The Auk 116(1):141–157, 1999

MOLECULAR SYSTEMATICS AND BIOGEOGRAPHY OF THE COCKATOOS (PSITTACIFORMES: CACATUIDAE)

DAVID M. BROWN[1] AND CATHERINE A. TOFT[2]

Section of Evolution and Ecology, Division of Biological Sciences, University of California, Davis, California 95616, USA

ABSTRACT.—We sequenced a 433-bp region of the mitochondrial 12S ribosomal subunit gene for 15 of the 18 recognized species of cockatoos and also examined previously published data on allozymes. Tests showed that the allozyme and mtDNA data have similar phylogenetic signals. The mtDNA phylogeny placed the Palm Cockatoo (*Probosciger aterrimus*) as the first extant cockatoo to split, followed by a subclade containing the black-cockatoos (*Calyptorhynchus* spp.), the Cockatiel (*Nymphicus hollandicus*), and the Gang-gang Cockatoo (*Callocephalon fimbriatum*); followed by the Galah (*Eolophus roseicapillus*) and Major Mitchell's Cockatoo (*Cacatua leadbeateri*), respectively; and finally followed by two subclades of "white" cockatoos: (1) the "corella" clade (Red-vented Cockatoo [*Cacatua haematuropygia*], Goffin's Cockatoo [*C. goffini*], Little Corella [*C. sanguinea*], Ducorps's Cockatoo [*C. ducorpsii*]); and (2) the "galerita" clade (Sulphur-crested Cockatoo [*C. galerita*], Salmon-crested Cockatoo [*C. moluccensis*], White Cockatoo [*C. alba*], Blue-eyed Cockatoo [*C. ophthalmica*], and Lesser Sulphur-crested Cockatoo [*C. sulphurea*]). If the mtDNA phylogeny accurately represents the evolutionary history of the cockatoos, then several of the phylogenetic problems within the group are resolved, including the positions and relationships of *Nymphicus hollandicus, Callocephalon fimbriatum, Eolophus roseicapillus,* and *Cacatua leadbeateri.* The mtDNA phylogeny supports some but not all of the nomenclature recently proposed for the Australian species. Biogeographic analysis of the mtDNA phylogeny supports the hypothesis that the cockatoos originated in Australia and that a combination of vicariant speciation and dispersal may have contributed to the diversification of the genus *Cacatua* in two separate radiations to the island regions of Indonesia, New Guinea, and the South Pacific. *Received 30 July 1997, accepted 18 June 1998.*

THE ORDER PSITTACIFORMES is a distinctive group of birds comprising approximately 350 species (Forshaw 1989). Several unique characteristics of the parrots suggest that they compose a monophyletic group, including a distinctive bill and a unique feather pigment (Smith 1975, Dixon 1994). Many classifications of the Psittaciformes have emerged since the classification by Linnaeus in 1758 (Sibley and Ahlquist 1990). Despite this long history, much uncertainty remains about how different groups of parrots are related to one another.

The cockatoos, family Cacatuidae, have long been recognized as a unique group within the Psittaciformes (Adams et al. 1984). Morphologically, cockatoos are distinguished from other parrots by having an erectile crest and lacking dyck texture in their feathers, which produces blue and green in the plumage of other parrots. Cockatoos possess a gall bladder, a non-pericyclic iris, paired patches of powder down in the lumbar region, and several other derived characters that separate them from other parrots (Adams et al. 1984). The monophyly of the cockatoos is also supported by karyological (Van Donzen and DeBoer 1984), allozyme (Adams et al. 1984), and DNA sequence data (Madsen et al. 1992).

The cockatoos have traditionally been organized into two major groups, the predominantly black Calyptorhynchini (*Calyptorhynchus* and *Probosciger*) and the predominantly white Cacatuini, including *Cacatua* (Adams et al. 1984). However, the phylogenetic branching of the various cockatoo groups (and thus their evolutionary relationships) remains unclear. Smith (1975) proposed evolutionary relationships (Fig. 1) for the five cockatoo genera that he recognized (*Probosciger, Calyptorhynchus, Cacatua, Nymphicus, Callocephalon*), but his hypothesis has not been tested.

[1] Present address: Department of Organismic Biology, Ecology, and Evolution, University of California, 621 Circle Drive South, Los Angeles, California 90095, USA.

[2] Address correspondence to this author. E-mail: catoft@ucdavis.edu

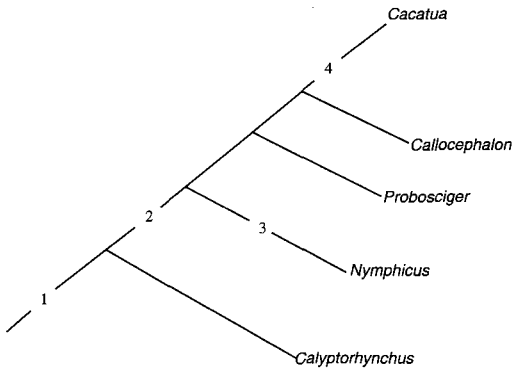

FIG. 1. Smith's (1975) phylogenetic hypothesis of the cockatoo genera. Characters are: (1) the loss of dyck texture; (2) loss of courtship feeding and acquisition of male incubation; (3) development of indirect head scratching; and (4) loss of feather barring.

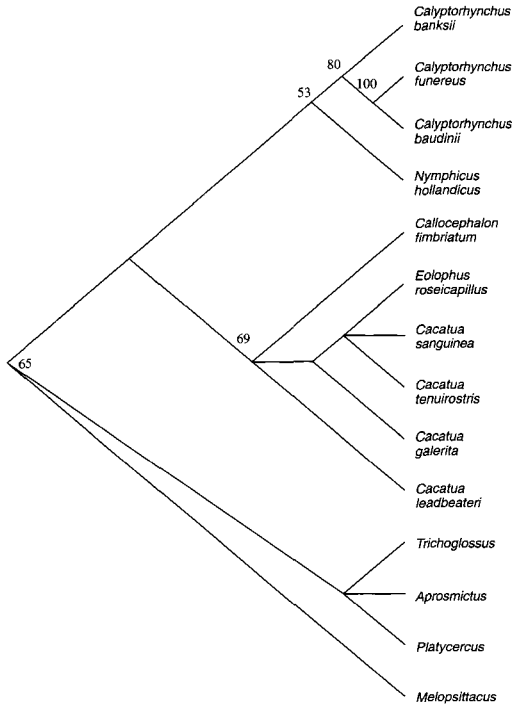

FIG. 2. Strict-consensus tree using allozyme data of Adams et al. (1984; from Dixon [1994]). Numbers are the percentage of bootstrap iterations (out of 1,000) that support particular nodes. Unlabeled nodes were supported by less than 50% of the bootstrap replicates.

A long-standing problem in cockatoo systematics is whether the monotypic Cockatiel (*Nymphicus hollandicus*) is a cockatoo, and if so, where it belongs within the cockatoo clade. Several workers have gathered morphological and behavioral evidence that the Cockatiel is a diminutive cockatoo (Adams et al. 1984). Others have placed the Cockatiel within other groups of parrots because of its indirect head scratching, auditory meatus, sequence of remigial molt, structure of pineal body, and wing spots in females and immatures. The allozyme evidence of Adams et al. (1984) indicates that the Cockatiel is a cockatoo (Fig. 2). This conclusion is supported by mtDNA (Ovenden et al. 1987), a tandem repeat in parrot nuclear DNA (Madsen et al. 1992, Dixon 1994), and egg shape (Saunders et al. 1984). Although this strong evidence places the Cockatiel with the cockatoos, its exact phylogenetic position within this group remains unresolved (i.e. whether it belongs in the Calyptorhynchinae, the Cacatuinae, or its own subfamily Nymphicinae, following Schodde [1997]). Similarly, there are unresolved questions about the phylogenetic positions (Fig. 2) of other species, including the Galah (*Eolophus roseicapillus*), the Gang-gang Cockatoo (*Callocephalon fimbriatum*), and Major Mitchell's Cockatoo (*Cacatua leadbeateri*; Adams et al. 1984).

