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ORIGINAL ARTICLE

On the phylogenetic position of the scrub-birds (Passeriformes: Menurae: Atrichornithidae) of Australia

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Abstract Evolutionary relationships of the scrub-birds *Atrichornis* were investigated using complete sequences of the recombination-activating gene RAG-1 and the proto-oncogene *c-mos* for two individuals of the noisy scrub-bird *Atrichornis clamosus*. Phylogenetic analysis revealed that *Atrichornis* was sister to the genus *Menura* (the lyrebirds) and that these two genera (the Menurae) were sister to the rest of the oscine passerines. A sister relationship between *Atrichornis* and *Menura* supports the traditional view, based on morphology and DNA hybridization, that these taxa are closely related. Similarly, a sister relationship with the remaining oscine passerines agrees with the morphological distinctiveness of *Atrichornis* and *Menura*, although this result contradicts conclusions based on DNA hybridization studies. Although *Atrichornis* is very well known morphologically, previous conclusions regarding its relationships were hampered by a lack of comparative knowledge of other passerines, making concurrence of the sequence data of particular significance.

Keywords *Atrichornis* · Menurae · Passeriformes · Phylogenetics · Scrub-birds

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Introduction

The Australian endemic family Atrichornithidae consists of two species of small passerine bird: the noisy scrub-bird *Atrichornis clamosus* (Gould 1844), an inhabitant of scrub and dry forest in southwestern Australia, and the rufous scrub-bird *A. rufescens* (Ramsay 1866), found in subtropical rainforests of eastern Australia. Both are ground-dwelling species of limited distribution, highly secretive and uncommon within their respective ranges; indeed, *A. clamosus* was considered extinct for many decades prior to its rediscovery in 1961 (Webster 1962a, b).

John Gilbert, collector of the first specimens of *A. clamosus*, considered the scrub-birds to be similar to the bristlebirds (genus *Dasyornis*), with whom they share ecological, behavioural and vocal features, and this was their original taxonomic placement (Gould 1865). They have also been considered to be closely related to other Australian ground-dwelling taxa, including the whipbirds (genus *Psophodes*; Chisholm 1951). For the past century, however, most systematists have considered scrub-birds to be the sister group to the lyrebirds (genus *Menura*, family Menuridae), a relationship first promulgated by Garrod (1876).

The broader relationships of *Atrichornis* have also received considerable attention. Garrod (1876) proposed a separate grouping within the oscines, the Acromyodi Abnormalis, for *Atrichornis* and *Menura*, with the remainder of the songbirds forming the Acromyodi Normalis. Sclater (1880) went further, characterizing *Atrichornis* and *Menura* as "the most anomalous forms of Passerine birds yet known" and considering them to constitute a suborder of Passeriformes removed from the oscines. This arrangement was followed by most ornithologists over the next 100 years (e.g., Mayr and Amadon 1951; Wetmore 1960),

although many morphologists (see Bock and Clench 1985) considered *Atrichornis* and *Menura* to be oscine.

Sibley's (1970, 1974) studies of egg-white proteins did not include *Atrichornis*, but indicated that the lyrebirds were oscines closely related to the bowerbirds (Ptilonorhynchidae) and birds of paradise (Paradisaeidae), and he suggested that the suborder Menurae (consisting of *Menura* and *Atrichornis*) be merged into the oscines. Results of his subsequent DNA hybridization studies (Sibley and Ahlquist 1985, 1990) indicated that *Atrichornis* and *Menura* were oscine birds embedded within the parvorder Corvida and that their nearest relatives were the bowerbirds (which the hybridization evidence indicated were not closely related to the birds of paradise).

Recent studies of passerines based on DNA sequence data (Barker et al. 2002, 2004; Ericson et al. 2002a, b) have found important differences compared to the DNA hybridization results (Sibley and Ahlquist 1985, 1990), especially in terms of the early radiations of Australasian songbirds. The results of these studies, for example, showed the Corvida (Sibley and Ahlquist 1985, 1990) to be a paraphyletic grade basal to other oscines, the most basal branches of which consisted exclusively or largely of Australasian taxa. Within this context, *Menura* was found to be sister to all other oscines. However, these studies were unable to incorporate sequence data from the genus *Atrichornis*. In this paper, we use DNA sequence data from the noisy scrub-bird, *A. clamosus*, to address the relationships of the scrub-birds both to *Menura* and, more generally, within the Passeriformes and to compare these results to those of studies based on morphology and DNA hybridization.

