

MOLECULAR PHYLOGENETIC AFFINITIES OF THE NIGHT PARROT (*GEOPSITTACUS OCCIDENTALIS*) AND THE GROUND PARROT (*PEZOPORUS WALLICUS*)

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ABSTRACT.—Although designating the Night Parrot (*Geopsittacus occidentalis*) and the Ground Parrot (*Pezoporus wallicus*) as each other's closest taxonomic relatives is generally accepted, placing this group with respect to other Australo-Pacific parrots has proven problematical. To examine the phylogenetic relationships of these two species, a 924-bp fragment of the cytochrome-*b* gene was sequenced from single representatives of the following genera: *Geopsittacus*, *Pezoporus*, *Neophema*, *Melopsittacus*, *Platycercus*, *Polytelis*, *Strigops*, and *Calyptorhynchus*. Maximum-parsimony, maximum-likelihood, and distance trees all supported a close association between *Geopsittacus* and *Pezoporus*. These two genera were also found to be closely linked with *Neophema* and *Melopsittacus*. Despite superficial morphological similarities, *Geopsittacus* and *Strigops* (Kakapo) were found not to be closely related. Received 21 December 1992, accepted 6 October 1993.

THE PSITTACIFORMES (parrots, lorikeets, and cockatoos) are distributed throughout the Neotropical, Ethiopian, Oriental and Australasian regions. Studies based on morphological (Brereton 1963, Smith 1975, Homberger 1980), biochemical (Christidis et al. 1991a), and chromosomal (Christidis 1990, Christidis et al. 1991b) data have shown that most diversity is centered within the Australasian region. Although these studies have identified major groupings among the Australasian psittaciforms, the placement of several genera and species is still poorly resolved. Two such species are the Night Parrot (*Geopsittacus occidentalis*) and the Ground Parrot (*Pezoporus wallicus*).

The monotypic genus *Geopsittacus* often has been considered to be allied to, or congeneric with, the monotypic genus *Pezoporus* (Brereton 1963, Ford 1969, Schodde and Mason 1980). The paucity of knowledge about the behavior and biology of *Geopsittacus* has hampered attempts to assess its links with *Pezoporus*. Until 1990, when a dead specimen was found (Boles et al. 1991, 1994), *Geopsittacus* had not been reliably documented since 1912. It is represented in museum collections by only 22 skins (excluding the 1990 specimen) and some bones (Forshaw et al. 1976). Schodde and Mason (1981) regarded *Geopsittacus* and *Pezoporus* as closely related vi-

carants, replacing each other in inland and wet coastal habitats of southern Australia, respectively. There is some similarity in the structure of their preferred low scrubby/heathland habitats. These two parrots share similar green plumage crossed with bands of black and yellow. Both are primarily terrestrial. *Geopsittacus* receives its common name from its nocturnal habits, and *Pezoporus* is essentially crepuscular (Forshaw 1981).

Superficially, *Geopsittacus* and *Pezoporus* resemble diminutive versions of the flightless New Zealand Kakapo (*Strigops habroptilus*), a fact commented on by Gould (1861). Like the two Australian taxa, *Strigops* is nocturnal and terrestrial, and has at least superficially similar green-barred plumage. Furthermore, *Strigops* and *Geopsittacus* possess enlarged fleshy ceres ringed by fine "hairlike" feathers. These are pronounced in the former, but small in the latter. Forshaw (1981, 1989) proposed that *Geopsittacus*, *Pezoporus*, and *Strigops* were closely related and constituted an ancient relict group. He also suggested that the Budgerigar (*Melopsittacus undulatus*) and *Neophema* linked this group with the "typical" platycercines or broad-tailed parrots. In the strictest sense, the broad-tailed parrot assemblage comprises the following Australian genera: *Platycercus*, *Barnardius*, *Northiella*, *Purpureice-*

phalus, *Lathamus*, *Psephotus*, *Pezoporus*, *Geopsittacus*, and *Neophema*. *Cyanoramphus* from New Zealand and the South Pacific is generally included (Forshaw 1989), and some authors also include other South Pacific genera such as *Eunymphicus* (Smith 1975, Homberger 1980) and *Prosopieia* (Homberger 1980). *Melopsittacus* shares with *Pezoporus*, *Geopsittacus*, and *Strigops* a yellow-green plumage marked with dark barring on the dorsum. Breteron (1963) placed *Geopsittacus* and *Pezoporus* with *Melopsittacus* in their own family, the *Pezoporidae*. Biochemical studies (Christidis et al. 1991a) do not support a close association between *Melopsittacus* and *Pezoporus*. Smith (1975) included *Melopsittacus*, *Geopsittacus*, and *Pezoporus* within the *platycercines* and kept *Strigops* in its own monotypic tribe. Several authors (e.g. Forshaw 1989, Sibley and Monroe 1990) have placed *Geopsittacus*, *Pezoporus*, and *Strigops* adjacent to each other in linear sequence, at least implying a relationship.