We sequenced part of the mitochondrial 12S ribosomal subunit gene for 15 species of cockatoos and then compared phylogenetic patterns derived from mtDNA with phylogenetic hypotheses from analysis of previously published allozyme data for 10 species of cockatoos (Adams et al. 1984), 7 of which were included in our study. We propose that the mtDNA phylogeny resolves the branching order of the cockatoo taxa and that current cockatoo taxonomy does not reflect accurately evolutionary relationships within the group. We suggest that Australia is the region of origin of cockatoos and that a combination of vicariance and dispersal resulted in two distinct radiations of the genus *Cacatua* in the islands north of the Australian continent.

METHODS

Materials and subjects.—Nomenclature follows Schodde (1997) for Australian species and Forshaw (1989) for non-Australian species. Tissue samples were acquired from captive birds, blood and shed feathers from living birds, and liver samples from birds that died of natural causes. Feather samples

were obtained for Palm Cockatoo (*Probosciger aterrimus*), Blue-eyed Cockatoo (*Cacatua ophthalmica*), and Red-vented Cockatoo (*C. haematuropygia*). Blood was taken from Red-tailed Black-Cockatoo (*Calyptorhynchus banksii*), Galah, Major Mitchell's Cockatoo, Sulphur-crested Cockatoo (*Cacatua galerita*), Lesser Sulphur-crested Cockatoo (*C. sulphurea*), Little Corella (*C. sanguinea*), Goffin's Cockatoo (*C. goffini*), Ducorps's Cockatoo (*C. ducorpsii*), Moluccan Cockatoo (*C. moluccensis*), Gang-gang Cockatoo, and Cockatiel. Liver samples were obtained for White Cockatoo (*Cacatua alba*).

We did not obtain material for Glossy Black-Cockatoo (*Calyptorhynchus lathami*), Yellow-tailed Black-Cockatoo (*C. funereus*), White-tailed Black-Cockatoo (*C. baudinii*), and Long-billed Corella (*Cacatua tenuirostris*). We assumed that the *Calyptorhynchus* group of black-cockatoos and the corella (*Cacatua*) group were adequately represented by *Calyptorhynchus banksii* and *Cacatua sanguinea*, respectively, based on previous work (Adams et al. 1984: figure 2). We emphasize that the focus of our study is at the generic level, and we did not set out to resolve relationships of the lower taxa (i.e. species and subspecies).

Taxa used as outgroups were: Rock Dove (*Columbia livia*; feather), Common Canary (*Serinus canariua*; liver), and Japanese Quail (*Coturnix japonica*; sequence obtained from Desjardins and Morais [1991]). Selection of an appropriate outgroup for parrots has been problematic, likely because of the old age of this lineage (Dixon 1994). We selected Rock Dove (Columbiformes) and Common Canary (Passeriformes) as outgroups because both orders have been suggested as potential sister groups to the parrots (Dixon 1994, Sibley and Ahlquist 1990), and Japanese Quail because it was used by Dixon (1994). One possible problem with outgroup selection is that overly distant outgroups may ruin ingroup topologies by randomly selecting the longest ingroup branch as the root. We tested for this problem in the cockatoo tree by deleting all of the outgroup species to see whether the ingroup topology changed. Because the ingroup topology did not change when outgroup species were deleted, we assume that this particular problem with outgroup selection is not evident in the cockatoo tree.

Genetic and phylogenetic analyses.—We extracted blood and liver DNA with Chelex (Walsh et al. 1991) and feather DNA using the method of Morin et al. (1994). A 433-bp region of the mitochondrial ribosomal small subunit (12S) gene was amplified using the polymerase chain reaction (PCR). The primers used were 5′-CCCAAGCTTGGGATTAGATACCCACTA-3′ and 5′-CCTCGAGGTGACGGGCGGTATGTACG-3′, modified from those used by Dixon (1994). Symmetric amplifications were performed in 25-μL reactions containing 1 to 10 μL DNA, 1 μL of a 10-mM solution of each primer, 2.5 μL of 10× buffer (including $MgCl_2$), 2 μL of a 1.0-mM solution of dNTPs, and 1 μL of *Taq* DNA polymerase, with up to 25 μL of water. The PCR protocol used was 1 cycle of 5 min at 95°C, 30 cycles of 45 s at 92°C, 45 s at 56°C, and 1 min at 72°C; and 1 cycle of 72°C for 4 min. Electrophoresis of 3 μL of amplification mixture in a 1% agarose gel verified the presence of desired amplified product. The PCR product was filtered (Microcon 100, Amicon) to remove excess dNTPs and primers with volume held constant. The DNA of some species were cloned into the PCRII vector (Original TA Cloning Kit, Invitrogen). Cloned DNA fragments were sequenced using the M13 forward and reverse primers. The remaining species were sequenced directly using internal primers in both forward and reverse directions. All amplified DNA products were sequenced on an automated sequencer. Sequences were edited using the program SeqApp (http://iubio.bio.indiana.edu) and aligned with the SeqApp application Clustal (Higgins and Sharp 1988). Several alternative sequence alignments were examined with taxa arranged in different orders, and all alignments produced the same results.

The distribution of and percent nucleotide variation along the region sequenced were measured with program MEGA (Kumar et al. 1994). Maximum parsimony as implemented in program PAUP* (Swofford 1996) was used to create phylogenetic trees from the mtDNA data using the branch-and-bound option. The maximum-likelihood approach was also used to construct phylogenies (Swofford and Olsen 1990). The 1-, 2-, and 6-parameter maximum-likelihood models in PAUP* were used with transition probabilities in the matrices, both estimated from the data and implemented using the default values. All maximum-likelihood models recovered the same trees.

We examined allozyme data in Adams et al. (1984) following Dixon (1994). Twenty-eight allozyme loci, 25 of which were parsimony-informative, were used as characters, and alleles were treated as character states, a method known as "qualitative coding" (Buth 1984, Swofford and Olsen 1990). This method is sensitive to sampling error because taxa that are polymorphic for alleles A and B would often be incorrectly scored as "fixed" if one allele were rare, unless sample sizes were large (Swofford and Olsen 1990). We constructed the allozyme phylogeny using maximum parsimony as implemented in PAUP*, with the heuristic option. We constructed bootstrap data sets for the mtDNA and allozyme data sets to establish how well particular branches were supported, using 1,000 bootstrap replicates for each data set.

The mtDNA phylogeny of our study and the allozyme phylogeny (Adams et al. 1984, Dixon 1994) used different outgroups and did not share all of the same species. The mtDNA phylogeny (Fig. 3) lacked *Calyptorhynchus funereus, C. baudinii,* and *C. tenuirostris*; the allozyme phylogeny (Fig. 2) lacked *P. aterri-*

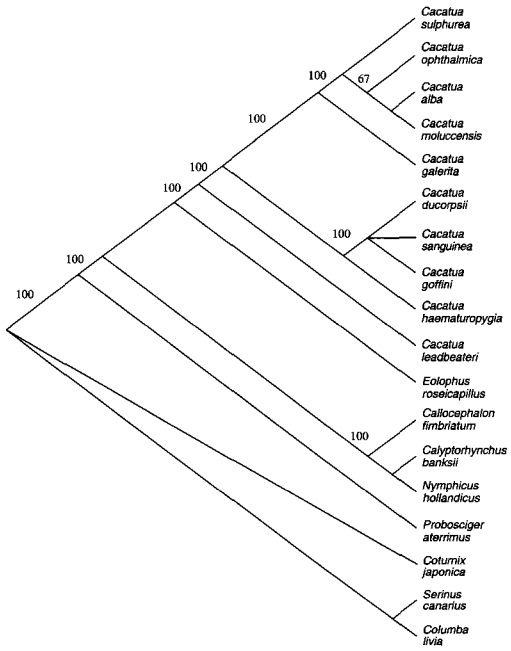

FIG. 3. Phylogenetic tree created from mtDNA sequence data using majority-rule consensus tree from 12 equally parsimonious trees. Values are percentage of trees out of 12 showing a particular node. Topology is the same as for all strict-consensus trees from maximum-likelihood analysis.

mus, Cacatua sulphurea, C. ophthalmica, C. alba, C. moluccensis, C. haematuropygia, C. goffini, and *C. ducorpsii.* Only seven cockatoo species are represented by both mtDNA and allozyme data: *Calyptorhynchus banksii, Callocephalon fimbriatum, Eolophus roseicapillus, Cacatua leadbeateri, C. galerita, C. sanguinea,* and *Nymphicus hollandicus.* To analyze the combined data, we constructed trees for only these seven species. There were no common outgroups present in the mtDNA and allozyme data sets. We rooted the trees at *C. banksii* and *N. hollandicus* because the mtDNA phylogeny suggests that these were the first species present in both data sets to split from the cockatoo ancestor. *Callocephalon fimbriatum* was not included as an outgroup because it is a member of the *C. banksii-N. hollandicus* clade only in the mtDNA tree and not in the allozyme tree, in which it is more closely related to the ingroup species. *Callocephalon fimbriatum* is thus treated as an ingroup taxon for this analysis. The allozyme and mtDNA data from the seven cockatoo species were combined into a single "total evidence" data matrix (Eernisse and Kluge 1993), which permits the evidence from each data set to complement the others. The allozyme characters were added to the mtDNA data, and all characters were analyzed as unordered.