Methods

Blood samples from individuals of *A. clamosus*, captured for translocation by the Western Australian Department of Conservation and Land Management (CALM), were donated to the Australian National Wildlife Collection (ANWC). DNA was extracted from two samples (01M01 and 01M04; ANWC 10646 and 10649, respectively) using the CTAB DNA extraction method (Doyle and Doyle 1987), with modifications as described below. A small amount of blood, previously preserved in EtOH, was placed in a 1.5-ml tube with 300 µl of 2× CTAB buffer in the presence of Proteinase K (20 mg/ml) at 20 µl/500 µl CTAB and β-mercapto-ethanol (0.6 µl/300 µl). This was incubated at 60°C overnight. The mixture was then extracted twice with equal volumes of $CHCL_3$:IAC (96:4) and centrifuged for 5–10 min at 13,000 rpm. The DNA was precipitated through the addition of 0.1 vol. 3 *M* NaOAc and 2.5 vol. EtOH (RT), mixed by inversion, incubated at RT for approximately 2 min and centrifuged at 13,000 rpm for 10 min. The pellet was washed with 70% ethanol and air-dried before resuspending in 50–100 µl 0.1× TE/10 µg/ml RNaseA.

Following Barker et al. (2002), we sequenced two nuclear exons – the recombination-activating gene RAG-1 (Schatz et al. 1989; Carlson et al. 1991) and the proto-oncogene *c-mos* (Schmidt et al. 1988; Saint et al. 1998) – for two individuals of *A. clamosus*. The primers used for amplification and sequencing have been published previously (Groth and Barrowclough 1999, Barker et al. 2002), except for 13C (5′-TCTGAATGGAAATTCAAGCTCTT-3′) and R659L (5′-GTCAAGAGAAAAAGCCAGCCC-3′), developed by J.G. Groth. Primer pairs used to amplify RAG-1 (13C/18, 17/22 and 21/2I) were chosen to generate three overlapping fragments. All amplifications were performed on an Eppendorf Mastercycler (gradient) in 200-µl striptubes, using a 50-µl reaction volume containing 200 μM dNTPs, 1.5 m*M* $MgCl_2$, 50 pmol of each of the primers, 1× PCR buffer and 0.5 U *Taq* DNA polymerase (Gibco-BRL, Gaitersburg, Md.). RAG-1 amplifications were conducted using a step-down PCR protocol: five cycles of denaturing at 96°C for 20 s (4 min in cycle 1), annealing at 58°C for 15 s and extension at 72°C for 1 min; five cycles with annealing at 56°C; five cycles with annealing at 54°C; 25 cycles with annealing at 52°C, followed by a final extension of 5 min. *C-mos* was amplified using primers CM5 and CM6 under the following conditions: five cycles of denaturing at 96°C for 20 s (4 min in cycle 1), annealing at 65°C for 30 s, extension at 72°C for 1 min; 30 cycles with annealing at 60°C, followed by a final extension of 5 min. The PCR products were visualized on an agarose gel and purified using the Qiagen gel extraction kit (Valencia, Calif.). The L-strand and H-strand were sequenced for both genes. RAG-1 primers 13C, 15, 23, 17, 19, R659L and 21 were used to sequence the L-strand, and RAG-1 primers 16, 18, 2I, 20, 22, and 24 to sequence the H-strand. *C-mos* sequencing was performed using the amplification primers CM5 and CM6. Sequencing was conducted using dye-terminator chemistry on an ABI 377 automated sequencer (Applied Biotechnologies, Foster City, Calif.). All sequences obtained for *A. clamosus* have been deposited in GenBank (accession numbers EF463007–EF463010).

Sequences were aligned and edited in SEQUENCHER ver. 4.1 (GeneCodes 2000) and combined with the data set of Barker et al. (2002). Phylogenetic analyses of the resulting 73-taxon data set were conducted using PAUP* ver. 4.0b10 (Swofford 2002) on the combined and individual genes. The 36-base ambiguous region of *c-mos* (Barker et al. 2002) was excluded from the analyses. Tree searches were performed using maximum parsimony and maximum likelihood (ML) methods, with *Gallus* designated the outgroup in all analyses. Parsimony searches were conducted using 500 random

