. This is a placement borne out by a more comprehensive sample of meliphagids currently under study (A. Driskell, personal communication). The three species of *Melipotés* all have a well-developed yellow facial apterium beginning anteriorly at the eye and which is wattle-like ventrally. This facial patch can flush red when the bird is excited. In *Macgregoria* the wattle is fully developed and anchored at the eye; unlike in *Melipotés* the wattle cannot flush red. Given the hypothesis that *Macgregoria* and *Melipotés* are sister taxa, the two conditions of the facial wattle should probably be considered homologous despite their differences. The apterium–wattle of *Melipotés* is probably the primitive condition.

The species of *Melipotés* are dark grey or black, with light mottling or spotting; the plumage of *Macgregoria* is deep black. The bill shape in the two genera is virtually identical. Both have a pinkish egg, with brown spotting that is more abundant at its large end (Rand 1940; Coates 1990, p. 266). Species in both genera are frugivores (Beehler 1983, 1988; Beehler *et al.* 1986). All of these data are consistent with the results of the molecular analysis. At the same time *Macgregoria* must be considered a highly derived meliphagid in being large and bulky, in having

Table 1. *Morphological characters and character-states for taxa in this study*

(Characters, character-states, and whether character was treated as ordered or unordered include the following. 1. Nasal septum: (0) absent; (1) present. Ordered. 2. Vomer: (0) relatively delicate, little expansion anteriorly, dorsoventrally flattened, with broad, shallow groove dorsally; (1) relatively delicate, flattened dorsoventrally, with lateral sides of distal end having short projections; (2) more robust, broadened distally, with distal end elaborated, with dorsal groove broad but deeper than in (0) or (1); (3) very robust, dorsal groove very deep and narrow; (4) robust, broadened distally, only moderately deep dorsal groove, braces nasal septum, distal end with robust anterior projections; (5) very broad distally, dorsal groove only moderately deep, braces nasal septum and mediopalatine process of premaxilla, robust anterior projections. Ordered, character-state tree: ((5)4,3)2,1)0. 3. Mediopalatine process of premaxilla: (0) absent; (1) present, does not extend posteriorly much beyond palatine-premaxilla junction; (2) extends well beyond junction. Ordered. 4. Maxillopalatine: (0) long, thin, delicate bone with expanded elongate club-shaped posterior end that is excavated laterally; (1) flat triangular or long narrow plate-like structure, not club-shaped and excavated. Ordered. 5. Zygomatic process and mandibular musculature: (0) zygomatic moderately well developed and tapering to point, does not divide temporal fossa; (1) zygomatic heavy, short, and blunt, separated from quadratocranial articulation, divides temporal fossa into two compartments, and is strongly excavated ventrally for muscles in lower compartment; (2) zygomatic long and thin, ends in sharp point, does not divide temporal fossa; (3) zygomatic short and blunt, does not divide temporal fossa; (4) zygomatic relatively short, excavated on lateral side for muscle attachment but does not divide temporal fossa. Unordered. 6. Temporal fossa: (0) relatively small, extends slightly beyond border of paroccipital process; (1) very small, confined anterior to border of process; (2) large, expands far posterior to border of process. Unordered. 7. Transpalatine processes: (0) relatively short and blunt at end; (1) relatively short and pointed at end; (2) very long, narrow, pointed at end. Unordered. 8. Interpalatine processes: (0) very short, blunt, nearly absent; (1) relatively long and thin. Unordered. 9. Palatine, ventral crest (= mediopalatine of Bock (1963)): (0) posterior end with sharp rise to level of articulation with pterygoids; (1) posterior end of crest grades smoothly to articulation. Ordered. 10. Ectethmoid, foot: (0) not well demarcated by strong constriction, not elongated and lying flat along jugal bar; (1) elongated, lying flat along jugal bar, with anterior projection. Ordered. 11. Ectethmoid, head: (0) not greatly expanded posteriorly or anteriorly, with relatively narrow articulation to frontal and, partially, to nasal-frontal hinge; (1) head not well developed, fused to frontal just posterior to nasal-frontal hinge by very narrow, neck-like connection; (2) head not connected to frontal, lacrimal intervenes; (3) head very large, expanded posteriorly along frontal and anteriorly along lateral nasal bar. Unordered. 12. Quadrate, orbital process: (0) tapers to end, foot poorly to only moderately developed and orientated more or less along axis of process; (1) foot well developed and orientated perpendicular to axis of process (T-shaped); (2) foot entirely absent, process tapers to blunt point. Unordered. 13. Quadrate, medial condyle: (0) projects ventrally to same degree as lateral condyle, or projects only slightly more ventrally; (1) medial condyle projects decidedly more ventrally relative to lateral condyle, which is strongly to moderately flattened, not rounded. Unordered. 14. Lacrimal: (0) absent or vestigial; (1) well developed, bracing lateral nasal bar and jugal. Ordered. 15. Ectethmoid, dorsal foramen in head: (0) absent; (1) present. Ordered. 16. Humerus, pneumatic and secondary pneumatic fossae: (0) secondary fossa present, deeply undercuts head of humerus, separated from pneumatic fossa by median crest (medial bar) so that two fossae are distinct and not broadly confluent; (1) secondary fossa absent, surface of bone external to internal tuberosity only slightly or moderately excavated for muscle attachment, attachment for supraspinatus not deep in pneumatic fossa, median crest well developed; (2) secondary fossa essentially absent but bone is moderately to strongly excavated, with median crest being reduced and present only proximally so that both pneumatic fossae are broadly confluent, supraspinatus attachment a very deep pit in pneumatic fossa. Unordered. 17. Humerus, attachment of brachialis: (0) triangular and shortened proximodistally, very deep pit; (1) elongated, tapering proximally, relatively shallow throughout. Ordered.)