We compared phylogenetic hypotheses produced from the mtDNA and allozyme data using several analyses. With the computer program COMPONENT (Page 1993), we used the quartet and nearest-neighbor interchange (NNI) metrics to compare similarities of the trees produced from the different data sets. The quartet metric examines all possible subsets of four taxa (quartets) and finds the percentage that agree. The NNI comparison reveals how many taxa must be moved to transform one tree into another (Page 1993, Zink and Blackwell 1996). We used the triples-distance method of Critchlow et al. (1996) to test the null hypothesis that the similarities between the two trees created from the different data sets can be explained by chance. The triples distance is the number of subtrees of three taxa (triplets) that differ between two trees. Critchlow et al. (1996) developed a method for determining the statistical significance of the triples distance between two trees. Finally, we used the partition-homogeneity test, which we interpreted according to Mason-Gamer and Kellogg (1996), to provide another estimate of the probability that two samples of data have the same phylogenetic history. In that analysis, there were 437 total characters, of which 30 were parsimony-informative.

Biogeographic analyses.—We inferred the geographic area of origin of the cockatoos using the cladistic ancestral-area method of Bremer (1992). This method approximates the ancestral area of groups from the topological information in cladograms of their geographic ranges. The range of each species is treated as a binary character with two states, present or absent. The species range character may be optimized on the cladogram under two different hypotheses that: (1) the ancestral area of the group is identical to the present range of the species in the group, or (2) none of the individual species' ranges is part of the ancestral area of the group.

Under hypothesis 1, the ancestral-area state for each area character is "present," and all area absences may be plotted as losses on the cladogram using reverse Camin-Sokal parsimony (i.e. specifying the ancestral area as present [1] along with the assumption of $1 \rightarrow 0$ irreversibility). Under hypothesis 2, the ancestral area state for each character is "absent," and all areas present may be plotted as gains on the cladogram using forward Camin-Sokal parsimony.

For any individual area character (i.e. species range), the number of gains and losses can be compared under the two optimization hypotheses. Initially, gains and losses are assumed to be equally possible. If losses exceed gains for any individual area, then hypothesis 1 is rejected as less parsimonious than hypothesis 2, and the area is excluded from the ancestral area of the group. If gains exceed losses for any individual area, hypothesis 2 is rejected, and the area is assumed to be part of the ancestral area (Bremer 1992). Cockatoo ranges were taken

from Blakers et al. (1984) and Forshaw (1989). The 12S ribosomal subunit tree was used as the area cladogram. We conducted the forward and reverse optimizations using PAUP* (Swofford 1996).

Results

Phylogenetic analysis.—Nucleotide variation was distributed throughout the 12S ribosomal subunit gene (Appendix). The percentages of each nucleotide were: adenine (19.7%), thymine (32.3%), cytosine (20.5%), guanine (27.6%). The mtDNA data for the 15 species of cockatoos in this study contained 409 total characters, 172 of which were variable and 81 parsimony informative (Appendix).

Maximum-parsimony analysis revealed 12 trees (I = 325). The 50% majority-rule consensus tree of these 12 trees and the strict consensus tree from all of the maximum-likelihood analyses (1-, 2-, and 6-parameter models) recovered the same topology (Fig. 3). This topology placed *Probosciger aterrimus* as sister group to the clade containing the rest of the cockatoos, followed in branching order by: a subclade containing *Calyptorhynchus banksii, Callocephalon fimbriatum,* and *Nymphicus hollandicus; Eolophus roseicapillus; Cacatua leadbeateri;* and two subclades together containing the rest of the white cockatoos, genus *Cacatua* (Fig. 3). In one subclade, *C. haematuropygia* was sister group to an unresolved trichotomy containing *C. ducorpsii, C. goffini,* and *C. sanguinea* (Fig. 3). In the other subclade of white cockatoos, *C. galerita* was sister taxon to the clade containing *C. sulphurea, C. ophthalmica, C. alba,* and *C. moluccensis* (Fig. 3). The order of descent of the more basal clades (Fig. 3) containing *Callocephalon banksii, C. fimbriatum, N. hollandicus, E. roseicapillus,* and *Cacatua leadbeateri* was not supported in more than 500 of the 1,000 bootstrap replicates and so was not entirely resolved (Fig. 4). Specifically, the sister-taxon status of *C. banksii* to *N. hollandicus* is supported by the bootstrap replicates, but not the clade containing these species with *Callocephalon fimbriatum.* The remaining relationships were more strongly supported by the bootstrap analysis (Fig. 4).

The heuristic maximum-parsimony analysis of the allozyme data (Adams et al. 1984, Dixon 1994) recovered a clade (Fig. 2) with the black-cockatoos (*Calyptorhynchus*) as sister group to *N. hollandicus,* a finding congruent with the mtDNA phylogeny (Figs. 3 and 4). Contrary to

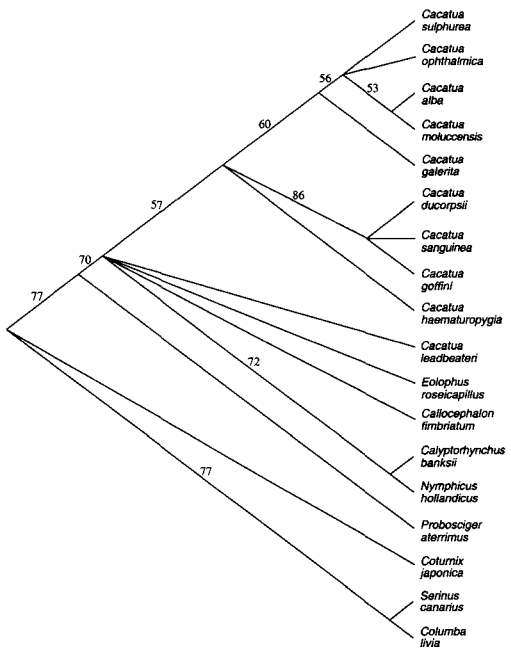

FIG. 4. Phylogenetic tree created from mtDNA sequence data using bootstrap tree created from 1,000 bootstrap replicates of mtDNA data. Values are percentage of trees out of 1,000 showing a particular node.

the mtDNA phylogeny, however, *Callocephalon fimbriatum, E. roseicapillus,* and *Cacatua leadbeateri* were grouped with *Cacatua galerita, C. sanguinea,* and *C. tenuirostris* (Fig. 2). The *Nymphicus-Calyptorhynchus* clade received moderate support from bootstrap replicates for both the mtDNA (Fig. 4) and allozyme trees (Fig. 2; 72 and 56%, respectively) in this study.