addition replicates. Character support for parsimony-based phylogenies was assessed via bootstrapping (Felsenstein 1985), using 100 heuristic searches with ten random addition replicates each, and branch support (Bremer 1988, 1994), which was computed using the computer programme TreeRot ver. 2 (Sorenson 1999). Likelihood analyses were conducted on the combined data using the parameters obtained from the computer programme Modeltest (Posada and Crandall 1998). Modeltest indicated that the most efficient model for the data set was TrN + I + G, and the following settings were used in the likelihood analysis: freq [A] = 0.2988, freq [C] = 0.2523, freq [G] = 0.2446, freq [T] = 0.2043; R [A-C] = 1.0000, R [A-G] = 5.0778, R [A-T] = 1.0000, R [C-G] = 1.0000, R [C-T] = 8.2490, R [G-T] = 1.0000; I = 0.4048; G = 1.1381. Likelihood analysis was also conducted using the parameters from Barker et al. (2002).

Results

We obtained 2872 bases of sequence from the RAG-1 locus and 613 bases from *c-mos* for both individuals of noisy scrub-bird. Sequences of RAG-1 were identical for both individuals, as were those of *c-mos*. RAG-1 sequence divergence between *A. clamosus* and other passerines ranged from 3.2% (from *Menura*) and 4.4% (from *Ptilonorhynchus*) to 8.3% (from *Sitta*); sequence divergence in *c-mos* ranged from 3.1% (from *Menura*) and 3.8% (from *Ptilonorhynchus*) to 8.9% (from *Muscicapa*). The data for the complete set of 73 taxa consisted of 2902 aligned bases of RAG-1 and 622 of *c-mos* (see also Barker et al. 2002).

Parsimony analyses of the combined data resulted in 54 most parsimonious trees [treelength = 5562; consistency index (CI) = 0.42; CI excluding uninformative characters = 0.35; RI = 0.45), the strict consensus of which indicated that *Menura novaehollandiae*, the superb lyrebird, was sister to *A. clamosus* (Fig. 1). Bootstrap support for this result was 100%; 25 characters unambiguously supported this relationship and the decay index for this node was 19. The analyses also indicated moderate bootstrap support (76%) for a sister relationship between *Atrichornis/Menura* and the remainder of the oscine passerines; seven characters unambiguously supported this relationship and the decay index for the node was two. Parsimony analyses of the RAG-1 data found 40 most parsimonious trees (treelength = 4308; CI = 0.45; CI excluding uninformative characters = 0.37; RI = 0.47), the strict consensus of which mirrored the results for the combined data, with 100% bootstrap support for the *Atrichornis/Menura* sister relationship and 57% support for these taxa as sister to the rest of the oscines. Parsimony analysis of the *c-mos* data resulted in less definitive trees, presumably due to the brevity of the sequences (see also Barker et al. 2002), and the relationships of *A. clamosus* were poorly resolved. More than 5000 most parsimonious trees were found (treelength = 1191; CI = 0.35; CI excluding uninformative characters = 0.28; RI = 0.46). The strict consensus of these trees included a polytomy at the base of the oscine passerines, one branch of which consisted of *A. clamosus*.

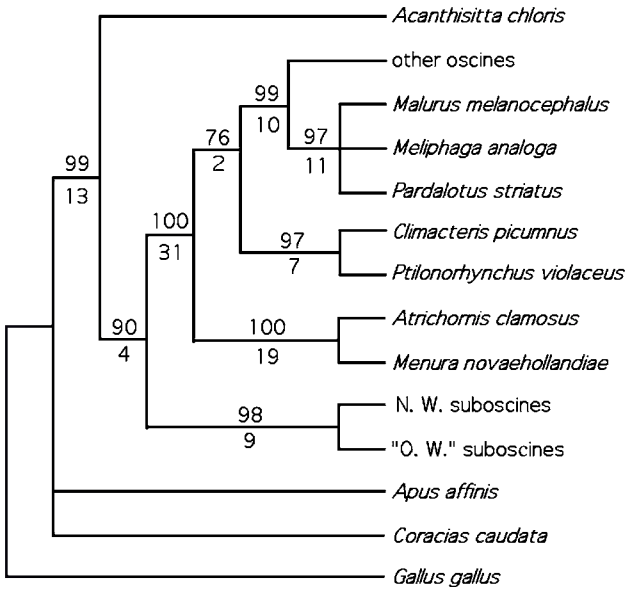

Fig. 1 Strict consensus of 54 most parsimonious trees. *Numbers above branches* are bootstrap support values; *numbers below branches* are decay (Bremer support) indices. Sampling for "Old World suboscines" includes four species; "New World suboscines," six species; "other oscines", 52 species (see Barker et al. 2002 for additional details). Topology resulting from maximum likelihood analyses was identical to the parsimony consensus tree