	character-states
taxon	0000000000111111 12345678901234567
<i>Turdus</i>	0000000000210000
<i>Catharus</i>	0000020000000000
<i>Phonygammus</i>	14111000001110010
<i>Manucodia</i>	14111000001110011
<i>Paradisaea rubra</i>	15211201001110011
<i>Paradisaea raggiana</i>	15211201001110011
<i>Diphylloides</i>	15211201001111011
<i>Cicinnurus</i>	15211201101111011
<i>Cyanocitta</i>	02103001001011011
<i>Corvus</i>	02110001001111011
<i>Coracina</i>	02103201000011011
<i>Gymnorhina</i>	13012021003011011
<i>Cnemophilus</i>	00003000000100110
<i>Loboparadisea</i>	00003000000100110
<i>Ptilonorhynchus</i>	00014211002001010
<i>Malurus</i>	01012111100200010
<i>Pardalotus</i>	01014111100200020
<i>Sericornis</i>	00002101100200020
<i>Acanthiza</i>	00002111100200020
<i>Melithreptus</i>	01012120110210020
<i>Meliphaga</i>	01000121113200020
<i>Macgregoria</i>	010021201131000??
<i>Melipotus</i>	01002120110100020
<i>Myzomela</i>	01012120110200020
<i>Philamon</i>	01002120113210020
<i>Manorina</i>	01000120113210020

Table 2. Morphological character transformations on trees of figure 2a that are relevant for the phylogenetic placement of the cnemophilines and *Macgregoria*

(Number refers to characters in table 1 that diagnose the relevant clade on all three most parsimonious trees; number in parentheses refers to the derived character-state. The characters under the cnemophilines exclude them from higher hierarchical levels; the numbers under *Macgregoria* include it at higher hierarchical levels within the Meliphagoidea.)

cnemophilines		<i>Macgregoria</i>	
clade	derived characters lacking in cnemophilines	clade	derived characters possessed by <i>Macgregoria</i>
<i>Coracina</i> + higher corvids	2(2), 3(1), 13(1), 17(1)	Meliphagoidea	2(1), 6(1), 9(1), 12(2)
<i>Gymnorhina</i> + higher corvids	1(1), 11(1)	all meliphagoids but <i>Malurus</i>	16(2) ^a
corvids + paradisaeid	12(1)		
Paradisaeidae	2(4), 5(1), 14(0)	Meliphagidae branches within meliphagids	7(2), 8(0), 10(1) ^a 13(1), 4(0), 11(3)
		<i>Macgregoria</i> + <i>Melipotés</i>	12(1)

^a Had a consistency on all trees of 1.00.

soft deep black plumage, and in having a large deep orange wing patch.

(b) Systematics of the cnemophilines

The cnemophilines have also had a somewhat confusing taxonomic history. In the days of their discovery many workers viewed the birds of paradise and bowerbirds to be very closely related and some united them in a single family. When *Cnemophilus macgregorii* was first described, DeVis (1891, pp. 39–40) placed this new genus and species in the Ptilonorhynchidae, presumably because their bright yellow and red pigments in their plumage resemble those of various bowerbirds, particularly *Amblyornis* and *Xanthomelus* (= *Sericulus*) to which he thought *Cnemophilus* to be closely allied. Likewise, early workers (Sclater 1895; W. Rothschild in Rothschild & Hartert (1896)) placed *Loria*, another cnemophiline, within ptilonorhynchids. At the same time, however, they were drawing attention to features they believed indicated a relationship between the cnemophilines and birds of paradise (Sclater 1891, 1895, p. 344). The preponderance of recent opinion, following Mayr (1962), Bock (1963), and Gilliard (1969), has placed cnemophilines with the birds of paradise.

Bock (1963, fig. 13) envisioned cnemophilines as being ancestral to both birds of paradise and bowerbirds, a conclusion that might be reached by a general phenetic analysis of morphological features but which cannot be supported by molecular and morphological data interpreted cladistically. The cnemophilines appear to be neither birds of paradise nor bowerbirds, but they share a primitive cranial anatomy with bowerbirds and, like bowerbirds, represent an early lineage of the corvids.