In an effort to resolve the systematic affinities of *Geopsittacus* and *Pezoporus*, we collected sequence data for a 924-base-pair fragment of the mitochondrial cytochrome-*b* gene from eight psittaciform genera, including *Strigops* and *Melopsittacus*.

MATERIALS AND METHODS

The following specimens were examined (with accession number, year of collection, and DNA source, in parentheses): *Geopsittacus occidentalis*, Night Parrot (36246, 1876, feather); *Pezoporus wallicus wallicus*, Ground Parrot (R8794, 1924, feather); *Strigops habroptilis*, Kakapo (R2402, 1907, feather); *Neophema petrophila petrophila*, Rock Parrot (MV254, 1989, frozen liver); *Melopsittacus undulatus*, Budgerigar (MV1058, 1992, frozen liver); *Platycercus icterotis xanthogenys*, Western Rosella (MV347, 1989, frozen liver); *Polytelis anthopeplus westralis*, Regent Parrot (MV340, 1989, frozen liver); and *Calyptorhynchus banksii graptogyne*, Red-tailed Black-Cockatoo (MV1616, 1989, feather). Specimens are lodged in the Museum of Victoria, Melbourne, Australia. The choice of an outgroup was compounded by the lack of conclusive evidence concerning the nearest relatives of Psittaciformes (summarized in Sibley and Ahlquist 1990). Consequently, two outgroups were chosen. A gruiform, *Grus rubicunda* (the Brolga; MV790, 1991, frozen liver) was sequenced. In addition, published cytochrome-*b* sequences from the passeriform *Pitta sordida* (the Hooded Pitta; Edwards et al. 1991) were used. The cytochrome-*b* sequences collected in the present study have been deposited in GenBank with the accession numbers U13620 to U13628.

Where feather tips were used, DNA extraction was performed as described in Leeton et al. (1993). For frozen liver samples, total DNA was extracted by grinding 0.1 to 0.3 g of tissue in 500 μ l of digestion solution (50 mM Tris HCl, 10 mM EDTA, 100 mM NaCl, pH 8.0) to which 10 μ l proteinase K (10 μ g/ml) was added. Digestion was performed at 37°C for 2 h. DNA was then extracted through two washes with equal volumes of phenol:chloroform (1:1), and precipitated following the addition of 2.5 volumes of ice-cold absolute ethanol. After drying, the DNA was resuspended in 100 μ l TE (10 mM Tris, 0.1 mM EDTA, pH 8.0).

The cytochrome-*b* sequence was amplified as a series of small segments (300–400 bp) using the primer pairs L14841/H15149 (Kocher et al. 1989), L15114/H15547, and L15424/H15767 (Edwards et al. 1991). Letters refer to light and heavy strands and numbers to positions of the 3' nucleotides in the human mtDNA sequence (Anderson et al. 1981). Double-stranded PCR amplifications were performed in a 50 μ l reaction mix (25 μ M of each appropriate primer, 2.5 mM dNTPs [Boehringer], 1 unit of Tth DNA polymerase [Toyobo], adjusted to appropriate specifications using 10 \times Tth buffer [Toyobo]). Thirty-five rounds of amplification were performed, with each cycle consisting of denaturation at 92°C for 60 s, reannealing at 52°C for 60 s, and extension at 72°C for 60 s. The final product was cleaned and concentrated using a microcentrifuge filter tube (Millipore), and resuspended in 50 μ l of TE (pH 8.0).

Asymmetric PCRs were carried out under similar conditions, in a reaction volume of 100 μ l using 1 μ l of double-stranded PCR product and 0.25 μ g of the appropriate primer (the addition of a limiting primer was not deemed necessary, due to small amounts of "carry over" following filtration). The final asymmetric PCR product was purified and concentrated following ethanol precipitation. Asymmetric products were sequenced directly by the protocol of Sanger et al. (1977) using a commercial kit (Sequenase, United States Biochemical). Sequences were obtained for the entire light strand and a portion of the heavy strand. There was complete congruence between the heavy- and light-strand sequences.

DNA sequences were aligned relative to the human mtDNA sequence (Anderson et al. 1981). No base insertions or deletions were detected. Sequence divergence, transition:transversion ratios, and evolutionary weightings were calculated from the data set. Following Brown et al. (1982), the transition:transversion ratio calculated for the least-diverged species pairs was used for all the taxa examined because the saturation of transitions for distantly related comparisons obscures the real transition:transversion bias.