The maximum likelihood analyses using the Modeltest parameters resulted in a single most likely tree (–Ln likelihood = 34456.86304), in which *M. novaehollandiae* was sister to *A. clamosus*. The basic structure of the tree was identical to that of the parsimony trees (Fig. 1), with the *Menura/Atrichornis* clade sister to the rest of the oscine passerines. The ML analyses using the parameters from Barker et al. (2002) also resulted in a single most likely tree that was identical in basic structure to the tree produced using the Modeltest parameters.

Discussion

Morphological data, DNA hybridization data, and now DNA sequence data have been used to address the evolutionary affinities of the genus *Atrichornis*, including its relationship with the genus *Menura* and its position more generally within the passerines. The sequence data identify

the scrub-birds and lyrebirds as sister taxa, corroborating long-standing conclusions based on morphology and, more recently, on DNA hybridization. However, the morphological case for the sister relationship is not as well supported as might be supposed (Rich et al. 1985), making concurrence of the molecular data of particular significance.

Despite the rarity of the two species of *Atrichornis*, the morphology of *A. clamosus* is now very well known, due to a remarkable series of studies of a modern anatomical specimen collected expressly for this purpose (published as *Records of the Australian Museum* 37:111–254). Character systems covered by this research included plumage (Clench and Smith 1985; Smith 1985), pterylosis (Clench 1985; Morlion 1985), osteology (Rich et al. 1985; Bock 1985) and myology (Bock 1985; Raikow 1985; Zusi 1985) of *A. clamosus*. Paradoxically, one of the themes to emerge from these and other studies of this rare species has been our lack of comparative knowledge of many of these systems across passerine birds generally (Bock and Clench 1985). For example, the study of the trunk and tail muscles of *A. clamosus* was the first for any passerine bird since Shufeldt's (1890) study of *Corvus corax*, and the evolutionary significance of the results proved impossible to evaluate due to a lack of similar studies (Zusi 1985).

Historically, the case for an *Atrichornis–Menura* sister relationship rested largely on features of the syrinx. Syringeal differences between the Menurae and other oscine birds were the basis for Garrod's (1876) division of the oscines into the Acromyodi Abnormales (*Atrichornis* and *Menura*) and the Acromyodi Normales (the other oscines). Similarly, Ames (1971) proposed that *Atrichornis* and *Menura* share a distinctive syringeal morphology (his "Division IV") with oscine passerines but that their syringes differ from those of oscines in terms of their relative lack of fusion of the cartilaginous rings and in the presence of three, rather than four, pairs of intrinsic muscles. Phylogenetic interpretation of these differences, however, is hindered by a lack of detailed comparative data and difficulties in determining homologies (Bock 1972; Sibley 1974). Moreover, the form of stapes present in *Atrichornis* and *Menura* (Feduccia 1975a, b; Feduccia personal communication; see also Feduccia and Olson 1982), often cited as evidence of their close affinity, is the ancestral avian type, which is homologous with the stapedial form in reptiles and many non-passerine birds and therefore of little use in assessing the relationship of scrub-birds to lyrebirds or to other passerines (Bock and Clench 1985).

The sequence data are in agreement with previous sequence-based conclusions (Barker et al. 2002, 2004; Ericson 2002b) concerning the place of the Menurae as sister to the rest of the oscine passerines, and they strengthen the case somewhat through inclusion of *Atrichornis*. That *Atrichornis* and *Menura* are oscines is also consistent with the DNA hybridization evidence. However, a sister relationship between the Menurae and the rest of the oscines is greatly at odds with conclusions based on DNA hybridization (Fig. 2), which placed the Menurae as sister to the Ptilonorhynchidae within the Corvida, one of two large parvorders deemed to constitute the oscines (Sibley and Ahlquist 1985, 1990). Despite assertions to the contrary (e.g. Sibley 1974), there is little other evidence for a Menurae-bowerbird sister relationship. Thorough osteological analyses provided no support for a sister relationship between these two groups and, indeed, the researchers carrying out these analyses concluded that their skulls and general osteology differ substantially (Feduccia and Olson 1982; Bock 1985). Sibley (1974) argued that egg white proteins were similar among the Menurae, the Ptilonorhynchidae and the Paradisaeidae (birds of paradise), but sister relationships were not determined, and the methodology used in his study has been questioned (Brush 1979).