The mtDNA and allozyme trees (Figs. 5 and 6) for the seven species represented by both data types differed in the placement of *Callocephalon fimbriatum, E. roseicapillus, Cacatua leadbeateri, C. sanguinea,* and *C. galerita.* The two trees (Figs. 5 and 6) were not congruent based on the quartet test. For these seven taxa, there were 35 possible quartets, 17 of which were compatible for the mtDNA and allozyme trees. The nearest-neighbor interchange (NNI) value was 3. The triples distance between the mtDNA and allozyme tree was 13. From the tables in Critchlow et al. (1996), there is a 5.2% probability that 13 or fewer incongruent triplets would occur by chance when the two trees are statistically independent under their uniform model. The analogous *P*-value under their Mar-

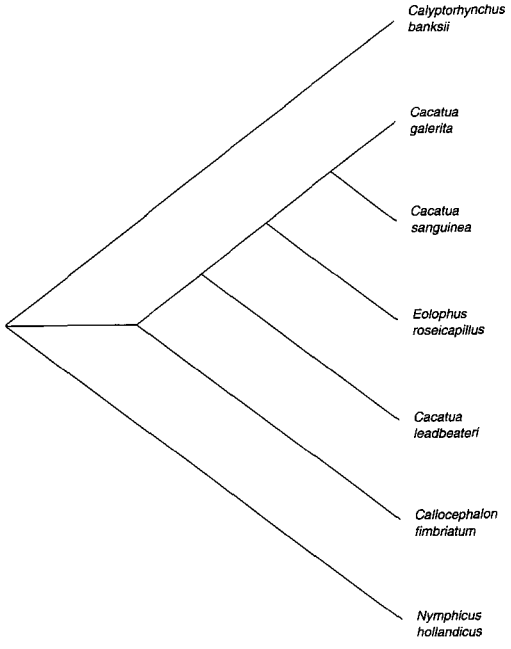

FIG. 5. Phylogenetic tree created from mtDNA data using the seven cockatoo species for which we had mtDNA sequence and allozyme data; trees are rooted by *Calyptorhynchus banksii* and *Nymphicus hollandicus*. Tree is identical to that of the total-evidence tree combining both mtDNA and allozyme data (see Fig. 6).

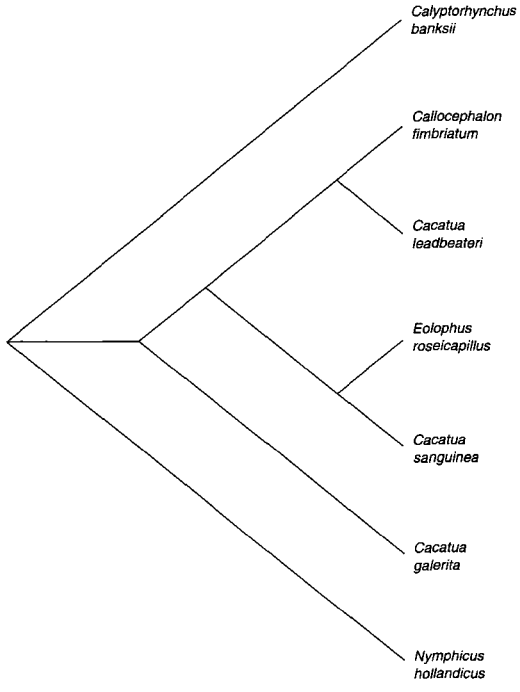

FIG. 6. Phylogenetic tree created from allozyme data using the seven cockatoo species for which we had both mtDNA sequence and allozyme data; trees are rooted by *Calyptorhynchus banksii* and *Nymphicus hollandicus*.

kov model is 3.8%. The *P*-value for the uniform model is near 5% and the *P*-value for the Markov model is less than 5% implying that the mtDNA and allozyme trees were more similar than expected by chance.

The total-evidence tree for the seven cockatoo species with allozyme and mtDNA data differed from the allozyme tree (Fig. 6) in placement of *Callocephalon fimbriatum, E. roseicapillus, Cacatua leadbeateri, C. galerita,* and *C. sanguinea.* The total-evidence tree was identical in placement of taxa to the mtDNA tree (Fig. 5), a result supported by all analyses (see below).

The total-evidence tree was identical to the mtDNA tree in the quartet test and NNI value; all 35 possible quartets were shared, and NNI = 0. The triples-distance test (Critchlow et al. 1996) revealed a statistically significant similarity in the phylogenetic patterns produced from the mtDNA and allozyme data, despite there being differences in tree topology between the data sets. When the allozyme and mtDNA data were combined as a total-evidence tree, the combined tree had the same topology as the mtDNA tree. In the partition-homogeneity test, the two data types (mtDNA and allozyme characters) were congruent with each other with a *P*-value of 1. Thus, we cannot reject the null hypothesis that the two samples of data arise from the same phylogenetic history (Mason-Gamer and Kellogg 1996). The congruence between the mtDNA and total-evidence tree thereby supports the hypothesis that the mtDNA tree represents the organismal phylogeny of the cockatoos, with the caveat that the two trees might be congruent simply because the number of DNA characters was greater than that of allozyme characters.

Biogeographic analysis.—Most of the more basal cockatoo species in the mtDNA phylogeny (*Calyptorhynchus banksii, Callocephalon fimbriatum, N. hollandicus, E. roseicapillus,* and *Cacatua leadbeateri*) have Australian distributions (Fig. 7), whereas most species in the genus *Cacatua* are distributed throughout New Guinea, Indonesia (e.g. Sulawesi, Moluccan Islands, and Bismarck Archipelago), and the Philippines

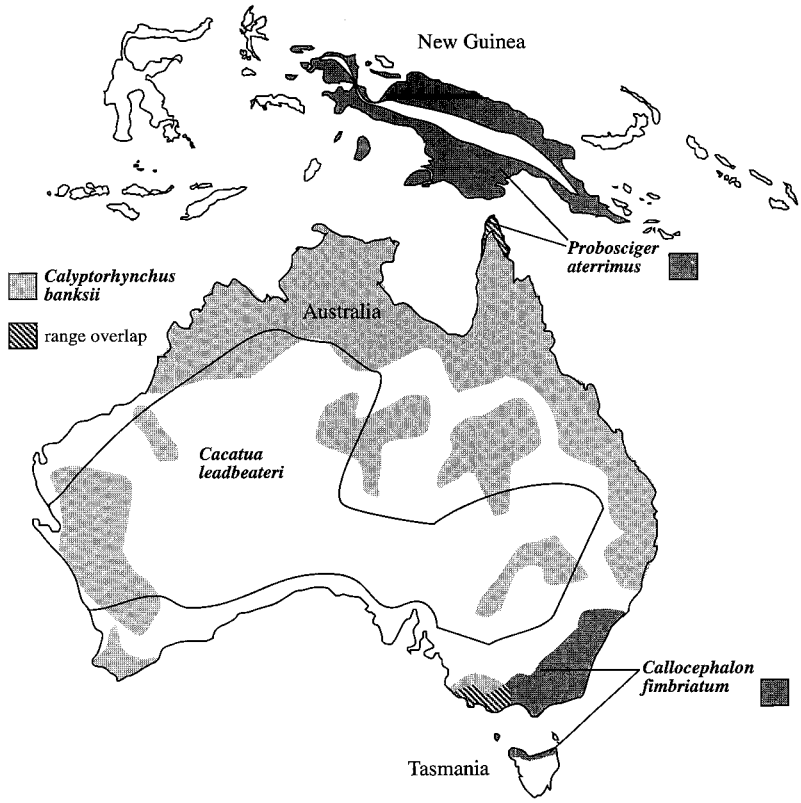

FIG. 7. Geographic ranges of cockatoo species that were in the more basal subclades in the mtDNA phylogeny of this study (see Fig. 3). Ranges are approximate and are adapted from Ford (1980), Blakers et al. (1984), Joseph 1988, and Forshaw (1989). Ranges of *Nymphicus hollandicus* and *Eolophus roseicapillus* (neither is shown) cover nearly all of interior Australia except for some areas near the coast.

(Fig. 8). One hypothesis for this arrangement of cockatoo distributions, relative to the phylogeny based on mtDNA, is that the cockatoos originated in Australia and then dispersed into other areas. Therefore, we tested the hypothesis that the cockatoos evolved in Australia using the cladistic method of Bremer (1992) for discerning the ancestral area of a group. Although this method is controversial (Ronquist 1995), we used it to provide some quantitative indication of where the cockatoos may have evolved.

The results of the analysis identified Australia as the most likely ancestral area of the cockatoos, with an ancestral area value of 1.0 (Table 1). Australia was the only region in the ancestral-area analysis to have a greater number of gains than losses under Camin-Sokal parsimony, rejecting the hypothesis that Australia is not part of the ancestral area. The ranges of all other cockatoo species have higher numbers of losses than gains when optimized onto the area cladogram, indicating that they were probably not part of the ancestral area of the cockatoos.