Maximum-parsimony trees were constructed using the exhaustive algorithm in PAUP version 3.1.1 (Swofford 1993). Initial analyses were based on all the characters without weighting (global parsimony). A series

TABLE 1. Sequence divergence measured between species pairs examined over the 924-bp cytochrome-*b* fragment. Above diagonal, Kimura (1980) two-parameter distance; below diagonal, frequency of sequence divergence.

Taxon	1	2	3	4	5	6	7	8	9	10
1 <i>Geopsittacus</i>	—	0.0903	0.1139	0.1735	0.1105	0.1348	0.1770	0.2340	0.2140	0.2266
2 <i>Pezoporus</i>	0.0840	—	0.1346	0.1682	0.1163	0.1297	0.1779	0.2378	0.2048	0.2312
3 <i>Melopsittacus</i>	0.1050	0.1220	—	0.1363	0.1101	0.1065	0.1587	0.2164	0.2076	0.2136
4 <i>Strigops</i>	0.1540	0.1490	0.1230	—	0.1586	0.1276	0.1405	0.2470	0.2193	0.2439
5 <i>Neophema</i>	0.1020	0.1070	0.1020	0.1420	—	0.1162	0.1631	0.2341	0.2164	0.2339
6 <i>Platycercus</i>	0.1220	0.1180	0.0980	0.1160	0.1070	—	0.1312	0.2129	0.2067	0.2222
7 <i>Polytelis</i>	0.1560	0.1570	0.1410	0.1270	0.1450	0.1190	—	0.1943	0.2300	0.2574
8 <i>Calyptorhynchus</i>	0.1990	0.2010	0.1860	0.2070	0.1990	0.1830	0.1690	—	0.2704	0.2475
9 <i>Grus</i>	0.1840	0.1770	0.1800	0.1880	0.1860	0.1800	0.1960	0.2250	—	0.2002
10 <i>Pitta</i>	0.1930	0.1960	0.1830	0.2060	0.1980	0.1890	0.2140	0.2420	0.1730	—

of conditional data sets was also analyzed: (1) weighting for differential evolutionary rates at the three codon positions (weighted parsimony); (2) excluding third positions; (3) transversions only (transversion parsimony). The resolving power of the sequence data was assessed using the bootstrap procedure (Felsenstein 1985) as implemented in PAUP and the jackknifing procedure as described by Lanyon (1985).

A maximum-likelihood analysis (Felsenstein 1981) using the DNAML option of PHYLIP version 3.5 (Felsenstein 1993) was performed including 100 bootstrap replicates. The data set was analyzed both with and without evolutionary weightings for the three codon positions. A transition : transversion bias of 4:3, generated from a consideration of all positions in the *Pezoporus-Geopsittacus* comparison, was included.

A distance matrix was constructed using the DNADIST program of PHYLIP employing Kimura's (1980) two-parameter method (Table 1). From the matrix, Fitch-Margoliash (Fitch and Margoliash 1967) and neighbor-joining (Saitou and Nei 1987) trees were generated using the FITCH and NEIGHBOR options of PHYLIP. Bootstrap resampling was implemented for both trees.

RESULTS

Within the 924-bp region of cytochrome *b* (Appendix), 301 positions were variable over all psittaciform taxa examined; 59 were at the first-codon position, 56 at the second, and 186 at the third. These converted to evolutionary weightings for the first-, second-, and third-codon positions of 3:3:1. The percent sequence divergence between psittaciform species pairs (Table 1) ranged from 8.4% (*Geopsittacus* and *Pezoporus*) to 20.7% (*Calyptorhynchus* and *Strigops*). Kimura (1980) two-parameter distances, within the psittaciforms, ranged from 0.0903 (*Geopsittacus* and *Pezoporus*) to 0.2470 (*Calyptorhynchus*

and *Strigops*), the pattern of divergences being similar to that of the percent differences (Table 1). Average percent divergences and two-parameter distances between the psittaciforms and the outgroups (*Grus*, *Pitta*) were 19.6% and 0.2403, respectively.

Transition : transversion ratios between species pairs varied considerably ranging from 1:1 (*Calyptorhynchus* : *Strigops*) to 4:3 (*Geopsittacus* : *Pezoporus*). The highest transition : transversion ratios occurred between those species that had the lowest percent divergences and Kimura (1980) two-parameter distances. The choice of either *Pitta* or *Grus* as the outgroup affected the topology and resolution of some of the analyses and, therefore, these are described separately below.