(c) Australasian avifaunal history

Investigating the history of corvidans within Australia necessarily begins with an understanding of their phylogenetic relationships. This study, although by no means comprehensive in its taxon sampling, is consistent with the hypothesis that the corvidans can be separated into two major lineages, the Corvoidea and Meliphagoidea. These results further corroborate the hypothesis that bowerbirds are close to, or at the base of, the corvids and postulate for the first time that the cnemophilines are

the next oldest branch. This raises the issue of when the cnemophiline lineage might have originated.

Ideally, an answer to this question would draw on fossil evidence, but in this case it is meagre. The oldest known passerine bird is from the early Eocene of Australia (about 54.6 million years before present (Myr BP); Boles 1995a, 1997), but its exact affinities cannot be resolved. If this fossil is related to either the Corvida or Passerida, it would set a minimum age for their divergence, and the age of the fossil is consistent with speculations that passeriforms began diverging at least 55 Myr BP (Sibley & Ahlquist 1985). Fossil evidence indicates that several distantly related corvidan lineages (menurids, orthonychids) had differentiated in Australia by about the early Miocene (Boles 1993, 1995b), thus implying a still more ancient origin for the group as a whole. Minimally, these observations suggest the Corvida have probably been in Australia since sometime in the early Tertiary. Using DNA hybridization data Sibley & Ahlquist (1985, 1990) proposed that the Corvida originated in Australia and asserted their separation from the remaining oscine passerines, the Passerida, to be 58–60 Myr BP (Sibley & Ahlquist 1985, p. 4). Considerable uncertainty must be ascribed to this conjecture as it derives from a dubious and poorly calibrated molecular clock.

The fossil evidence (reviewed in Boles (1997), and above) permits the inference that the major split between the Passerida and Corvida took place at least by the early Tertiary. That age therefore places a minimal boundary on interpreting the molecular data and their potential for inferring something about the temporal depth of the corvidan radiation within Australia. Because transversion distances are thought to be roughly linear with time (e.g. Miyamoto & Boyle 1989; Matthee & Robinson 1999), they can be employed as a general index to relative times of divergence. Transversion differences from the thrush (Passerida) outgroups to the corvine ingroups range from 5.8 to 7.9%; from meliphagoid taxa to the corvids, 5.6 to 7.9%; from *Ptilonorhynchus* to other corvids, 6.3 to 7.5%; and from cnemophilines to other corvids (except *Ptilonorhynchus*), 5.6 to 6.9%. Conservatively, two conclusions might be drawn from these data. First, the variability in distances within and among these sister groups suggests the existence of variable evolutionary rates of

transversional change. The degree to which this is the case, however, cannot be investigated meaningfully until taxon samples are increased, as inadequate sampling itself could lead to apparent rate variability of some lineages. Second, the distances, especially the high values, indicate that the separation of the Passerida and Corvida, and the subsequent diversification of the basal lineages within the latter, appear to be nearly contemporaneous. This seems to be true of the cnemophilines as well, and thus these data suggest they represent a relatively old, possibly Eocene or Oligocene element, within the Australian avifauna.

Previous genetic studies have supported the hypothesis that honeyeaters (Meliphagidae) are also an ancient radiation within Australasia (Sibley & Ahlquist 1985, 1990; Christidis 1991; Christidis & Schodde 1991), a conclusion consistent with a maximal transversion distance within the family of 5.2% observed in the small sample of this study (table 1). *Macgregoria* is 2.6% transversional distance (10.5% uncorrected *p*-distance) from *Melipotus*, which indicates the two groups have been separated for a moderate amount of time.

(d) *Implications for understanding evolution of the birds of paradise*

Virtually all discussions of paradisaeid evolution—morphological, behavioural, ecological—have been predicated on the assumption that cnemophilines and *Macgregoria* are paradisaeids and occupy a primitive position within the family. But placing these two taxa near the base of the paradisaeid tree results in their characters having an influence on postulated evolutionary transformations within the family. This has been true for features such as mating systems, sexual dimorphism, ancestral plumage pattern, and ancestral distributions. Removing the cnemophilines and *Macgregoria* from the birds of paradise will necessitate a re-evaluation of their morphological and behavioural evolution once relationships within the family are better understood. Thus, although the manucodines are the strongly supported sister taxon to the paradisaeines, compelling evidence for basal relationships within the core birds of paradise (Paradisaeinae) has not yet been presented.

(e) *Vernacular names*

The removal of the cnemophilines and *Macgregoria* from the paradisaeids necessitates a change in their vernacular names since all are referred to as birds of paradise. The cnemophilines have no readily available vernacular name, hence it is proposed here that the three biological species be called Loria's cnemophilus (*Cnemophilus loriae*), crested cnemophilus (*C. macgregorii*), and yellow-breasted cnemophilus (*Loboparadisea sericea*). The word 'cnemophilus' refers to being a lover of the mountain slope (Frith & Beehler 1998, p.178), which characterizes all the species. *Macgregoria pulchra* can now be called Macgregor's honeyeater.

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