DISCUSSION

Phylogeny of the cockatoos.—The branching order produced by the mtDNA phylogeny (see Fig. 3) differed from the cockatoo radiation hypothesized by Smith (1975). He proposed that the black-cockatoos (*Calyptorhynchus*) split first, followed respectively by the splitting of *Nymphicus, Probosciger, Callocephalon,* and *Cacatua.* His arrangement was based on several morphological and behavioral characters (Fig. 1). The mtDNA tree and Smith's radiation hypothesis both place the genus *Cacatua* as the terminal taxon in the cockatoo lineage. The branching order of the cockatoos cannot be inferred

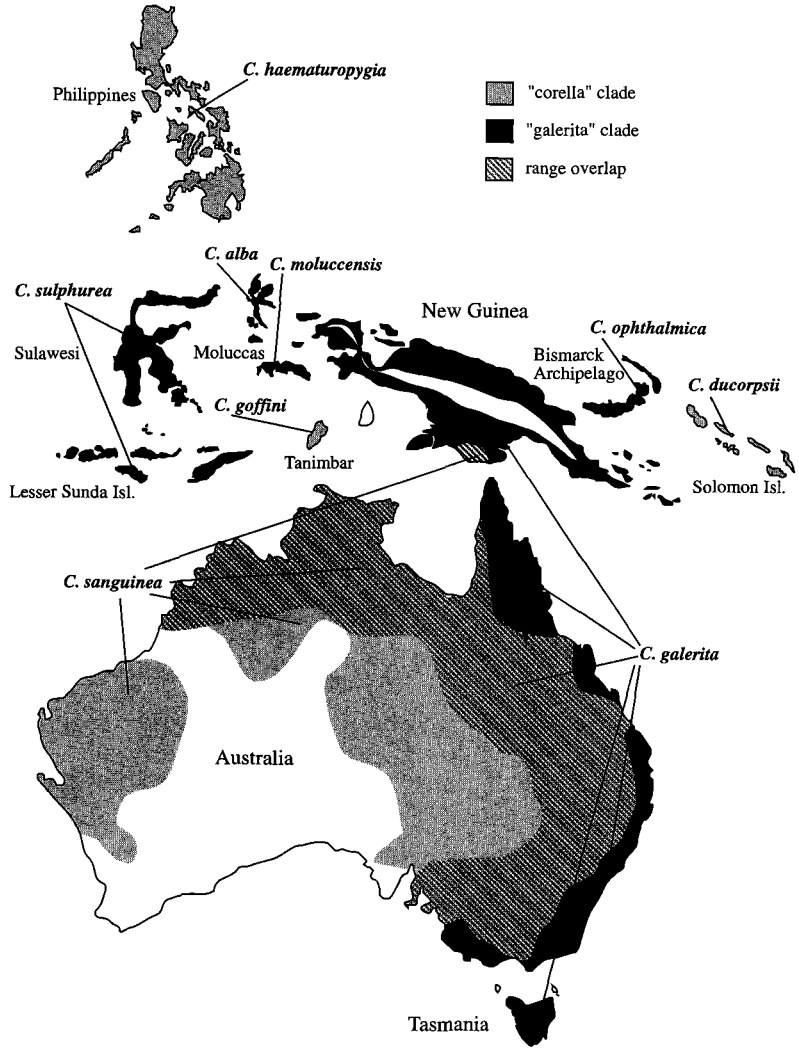

FIG. 8. Geographic ranges of cockatoo species in the two subclades of *Cacatua* used in the mtDNA phylogeny (see Fig. 3). Ranges are approximate and are adapted from Ford (1980), Blakers et al. (1984), Joseph (1988), and Forshaw (1989).

from the allozyme data of Adams et al. (1984) because phylogenetic analysis of their data does not clearly resolve the order in which the "black" and "white" lineages split from their common ancestor (Fig. 2).

Our study places *N. hollandicus* and *Callocephalon fimbriatum* (both of which are monotypic) in a clade with *Calyptorhynchus banksii* in the mtDNA phylogeny. *N. hollandicus* also forms a clade with the *Calyptorhynchus* species in the analysis of allozyme data (Adams et al. 1984; Fig. 2). The allozyme-based phylogeny, however, grouped *Callocephalon fimbriatum* with the white cockatoos. The *Calyptorhynchus* species, *N. hollandicus*, and *Callocephalon fimbriatum* share patterns of marked sexual dimorphism, typically involving presence or absence of a non-melanistic face or a face patch and barred-and-spotted feathers (Adams et al. 1984). These characters are unique to these species within the cockatoos and would be synapomorphies if these species truly formed a single clade.

The mtDNA phylogeny revealed two sister clades within the *Cacatua*. The genus *Cacatua* has traditionally been thought to contain two groups based on morphological characters (Ad-

TABLE 1. Grain and loss values (i.e. number of necessary gains and losses under forward and reverse, respectively, Camin-Sokal parsimony) for the cladogram of geographic ranges of cockatoo species considered in this study. Ancestral-area values are the gain/loss quotients rescaled to a maximum value of 1 by dividing by the largest gain/loss value (Bremer 1992).

Area	No. of gains	No. of losses	Gains/losses	Ancestral-area value
Australia	6	3	2.000	1.000
New Guinea	3	6	0.500	0.250
Philippines	1	6	0.167	0.083
Aru Islands	2	5	0.400	0.200
Sunda Islands	1	7	0.143	0.071
Bismarck Archipelago	1	8	0.125	0.063
Southern Moluccas	1	9	0.111	0.056
Northern Moluccas	1	9	0.111	0.056
Tanimbar Islands	1	8	0.125	0.063
Eastern Solomon Islands	1	8	0.125	0.063

ams et al. 1984). One group ("galerita") includes the species with round wings, heavy bills, and prominent colored crests and comprises *C. galerita, C. sulphurea, C. ophthalmica, C. alba,* and *C. moluccensis.* The other group ("corella") includes species that are slender winged, small billed, and short crested and comprises *C. sanguinea, C. pastinator, C. tenuirostris, C. ducorpsii, C. goffini,* and *C. haematuropygia.* For the Australian species, Schodde (1997) recognizes these two clades as subgenera: *Cacatua (Cacatua)* for *C. galerita* and *Cacatua (Licmetis)* for *C. sanguinea, C. pastinator, C. tenuirostris.* The mtDNA phylogeny of the present study supports taxonomic recognition of these two lineages within the *Cacatua,* presumably also including the non-Australian species *C. sulphurea, C. ophthalmica, C. alba,* and *C. moluccensis* in Schodde's (1997) subgenus *Cacatua (Cacatua)* and *C. ducorpsii,* and *C. goffini* in his subgenus *Cacatua (Licmetis).*

The mtDNA phylogeny indicated that both *Eolophus roseicapillus* and *Cacatua leadbeateri* split prior to the radiation of *Cacatua* (Fig. 3). The phylogenetic positions of *E. roseicapillus* and *C. leadbeateri* within the cockatoo lineage have traditionally been uncertain. Authors have variously placed *roseicapillus* in *Cacatua* or *Eolophus* (Adams et al. 1984, Boles 1993, Bonaparte 1854 *in* Schodde 1997); the latter is currently recognized (Schodde 1997). The mtDNA phylogeny supports the placement of *roseicapillus* in the monotypic *Eolophus.* Major Mitchell's Cockatoo was moved from the original genus *Lophocroa* (Bonaparte 1897 *in* Schodde 1997) to *Cacatua;* its position within the white cockatoo radiation has been uncertain because it shares a small whitish bill and yodeled contact call with the "corella" group and an upcurving, colored crest and broadly rounded wings with the "galerita" group (Adams et al. 1984). The phylogeny based on the mtDNA, and corroborated by the total-evidence tree of the combined mtDNA and allozyme characters, indicates that both Major Mitchell's Cockatoo and the Galah are clearly basal to the major radiation of species in the genus *Cacatua.*

The mtDNA phylogeny was not entirely in agreement with the currently proposed nomenclature (e.g. Schodde 1997), although it did support several important features of the current classification and previous phylogenetic hypotheses, namely: (1) the basal position and monogeneric status of *Probosciger aterrimus* in the Microglossinae (Schodde 1997); (2) the intermediate and terminal positions of Schodde's Calyptorhynchinae and Cacatuinae, respectively; and (3) the placement of species in the subgenera *Cacatua (Cacatua)* and *Cacatua (Licmetis).*

The most significant deviations from Schodde's (1997) classification revealed by the mtDNA phylogeny are the intermediate relationships in the cockatoo phylogeny. Foremost, *Nymphicus* was clearly most closely allied to *Calyptorhynchus* and secondarily to *Callocephalon,* and the three genera formed a single clade in the majority-rule consensus tree. Thus, the mtDNA phylogeny did not support separating *N. hollandicus* into a monogeneric subfamily. The placement of *Callocephalon fimbriatum* with the more distantly related species in the subfamily Cacatuinae also was not supported. Although the bootstrap analysis did not provide

robust support for the branching of species intermediate in the phylogeny, the mtDNA data implied that these three genera form a single group at the subfamily level.