A global-parsimony analysis, without weighting and using *Grus* as the outgroup, produced two equally most-parsimonious trees of length 668 steps, which differed from one another only in the relative positioning of *Calyptorhynchus* and *Strigops*. In one, *Polytelis* and *Calyptorhynchus* were sister taxa and, in the other, *Strigops* and *Polytelis* were sister taxa. Bootstrap analysis supported only the former topology. In the bootstrap consensus topology (Fig. 1), *Geopsittacus* and *Pezoporus* were sister taxa, and these were linked with *Neophema*, *Melopsittacus*, and *Platycercus* in a stepwise pattern. Bootstrap values at each of these nodes were 94, 77, 72, and 73%, respectively. A consideration of near-parsimonious trees revealed 4 with 671 steps or less and their strict consensus was identical in topology to the above. Weighted parsimony provided less resolution; the *Geopsittacus-Pezoporus-Neophema* clade was present, and *Polytelis* was aligned with *Strigops*, but with a low boot-

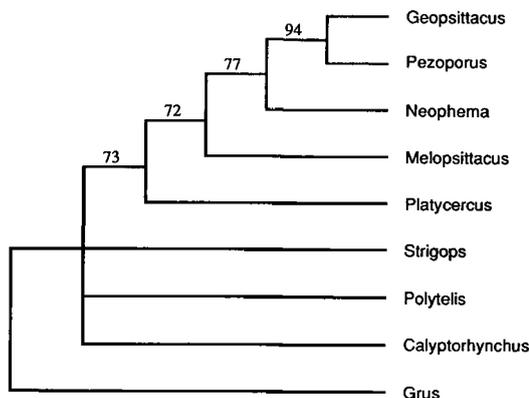


Fig. 1. PAUP maximum-parsimony analysis based on unweighted characters for psittaciform genera examined and using *Grus* as the outgroup. Length of two equally most-parsimonious trees, before bootstrapping, was 668 and consistency index was 0.669. Bootstrap values greater than 50% indicated at nodes.

strap value of 56%. Global parsimony using *Pitta* as the group produced a single most-parsimonious tree with 683 steps (not shown). This topology differed from the above (Fig. 1) in that *Platycercus* was now linked with *Strigops*, although this node was not supported following bootstrapping. The *Pezoporos-Geopsittacus* clade was supported in all of the bootstrap replicates, while nodes linking *Neophema* and *Melopsittacus* to this clade were well supported with bootstrap values of 91 and 71%, respectively. The *Polytelis-Calyptorhynchus* clade was supported by a bootstrap of 78%. A consideration of near-parsimonious trees revealed 7 with 687 steps or less, and their strict consensus was identical in topology to the above. Weighted parsimony, with *Pitta* as outgroup, differed in that *Polytelis* was aligned with *Strigops*, but this node had a low bootstrap value (55%). Following the jack-knife procedure, only the *Geopsittacus-Pezoporos-Neophema* clade was identified in all replicates, regardless of choice of outgroup. Moreover, in all replicates that included *Neophema*, both *Melopsittacus* and *Platycercus* were aligned with the *Geopsittacus-Pezoporos-Neophema* clade.

When first- and second-codon positions only were considered, with *Pitta* as the outgroup, *Calyptorhynchus* was separated from the remaining parrots, but only with a bootstrap value of 51%. The only other resolution was a node linking *Polytelis* with *Strigops* with a low bootstrap value of 62%. When *Grus* was used as the out-

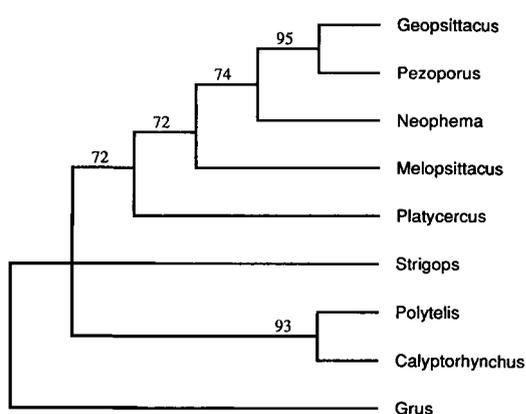


Fig. 2. Maximum-likelihood tree based on unweighted characters for psittaciform genera examined and using *Grus* as the outgroup. Log likelihood before bootstrapping was -4355.78900 . Bootstrap values greater than 50% indicated at nodes.

group, no resolution was obtained following bootstrapping.

Transversion parsimony using *Pitta* as the outgroup (not shown) produced three clades: (1) *Geopsittacus-Pezoporos*; (2) *Neophema-Platycercus-Melopsittacus*; and (3) *Polytelis-Strigops*. The first two were sister clades and *Calyptorhynchus* pulled out as the most divergent lineage. Following bootstrapping, however, only the *Geopsittacus-Pezoporos* clade (75%) was supported. When *Grus* was used as the outgroup, *Calyptorhynchus* was again the most divergent lineage, *Geopsittacus* and *Pezoporos* were linked with *Neophema*, *Melopsittacus* and *Platycercus*, and *Polytelis* was linked with *Strigops*. Following bootstrapping, the node separating *Calyptorhynchus* from the rest had a bootstrap of 63%; the only other nodes with values higher than 50% were *Geopsittacus-Pezoporos* (68%) and *Strigops-Polytelis* (55%).