The DNA sequence data, in contrast, provide support for a sister relationship between the Menurae and the rest of the oscines, and for a sister relationship between the Ptilonorhynchidae and the Climacteridae (Australo-Papuan treecreepers); the latter pair was found to be sister to the remainder of the oscines that was apart from the Menurae (Figs. 1, 2). A sister relationship between the Menurae and

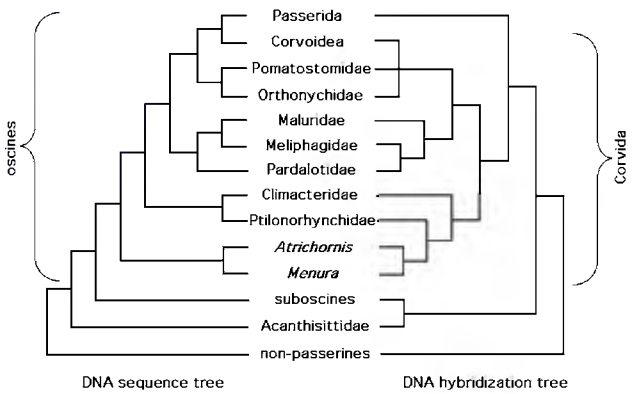

Fig. 2 Evolutionary relationships of *Atrichornis*, as determined using DNA–DNA hybridization (*right side*; adapted from Sibley and Ahlquist 1990) and maximum likelihood (ML) analysis of DNA sequences (*left side*). Although both topologies recover a sister relationship between *Atrichornis* and *Menura*, the DNA hybridization tree indicates that these taxa form part of the Corvida, one of two suborders constituting the oscines (the other being the Passerida), whereas the DNA sequence tree places *Atrichornis* and *Menura* as sister group to the rest of the oscines. *Corvoidea* here includes the "core Corvoidea" of Barker et al (2002) as well as the clade formed by *Melanocharis*, *Oedistoma*, *Toxorhamphus* and *Tregellasia*. The Pomatostomidae and Orthonychidae form part of the "core Corvoidea" under DNA hybridization (Sibley and Ahlquist 1990), and there are other slight differences with the sequence results in composition of the Corvoidea and Passerida

the remaining oscines concurs with the traditional morphological view of the distinctiveness of *Menura* and *Atrichornis* relative to other oscines (Bock and Clench 1985), and with other biochemical studies using *Menura* as the sole representative of the group (Christidis and Schodde 1991; Barker et al. 2002; Ericson et al. 2002b). The presence of this sister relationship in phylogenies constructed using different types of characters, varying taxon sampling schemes, and alternative methods of data analysis attests to the robustness of the result.

Zusammenfassung

Über die phylogenetische Stellung der Dickichtvögel (Passeriformes, Menurae, Atrichornithidae) Australiens

Die evolutionären Beziehungen der Dickichtvögel wurden mit Hilfe vollständiger Sequenzen des rekombinationsaktivierenden Gens RAG-1 und des Proto-Onkogens c-mos für zwei Individuen des Braunbauch-Dickichtvogels (*Atrichornis clamosus*) untersucht. Phylogenetische Analysen zeigten, dass *Atrichornis* eine Schwestergattung zur Gattung *Menura* (Leierschwänze) ist und dass diese zwei Gattungen (die Menurae) eine Schwesterbeziehung haben zu den restlichen Oscinae. Eine Schwesterbeziehung zwischen *Atrichornis* und *Menura* unterstützt die traditionelle Ansicht, basierend auf Morphologie und DNA-Hybridisierung, dass diese Taxa eng verwandt sind. In ähnlicher Weise stimmt eine Schwesterbeziehung mit den restlichen Oscinae mit der morphologischen Unterscheidbarkeit von *Atrichornis* und *Menura* überein, wenn diese Ergebnisse auch Schlussfolgerungen auf der Grundlage von DNA-Hybridisierungen widersprechen. Obwohl *Atrichornis* morphologisch sehr gut bekannt ist, wurden frühere Schlussfolgerungen zu seiner Verwandtschaft durch den Mangel an vergleichbarem Wissen über andere Singvögel behindert, was ihre Übereinstimmung mit den Schlussfolgerungen aus den Sequenzanalysen besonders gewichtig erscheinen lässt.

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