Based on Schodde's (1997) classification and the mtDNA phylogeny, a case could be made for returning *leadbeateri* to the monotypic genus *Lophocroa,* a placement that is consistent with the treatment of *Eolophus roseicapillus.* Indeed, raising the three subgenera of Schodde (1997) to the generic level would be supported by the mtDNA phylogeny, although a more thorough investigation of species in the "corella" clade is warranted.

Biogeography of the cockatoos.—The most basal cockatoo in the mtDNA phylogeny, *Probosciger aterrimus,* had a range that includes both Australia and New Guinea (Fig. 7), the regions with the first- and second-highest ancestral-area values, respectively, in our analysis. This distribution could be interpreted to mean that New Guinea was the ancestral home of the cockatoos, but this possibility was unsupported by Bremer's method and by fossil evidence. The earliest known cockatoo fossil is from the early to middle Miocene of Queensland, Australia (Boles 1993), and appears to be a modern form resembling *Eolophus* or *Cacatua.* New Guinea was submerged during the period that this fossil taxon would have been living. The colonization of New Guinea by plants and animals occurred during the mid- to late Tertiary (Schodde and Calaby 1972). Phylogenetic evidence (this study) combined with fossil evidence (Boles 1993) suggests that the cockatoos evolved prior to this time.

The cockatoo species with distributions outside of Australia (Fig. 8), all of which occur in the subgenera *Cacatua* (*Cacatua*) and *Cacatua* (*Licmetis*), have undergone an extensive radiation throughout the islands of New Guinea and Indonesia. One hypothesis for this diversification is that an ancestral form of *Cacatua* dispersed from Australia throughout these islands, and populations subsequently underwent allopatric speciation. Alternatively, de Boer and Duffels (1996) proposed that many radiations in this region resulted from vicariance rather than dispersal. The islands and archipelagoes of Wallacea occur in the geologically unstable area between Asia, Australia, and the Papuan region and have changed positions relative to one another because of rifting and plate movements (de Boer and Duffels 1996). de Boer and Duffels (1996) propose that the distribution patterns of animals and plants in Wallacea and the Papuan region were determined largely by these complex geotectonic movements and that the active dispersal of Asian and Australian species that occurred after the area had reached its present configuration probably played a minor role.

de Boer and Duffels (1996) propose that a phylogeny of a monophyletic group of a sufficient age that shows a high rate of endemism in a given area should reflect the area's geotectonic history. The radiation within the two clades of *Cacatua* show patterns similar to those of cicada phylogenies and that may reflect the geotectonic history of Wallacea (Duffels and de Boer 1990).

In the "galerita" clade, *C. ophthalmica* is endemic to the Bismarck Archipelago and is a sister species to *C. alba* and *C. moluccensis* in the mtDNA cockatoo phylogeny, thereby suggesting a biogeographic link between the Moluccan Islands and the Bismarck Archipelago. This pattern is also present in some cicada groups (Duffels and de Boer 1990). The Moluccan Islands and the Bismarck Archipelago are presently separated by New Guinea, but de Boer (1995) hypothesized that the North Moluccan island Hamalera and the Bismarck islands once were connected in one landform. If the phylogenies of the cockatoo and the cicada groups accurately reflect the geotectonic history of these islands, then *C. ophthalmica* and the *C. alba-C. moluccensis* group may have split in a vicariant speciation event, assuming that their common ancestor was on the landform that became Hamalera and the Bismarck Archipelago.

The sister-group relationship of *C. alba* and *C. moluccensis* displayed a biogeographic discontinuity between the North and South Moluccan islands that is also found in the phylogenies of the *Diceropyga, Baeturia,* and *Cosmopsaltria* cicada groups. The South Moluccan Islands have probably emerged within the last one million years, making the terrestrial life on these islands of relatively recent origin (de Boer 1995). de Boer (1995) attributes the biogeographic discontinuity in cicadas between the North and South Moluccas to dispersal from north to south during a period of lower sea levels. Thus, *C. alba* in the North Moluccas and *C. moluccensis* in the South Moluccas may have di-

verged after the dispersal of the *C. moluccensis* ancestor from the North Moluccas to the South Moluccas. The North-South Moluccan Islands discontinuity is also found in the butterfly genus *Idea* (Kitching et al. 1987). The divergence of the "galerita" cockatoo clade thereby appears to reflect a combination of vicariance and dispersal.

Moreover, the ranges of the species of *Cacatua* in the two subclades present a pattern (Fig. 8) suggestive of two separate radiations of *Cacatua* ancestors northward from the continent of Australia, if the mtDNA data represent the true phylogeny. As we discussed above, in the "galerita" clade, *Cacatua galerita* is widespread in eastern Australia and on much of the island of New Guinea, with *C. alba, C. moluccensis,* and *C. sulphurea* occurring on islands to the east of New Guinea, and *C. ophthalmica* occurring on islands to the west of New Guinea. Similarly, in the "corella" clade, *C. (Licmetis) sanguinea* occurs widely in Australia and on part of New Guinea; its presumed sister species, *C. tenuirostris,* also occurs in Australia but has a more restricted range. The species *C. goffini* (on Tanimbar), *C. haematuropygia* (on the Philippines), and *C. ducorpsii* (on the Solomon Islands) occur on islands on either side of New Guinea. However, hypotheses concerning the divergence of these species are more uncertain because of the unresolved trichotomy in that subclade. In summary, the mtDNA phylogeny of the cockatoos reveals distinct biogeographic patterns that are consonant with patterns seen in distantly related taxa and that match hypotheses on the tectonic history of the Australasian region.

Acknowledgments

We thank C. Langley, M. Sanderson, M. Dixon, and M. Plotkin for helping with the molecular biology and phylogenetic analysis. J. Halverson, A. Romagnano, D. Rimlinger, S. Healy, B. Speer, L. Tell, D. Gordon, and B. Arbon provided cockatoo material. A. de Boer, H. Duffels, T. Frazier, L. Joseph, T. Low, C. Nice, R. Zink, and two anonymous reviewers provided helpful comments on the manuscript. This study was supported by NSF grants GER 90-23789 to C. Toft and DEB 95-09548 to C. Langley.

Literature Cited

Adams, M., P. R. Baverstock, D. A. Saunders, R. Schodde, and G. T. Smith. 1984. Biochemical systematics of the Australian cockatoos (Psittaciformes: Cacatuinae). Australian Journal of Zoology 32:363–377.

Blakers, M., S. J. J. F. Davies, and P. N. Reilly. 1984. The atlas of Australian birds. Royal Australasian Ornithologists Union. Melbourne University Press, Carlton, Victoria.

Boles, W. E. 1993. A new cockatoo (Psittaciformes: Cacatuidae) from the Tertiary of Riversleigh, northwestern Queensland, and an evaluation of rostral characters in the systematics of parrots. Ibis 135:8–18.

Bremer, K. 1992. Ancestral areas: A cladistic reinterpretation of the center of origin concept. Systematic Biology 41:436–445.

Buth, D. G. 1984. The application of electrophoretic data in systematic studies. Annual Review of Ecology and Systematics 15:501–522.

Critchlow, D. E., D. K. Pearl, and C. Qian. 1996. The triples distance for rooted bifurcating phylogenetic trees. Systematic Biology 45:323–334.

de Boer, A. J. 1995. Islands and cicadas adrift in the West Pacific. Biogeographic patterns related to plate tectonics. Tijdschrift voor Entomologie 138:169–244.

de Boer, A. J., and J. P. Duffels. 1996. Historical biogeography of the cicadas of Wallacea, New Guinea and the West Pacific: A geotectonic explanation. Palaeogeography Palaeoclimatology Palaeoecology 124:153–177.