The maximum-likelihood tree (Fig. 2), using *Grus* as the outgroup, had a topology comparable to that obtained with global parsimony (Fig. 1). *Polytelis* and *Calyptorhynchus* were linked with *Strigops*, although this node had a bootstrap value of only 40%. All other nodes were supported by bootstrap values of 72% and higher. A consideration of evolutionary weightings did not alter the topology or resolution of the maximum-likelihood tree. When *Pitta* was used as the outgroup, the position of *Platycercus* was not resolved following bootstrapping, but *Strigops* was linked with *Polytelis-Calyptorhynchus* with a bootstrap of 64%.

The Fitch tree, using *Grus* as the outgroup (not shown), was identical in topology to the maximum-likelihood tree, and there was only one topological difference between the Fitch and neighbor-joining (Fig. 3) trees. In the latter, *Strigops* was aligned with the *Geopsittacus-Platycercus* clade, and this node was supported by a bootstrap of 51%. When *Pitta* was used as the outgroup, the neighbor-joining tree was identical in topology to the maximum-likelihood tree, while in the Fitch tree, *Platycercus* was aligned with the *Strigops-Calyptorhynchus-Polytelis* clade and this node was supported by a bootstrap of 51%.

DISCUSSION

Phylogenetic position of Geopsittacus and Pezoporos.—Cytochrome-*b* data are unequivocal and consistent in their linking of *Geopsittacus* with *Pezoporos*. The two genera differ by 8.4% sequence divergence (Table 1), which is comparable to divergences for other congeneric avian species. Edwards et al. (1991) reported values ranging from 6.2 to 12.0% between congeners in *Pomatostomus*, while Smith et al. (1991) recorded values of 5.7 to 13.0% within the genus *Laniarius*. The present data are consistent with the conclusions of Ford (1969) and Schodde and Mason (1980) that *Geopsittacus* and *Pezoporos* should be treated as congeneric species. *Geopsittacus occidentalis*, therefore, becomes *Pezoporos occidentalis*. The pattern of distribution and preferred habitats for these species parallels those in the genus *Neophema*, which also has both inland (*bourkii* and *splendida*) and coastal species (*chrysogaster*, *chrysostoma*, *pulchella*, *petrophila*, and *elegans*).

In concert with the shared patterns of distribution, *Geopsittacus* and *Pezoporos* were consistently allied with *Neophema* by the cytochrome-*b* data. *Melopsittacus* also was aligned with this assemblage in all analyses. On the basis of morphological characters, such as lack of a nape spot and presence of barred feathers, Brereton (1963) linked *Melopsittacus* with *Pezoporos* and *Geopsittacus*; however, lack of a nape spot appears to be the ancestral condition within the Psittaciformes. Only the other Australian platycercine genera and *Cyanoramphus* possess a nape spot. Although Smith (1975) listed *Eunymphicus* as possessing a nape spot, our examination found that it in fact lacks one. If the *Geopsittacus-Melopsittacus* assemblage, as identified in our study,

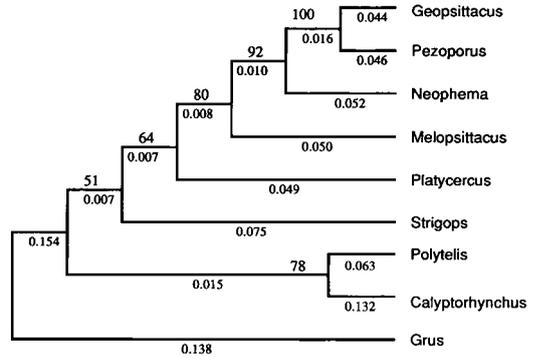


Fig. 3. Neighbor-joining tree based on the Kimura (1980) two-parameter distances for psittaciform genera examined, using *Grus* as the outgroup. Bootstrap values greater than 50% indicated above nodes. Numbers below nodes refer to branch lengths.

is part of the platycercines, then two scenarios are possible to explain the occurrence of a nape spot in the various genera. In the first (Fig. 4A), the nape spot evolved early in the evolution of the platycercines and has since been lost twice, in *Melopsittacus* and in *Geopsittacus-Pezoporos*. The alternative scenario (Fig. 4B) is that the nape spot evolved in the "core" platycercines (sensu Christidis et al. 1991a) after their divergence from the lineage, giving rise to the *Geopsittacus-Melopsittacus* assemblage, and also evolved independently in *Neophema*. There are no data at present to favor one hypothesis over the other.