Desjardins, P., and R. Morais. 1991. Nucleotide sequence and evolution of coding and noncoding regions of a quail mitochondrial genome. Journal of Molecular Evolution 32:135–161.

Dixon, M. 1994. Phylogenetic analysis of Psittaciformes (Aves). Ph.D. thesis, University of Texas, Austin.

Duffels, J. P., and A. J. de Boer. 1990. Areas of endemism and composite areas in East Malesia. Pages 249–272 *in* The plant diversity of East Malesia: Proceedings of the Flora Malesiana Symposium commemorating Professor Dr. C. G. G. J. van Steenis (P. Baas, K. Kalkman, and R. Geesink, Eds.). Kluwer Academic Publishers, Dordect, The Netherlands.

Eernise, D. J., and A. G. Kluge. 1993. Taxonomic congruence versus total evidence, and amniote phylogeny inferred from fossils, molecules, and morphology. Molecular Biology and Evolution 10:1170–1195.

Ford, J. 1980. Morphological and ecological divergence and convergence in isolated populations of the Red-tailed Black Cockatoo. Emu 80:103–120.

Forshaw, J. M. 1989. Parrots of the world. Lansdowne Press, Melbourne, Australia.

Higgins, D. G., and P. M. Sharp. 1988. Clustal: A package for performing multiple sequence

alignment on a microcomputer. Gene 73:237–244.

JOSEPH, L. 1988. A review of the conservation status of Australian parrots in 1987. Biological Conservation 46:261–280.

KITCHING, I. J., R. I. VANE-WRIGHT, AND P. R. ACKERY. 1987. The cladistics of *Ideas* (Lepidoptera, Danainae). Cladistics 3:14–34.

KUMAR, S., K. TAMURA, AND M. NEI. 1994. MEGA: Molecular evolutionary genetics analysis software for microcomputers. Computer Applications in the Biosciences10:89–191.

MADSEN, C. S., D. H. DEKLOET, J. E. BROOKS, AND S. R. DEKLOET. 1992. Highly repeated DNA sequences in birds: The structure and evolution of an abundant tandemly repeated 190-bp DNA fragment in parrots. Genomics 14:462–469.

MASON-GAMER, R. J., AND E. A. KELLOGG. 1996. Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). Systematic Biology 45:524–545

MORIN, P. A., J. MESSIER, AND D. S. WOODRUFF. 1994. DNA extraction, amplification, and direct sequencing for hornbill feathers. Journal of the Science Society of Thailand 20:31–41.

OVENDEN, J. R., A. G. MACKINLEY, AND R. H. CROZIER. 1987. Systematics and mitochondrial genome evolution of Australian rosellas. Molecular Biological Evolution 4:526–543.

PAGE, R. D. M. 1993. Component, version 2.0. The Natural History Museum, London.

RONQUIST, F. 1995. Ancestral areas revisited. Systematic Biology 44:572–575.

SAUNDERS, D. A., G. T. SMITH, AND N. A. CAMPBELL. 1984. Egg shape within the Australian Psittaciformes with comments on eggs of *Nymphicus hollandicus*. Emu 8:36–37.

SCHODDE, R. 1997. Cacatuidae. Pages 64–108 *in* Zoological Catalogue of Australia. Vol. 37.2, Aves (Columbidae to Coraciidae)(R. Schodde and I. J. Mason, Eds.). CSIRO Publishing, Melbourne, Australia.

SCHODDE, R., AND J. H. CALABY. 1972. The biogeography of the Australo-Papuan bird and mammal faunas in relation to Torres Strait. Pages 257–300 *in* Bridge and barrier: The natural and cultural history of Torres Strait (D. Walker, Ed.). Australian National University Publishers, Canberra, Australia.

SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds: A study in molecular evolution. Yale University Press, New Haven, Connecticut.

SMITH, G. A. 1975. Systematics of parrots. Ibis 117: 18–68.

SWOFFORD, D. L. 1996. PAUP. Illinois Natural History Survey, Champaign.

SWOFFORD, D. L., AND G. J. OLSEN. 1990. Phylogeny reconstruction. Pages 411–501 *in* Molecular systematics (D. M. Hillis and C. Moritz, Eds.). Sinauer Associates, Sunderland, Massachusetts.

VAN DONZEN, M. W. M., AND L. E. M. DEBOER. 1984. Chromosome studies on 8 species of parrots in the families Cacatuidae and Psittacidae (Aves: Psittaciformes). Genetica 65:109–117.

WALSH, P. S., D. A. METZGER, AND R. HIGUCHI. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques 10:506–513.

ZINK, R. M., AND R. C. BLACKWELL. 1996. Patterns of allozyme, mitochondrial DNA, and morphometric variation in four sparrow genera. Auk 113: 59–67.

Associate Editor: R. M. Zink

APPENDIX. Aligned sequence of the 433-bp region of the 12S mitochondrial DNA gene for species of cockatoos and outgroups in this study. Unreadable nucleotides are denoted by X.

	10	20	30	40	50
C. sulphurea	TGCCCGGCCC	TAAATCTTGA	TGCTTAC-CG	CACATAAACC	ATCCGCCT-G
C. ophthalmica	....C.....	.....C....	..C....-T.	....T.....	.........-.
C. alba	....C....T	.....X....	..C...--T.	A.A.T.....	.........-.
C. moluccensis	....C.....	....	..C....-..	....T.....	.......C-.
C. galerita	....C.....	.....X....	..T....-.A	....T.....	.........-.
C. ducorpsii	....TX....	.....T....	.......-..	....-.....	.........-.
C. sanguinea	....	.......C..	.......-..	....-.....	.........-.
C. goffini	....X.....	....	.......-..	....-.....	.........-.
C. haematuropygia	....C.....	.....C....	.......-..	....-.....	.........-.
C. leadbeateri	....C.....	.......A..	......A-..	T...-...A.	.........-.
E. roseicapillus	....	.....X....	..C....-..	....-...A.	.........-.
C. fimbriatum	....	.....C....	...X.T.-..	....-.....	.........-.
C. banksii	.....A....	.........G	.A...C.-T.	....G.G.-.	.C.....C-.
N. hollandicus	....	....	.....X.-..	A...X....A	T....X.CG.
P. aterrimus	.....A....	.....C....	....CC.-T.	....-...A.	.......C-.
C. japonica	.....A....	.....C.A..	.ACCC..--.	T..TT.TG-T	.........-.
S. canarius	....	....	..C....-AC	.TACT...G.	.......C-.
C. livia	....	....X.....	..C..TTAT.	T.ACC...G.	....X...-.
	60	70	80	90	100
C. sulphurea	AGAACTACGA	GCATAAACGC	TTAAAACTCT	AAGGACTTGG	CGGTGCCCTA
C. ophthalmica	....	....	........C.	....	....
C. alba	....X..X..	....	......X.X.	....	....
C. moluccensis	....	....	......X.T.	....	....
C. galerita	....	X	........T.	.G........	....
C. ducorpsii	....X.....	....	........C.	....	....
C. sanguinea	....	....	........C.	....	....
C. goffini	....	....	........X.	....	....
C. haematuropygia	....	....	........C.	.........A	....
C. leadbeateri	....	....	........X.	....	....A.....
E. roseicapillus	....	....	........X.	....	....
C. fimbriatum	..G.......	....	........C.	....	....
C. banksii	....	....	......T.T.	....	....
N. hollandicus	G...TX.G.G	.AX....G.T	......T.T.	.G.A.T.G..	G.X.C..T..
P. aterrimus	....	...C......	........C.	.........A	....
C. japonica	....	...C......	........C.	....	........C.
S. canarius	....	...CT.....	........X.	....	.....T..C.
C. livia	....	...C......	......T.T.	.....X....	........C.

APPENDIX. Continued.