The distribution of barred feathers within the platycercines also has two possible explanations. Barred feathers may have arisen early in the evolution of the *Geopsittacus-Melopsittacus* assemblage and then been lost secondarily in *Neophema* (Fig. 4A). Alternatively, barred feathers may have evolved independently in both *Melopsittacus* and *Geopsittacus-Pezoporos* (Fig. 4B). To differentiate between these two hypotheses, we examined in detail the barred feathers in *Pezoporos*, *Geopsittacus*, *Strigops*, *Melopsittacus*, and *Psittacella*. Other than their darker green color, the barred feathers of *Pezoporos* are very similar to those of *Geopsittacus*, agreeing in details of pattern on each part of the body. The most obvious difference is the barring of underpart feathers, which in *Pezoporos* extends to the borders of the webs, whereas in *Geopsittacus* it does not. *Melopsittacus* does not exhibit this same agreement of feather patterns. On no part of the body does its pattern of barring appear homologous with that in *Pezoporos-Geopsittacus*.

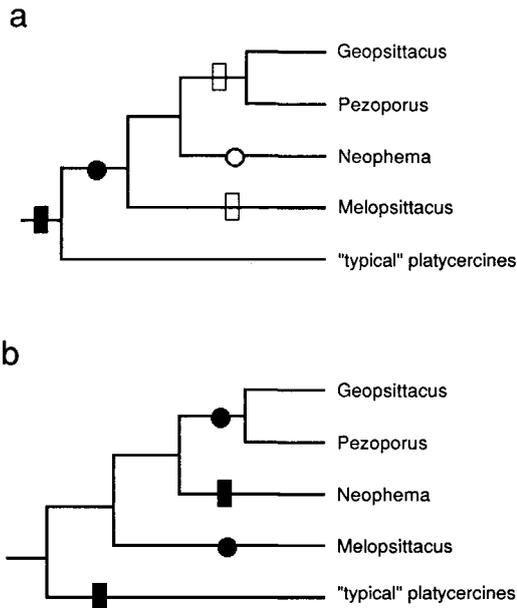


Fig. 4. Possible pathways for evolution of nape spots and barred feathers in platycercines with (A) character loss, or (B) characters arising more than once. Closed rectangles represent gain of nape spot; open rectangles represent loss of nape spot. Closed circles represent gain of barred feathers; open circles represent loss of barred feathers.

This adds support to the idea that barred patterns evolved independently in each group. The barred feathers of *Strigops* show even more substantial differences from those of *Geopsittacus*-*Pezoporos*, and are more likely to have been independently derived. New Guinean *Psittacella* is similar to *Geopsittacus* and *Pezoporos* in its underparts and to *Melopsittacus* in its upperparts. It was shown to be linked with the platycercines by Christidis et al. (1991a), but was not treated by Brereton (1963) or included in this study. The relationship of *Psittacella* to these other genera needs to be assessed and further studies should include it.

Neophema, *Melopsittacus*, and *Geopsittacus* share a Type A-1 carotid formula (no data are available for *Pezoporos*), whereas the other platycercines (including *Cyanoramphus*) are Type A-2 (Garrod 1873, 1874, 1876, Glenny 1957). Apart from *Nestor*, *Psittichas*, and *Prosopieia* (which are Type A-2), other Australasian and Asian genera examined have a Type A-1 carotid formula. Beddard (1898) listed *Eunymphicus* (which he called *Nymphicus cornutus*) as possessing a Type A-2

carotid formula, citing Garrod (1873, 1874, 1876) as the source. This appears to be in error, as Garrod (1873, 1874, 1876) did not examine *Eunymphicus*. Similarly, Smith (1975) listed *Psittacella* as possessing a Type A-1 carotid formula, but his cited sources (i.e. Garrod 1874, Beddard 1898, Glenny 1957) did not mention *Psittacella*. The African Psittacini and all South American genera examined are Type A-2. It can be argued that the Type A-1 carotid formula is ancestral for the Australasian genera and that a Type A-2 formula evolved in the "core" platycercines after this lineage diverged from the one leading to the *Geopsittacus*-*Melopsittacus* assemblage.

Based on 924 bp of cytochrome-*b* sequences, no association was apparent between *Strigops* and either *Geopsittacus* or *Pezoporos* (cf. Forshaw 1989). Thus, the similarities in appearance between *Strigops* and *Geopsittacus* are convergent, presumably brought about by similar life habits. Predominantly green plumage crossed with bands of black and yellow may serve as camouflage for these ground-dwelling species, which shelter in tussocks or clumps of vegetation by day. The "hairlike" feathers present in both *Geopsittacus* and *Strigops* have also evolved convergently, possibly acting as tactile sensors when the birds are moving through thick ground cover.

Deeper relationships within Psittaciformes.—The platycercine assemblage is generally considered to include *Neophema*, *Pezoporos*, and *Melopsittacus* (Smith 1975, Homberger 1980). Although the qualitative and distance analyses given above generally aligned *Platycercus* with the *Pezoporos*-*Melopsittacus* clade, bootstrap analysis revealed that the position of *Platycercus* could not be resolved confidently by the cytochrome-*b* sequences. Moreover, resolution of the position of *Platycercus* was affected by the choice of outgroup. To resolve this inconsistency regarding the position of *Platycercus*, sequence data are required from other typical platycercines such as *Northiella*, *Psephotus*, and *Barnardius*. Such studies are currently in progress. If one assumes that the *Melopsittacus* to *Pezoporos* clade is part of the platycercine assemblage, it probably represents a highly divergent group of taxa. Christidis et al. (1991a), based on allozyme studies, argued for two successive radiations among the platycercines. The first involved the divergence of *Pezoporos* (and presumably *Geopsittacus*, which was not included in that study), *Neophema*, and *Melopsittacus* from the core platycercine group.

The second, more recent one, gave rise to *Platycercus*, *Barnardius*, *Purpuricephalus*, *Northiella*, *Lathamus*, and *Psephotus*. Christidis et al. (1991a) also reported a close association between the polytelitines and platycercines, but this was not apparent in the present study. Although *Polytelis* was aligned with *Calyptorhynchus* in most analyses, the relatively high sequence divergence between the two (17.1%) suggests that an examination of additional taxa is required to accurately assess their relationships. Moreover, bootstrapping and jackknifing indicated that the relationships of *Polytelis*, *Strigops*, and *Calyptorhynchus* could not be resolved from the present data set.

The patterns of resolution obtained in this study indicate that the cytochrome-*b* gene is particularly useful in determining relationships between closely related genera, but that for deeper branches, transition bias needs to be considered. The cockatoos, represented in our study by *Calyptorhynchus*, are generally considered to be the sister group to a large assemblage that includes all the Australian genera examined here (Smith 1975, Homberger 1980, Christidis et al. 1991a, b). Only when the transition bias was taken into consideration was such a relationship apparent from the present sequence data. Moreover, the levels of sequence divergence between *Calyptorhynchus* and the other psittaciforms examined were of similar magnitude to those recorded between the psittaciforms and the two outgroups *Grus* and *Pitta*, indicating that the level of transition divergence had reached saturation in those comparisons.

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LITERATURE CITED

- ANDERSON, S., A. T. BANKIER, B. G. BARRALL, M. H. L. BRUIJN, A. R. COULSON, J. DROUIN, I. C. EPERON, D. P. NIERLICH, B. A. ROE, F. SANGER, P. H. SCHREIRER, A. J. H. SMITH, R. STADEN, AND I. G. YOUNG. 1981. Sequence and organization of the human mitochondrial genome. *Nature* 290:457-465.
- BEDDARD, F. E. 1898. The structure and classification of birds. Longmans Green, London.
- BOLES, W. E., N. W. LONGMORE, AND M. C. THOMPSON. 1991. The fly-by-night parrot. *Aust. Nat. Hist.* 9: 689-695.
- BOLES, W. E., N. W. LONGMORE, AND M. C. THOMPSON. 1994. A recent specimen of the Night Parrot, *Geopsittacus occidentalis*. *Emu* 94:37-40.
- BRETERON, J. LE GAY. 1963. Evolution within the Psittaciformes. Pages 411-501 in *Proceedings XIII International Ornithological Congress* (C. G. Sibley, Ed.). Ithaca, New York, 1962. American Ornithologists' Union, Washington, D.C.
- BROWN, W. M., E. M. PRAGER, A. WANG, AND A. C. WILSON. 1982. Mitochondrial DNA sequences of primates: Tempo and mode of evolution. *J. Mol. Evol.* 18:225-239.
- CHRISTIDIS, L. 1990. Animal cytogenetics—Aves. *Gebürder Borntraeger*, Berlin.
- CHRISTIDIS, L., R. SCHODDE, D. D. SHAW, AND S. F. MAYNES. 1991a. Relationships among the Australo-Papuan parrots, lorikeets, and cockatoos (Aves: Psittaciformes): Protein evidence. *Condor* 93:302-317.
- CHRISTIDIS, L., D. D. SHAW, AND R. SCHODDE. 1991b. Chromosomal evolution in parrots, lorikeets and cockatoos (Aves: Psittaciformes). *Hereditas* 114: 47-56.
- EDWARDS, S. V., P. ARCTANDER, AND A. C. WILSON. 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. *Proc. R. Soc. Lond. B. Biol. Sci.* 243:99-107.
- FELSENSTEIN, J. 1981. Evolutionary trees from DNA sequences: A maximum likelihood approach. *J. Mol. Evol.* 17:368-376.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783-791.
- FELSENSTEIN, J. 1993. PHYLIP, manual version 3.5. Department of Genetics, Univ. Washington, Seattle.
- FITCH, W. M., AND E. MARGOLIASH. 1967. Construction of phylogenetic trees. *Science* 155:279-284.
- FORD, J. 1969. Distribution and taxonomic notes of some parrots of Western Australia. *S. Aust. Ornithol.* 25:99-105.
- FORSHAW, J. M. 1981. Australian parrots, 2nd rev. ed. Lansdowne, Melbourne.
- FORSHAW, J. M. 1989. Parrots of the world, 3rd rev. ed. Lansdowne, Willoughby, Sydney.
- FORSHAW, J. M., P. J. FULLAGAR, AND J. I. HARRIS. 1976. Specimens of the Night Parrot in museums throughout the world. *Emu* 76:120-126.
- GARROD, A. H. 1873. On the carotid arteries of birds. *Proc. Zool. Soc. Lond.* 1873:457-472.
- GARROD, A. H. 1874. On some points in the anatomy