	110	120	130	140	150
C. sulphurea	AACCCGCCTA	GAGGAGCCTG	TTCTATAA-T	CGATAA-CCC	ACGATACACC
C. ophthalmica	.....G....	....	........-.	......-...	....
C. alba	.....G....	....	..T.....-.	......-...	....
C. moluccensis	.....G....	....	........-.	......-...	....
C. galerita	.....A....	....	.....C..-.	......-...	....
C. ducorpsii	....	....	........-.	X.....-...	....
C. sanguinea	....	....	........-.	......-...	....
C. goffini	....	....	........-.	......-...	....
C. haematuropygia	....	....T.....	...A....-.	......-...	.........T
C. leadbeateri	....	....	........-.	......-...	....
E. roseicapillus	....	....	........-.	......-...	....
C. fimbriatum	.....T....	....	.........-C	......T...	....
C. banksii	..A.......	....	........-.	......T-..	....
N. hollandicus	..-...X..T	.G..GX...T	..T..X..T.	.....--..	....
P. aterrimus	....	....	........-.	......T-..	....
C. japonica	....	....	.........-C	......T-..	.....CT...
S. canarius	....	....	........-.	....G.T-..	......T...
C. livia	....	....	....G...-X	......--T..	.........-.
	160	170	180	190	200
C. sulphurea	CGACCCCTCC	TTGCCA-AAG	CAGCCTACAT	ACCGCCGTCG	CCAGCTCACC
C. ophthalmica	.....T....	......-..A	....	....	.....T....
C. alba	....	......-...	....	....	.....T....
C. moluccensis	....	......-...	....	....	.....T....
C. galerita	....	......-..G	....	....	.....T....
C. ducorpsii	....	......-...	....	....	.....C....
C. sanguinea	....	......-...	....	....	....
C. goffini	....	......-...	....	....	....
C. haematuropygia	....	......-...	....	....	.....T....
C. leadbeateri	......T...	......-...	....	....	.....T....
E. roseicapillus	....	......-...	....	....	....
C. fimbriatum	.....A....	......-...	....	....	....
C. banksii	.A...A.C..	......-...	....	....	....
N. hollandicus	.....A.C..	......-...	....	.........T.	......A...
P. aterrimus	.....A....	......-...	....	....	....
C. japonica	.A...A.C..	.......-.C.	....	....	.........T
S. canarius	T....AT...	.......-G..	....	.........T	....TT....
C. livia	.....A..T.	......TGG.	....	.........A	.....T..G.

APPENDIX. Continued.

	210	220	230	240	250
C. sulphurea	T-TTATGAAA	GCACAACAGT	-GAGCCCAAT	AGTCC-ACAA	CCACTAACAA
C. ophthalmica	.-.T.....	....	-.........	..C..-G...	T.........
C. alba	.-XT.....	.T........	-.........	...XT-....	T.........
C. moluccensis	.-CT.....	.....G....	-.........	.....-....	T.........
C. galerita	.-.T.....	.....G....	-.........	....-....	....
C. ducorpsii	.-.C.....	...T......	-.........	....T-....	X.........
C. sanguinea	.-........	...T......	-.........	.....-....	T.........
C. goffini	.-.....G.	...T......	-.........	.....-....	T.........
C. haematuropygia	.-........	....	-.........	.....-....	......G...
C. leadbeateri	.-C.....G.	......T...	-........C	.....-....	....
E. roseicapillus	.-........	......T...	-....T....	...TT-....	....
C. fimbriatum	.-........	....	-.G......C	.....-....	....
C. banksii	.-.T....G.	......T...	-.G..T...C	....T-...C	....
N. hollandicus	.TC.......	......T...	-........C	..C..-....	.........-.
P. aterrimus	.-C.....G.	.....G....	-.........	..C..-.T.C	....
C. japonica	.A--......	.A........	-....T....	..C.-----G	.......T..
S. canarius	.AC.C.....	..C.......	-....G...C	..C..-CACC	A.G....T-.
C. livia	.CCTC...G.	.T..T...A.	G....A....	C.C..T.ACC	..G.......

	260	270	280	290	300
C. sulphurea	-GACAGGTCA	AGGTATAGCC	TATGGAGTGG	AAG-AAATGG	GCTACATTTT
C. ophthalmica	-.........	....	....	...-......	....
C. alba	-.........	.........T	....	...-......	....
C. moluccensis	-.........	.........T	....	...-......	....
C. galerita	-.........	....	....	...-......	....
C. ducorpsii	-.........	....	..C.......	...-......	....
C. sanguinea	-.........	....	..C....C..	...-......	....
C. goffini	-.........	....	..C.......	...-......	....
C. haematuropygia	-.........	....	..C....C..	...-......	....
C. leadbeateri	-.........	....	C.........	...-......	....
E. roseicapillus	-.........	....	....	...-......	....
C. fimbriatum	-.........	....	C.........	...-......	....
C. banksii	G.........	....	C.....X...	...-......	....
N. hollandicus	C.........	....	C.........	..A-......	.........C.
P. aterrimus	-.........	....	....	...-......	....
C. japonica	-.........	....	.....GA...	...-......	....
S. canarius	C.........	....	......A...	T..-C.....	....
C. livia	-.........X	.......X.X	....A.X...	...A......	....

APPENDIX. Continued.

	310	320	330	340	350
C. sulphurea	CTAAAATAGA	CAAACCCAAC	GG-AAAGAGG	CCTGAAACCT	-GCCTCTAGA
C. ophthalmica	....	T.........	..-......G	C	-.........
C. alba	X.........	....	..-......G	C	-....X....
C. moluccensis	....	....	..-......G	C	-.........
C. galerita	....	....	..-......G	....	-.........
C. ducorpsii	....	.C........	..-......A	C	-.T.......
C. sanguinea	....	.C........	..-.......	C	-....X....
C. goffini	....	.C........	..-.......	C	-.T.......
C. haematuropygia	....	.T........	..-.......	....	-.T...C...
C. leadbeateri	....	......T...	.A-.......	....	-.........
E. roseicapillus	....G.....	....	.A-.......	.T........	-.........
C. fimbriatum	....G.....	T.....T...	.A-..G....	.T........	-.T.....A.
C. banksii	....G.....	......T...	.A-..G..AG	........T.	-...-.C...
N. hollandicus	........A.	T-....T...	.A-......G	....	-.....C...
P. aterrimus	....	T..G..T...	.A-.......	.T........	-.........
C. japonica	....	AC..----..	.A-...AG..	.A........	G.T.CT.G..
S. canarius	....G....-	--...ATG..	..CX...G.G	TA.....-TA	-A..C.....
C. livia	....XC..X.	-...T..C..	.A-....G.G	.A.....--.	A...C.....
	360	370	380	390	400
C. sulphurea	AGGTGGATTT	AGCAGTAAAG	AGGGACAATA	GG-GCCCTCT	TTAAGTCGGC
C. ophthalmica	....	....	....	..-.......	.....T....
C. alba	...T......	G.........	....	.G-.......	.....T....
C. moluccensis	...T......	....	....	.C-.......	.....T....
C. galerita	...C......	....	....	.A-.......	.....T....
C. ducorpsii	...X......	....	....	.C-.......	.....A....
C. sanguinea	...T......	....	....	.T-.......	.....A....
C. goffini	....	.........A	.........G	AC-.......	.....AT...
C. haematuropygia	....	....	G.........	.C-.....X.	.....G...T
C. leadbeateri	....	.........A	....	..-.....T.	....AC....
E. roseicapillus	....	....	....	..-.......	.....C....
C. fimbriatum	....	....	.X........	..-.......	.....T.X..
C. banksii	....	....	.A........	AT-.......	.....TT...
N. hollandicus	....	....	G....T....	A.T....C..	....TT....
P. aterrimus	....	....	.....T..C.	A.-A......	.....C....
C. japonica	...A......	.........A	T....TC.CT	TT-....A..	.....AT...
S. canarius	....	....	T........C	..-.......	.....C....
C. livia	....	....	.....T..X.	T.AX...C..	.....CT...

APPENDIX. Continued.

	409
C. sulphurea	TCTAGGGCA
C. ophthalmica	....
C. alba	.X.......
C. moluccensis	....
C. galerita	....
C. ducorpsii	....
C. sanguinea	....
C. goffini	....
C. haematuropygia	.T.......
C. leadbeateri	.......T.
E. roseicapillus	....
C. fimbriatum	C........
C. banksii	....
N. hollandicus	....
P. aterrimus	C........
C. japonica	C..GA....
S. canarius	C..G..A..
C. livia	...GX....