ANDERSON, S., A. T. BANKIER, B. G. BARRALL, M. H. L. BRUIJN, A. R. COULSON, J. DROUIN, I. C. EPERON, D. P. NIERLICH, B. A. ROE, F. SANGER, P. H. SCHREIRER, A. J. H. SMITH, R. STADEN, AND I. G.

- of the parrots which bear on the classification of the suborder. *Proc. Zool. Soc. Lond.* 1874:586-598.
- GARROD, A. H. 1876. Notes on the anatomy of certain parrots. *Proc. Zool. Soc. Lond.* 1876:691-692.
- GLENNY, F. H. 1957. A revised classification of the Psittaciformes based on the carotid artery arrangement patterns. *Ann. Zool. Agra* 2:47-56.
- GOULD, J. 1861. On a new genus and species of parakeet from Western Australia. *Proc. Zool. Soc. Lond.* 1861:100-101.
- HOMBERGER, D. G. 1980. Funktionell-Morphologische Untersuchungen zur Radiation der Ernährungs- und Trinkmethoden der Papageien (Psittaci). *Bonn. Zool. Monogr.* 13:1-192.
- KIMURA, M. 1980. A simple method for estimating evolutionary rate of base substitution through comparative studies of nucleotide sequences. *J. Mol. Evol.* 116:111-120.
- KOCHER, T. D., W. K. THOMAS, A. MEYER, S. V. EDWARDS, S. PAABO, F. X. VILLA BLANCA, AND A. C. WILSON. 1989. Dynamics of mitochondrial DNA evolution in animals: Amplification and sequencing with conserved primers. *Proc. Natl. Acad. Sci. USA* 86:6196-6200.
- LANYON, S. M. 1985. Detecting internal inconsistencies in distance data. *Syst. Zool.* 34:397-403.
- LEETON, P. R., L. CHRISTIDIS, AND M. WESTERMAN. 1993. Feathers from museum skins—A good source of DNA for phylogenetic studies. *Condor* 95:465-466.
- SAITOU, N., AND M. NEI. 1987. The neighbour-joining method: A new method for reconstructing phylogenetic trees. *Mol. Biol. Evol.* 4:406-425.
- SANGER, F., S. NICKLEN, AND A. R. COULSON. 1977. DNA sequencing with chain-terminating inhibitors. *Proc. Natl. Acad. Sci. USA* 74:5463-5467.
- SCHODDE, R., AND I. J. MASON. 1980. Nocturnal birds of Australia. Lansdowne, Melbourne.
- SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds. Yale Univ. Press, New Haven.
- SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale Univ. Press, New Haven.
- SMITH, G. A. 1975. Systematics of parrots. *Ibis* 131:18-68.
- SMITH, E. F. G., P. ARCTANDER, J. FJELDSÅ, AND O. G. AMIR. 1991. A new species of shrike (*Laniidae: Laniarius*) from Somalia, verified by DNA sequence data from the only known individual. *Ibis* 133:227-235.
- SWOFFORD, D. L. 1993. PAUP manual version 3.1:1. Illinois Natural History Survey, Champaign.

APPENDIX. Continued.

<i>Geopsittacus</i>	MetTrpPheTrpGlyAlaThrValIleThrAsnLeuPheSerAlaIleProTyrValGlyGlnThrLeuValGluTrpAlaTrpGlyGlyPheSerValAspAsn
<i>Pezoporus</i>	ATATGATTCTGAGGGGCAACACTAATTACCAACCTATTCTCAGCAATCCCTACCTCGGGCAACACTAGTAGAATGACCTGAGGTGGTTCTCCGTAGACAAC
<i>Melospittacus</i>T.....A.....C.....TA.A.....C.....G.....A.....A.....G.....A.....A.....T.....
<i>Strigops</i>T.....A.....A.....C.....A.....A.....C.....A.....A.....A.....G.....A.....G.....A.....G.....
<i>Neophema</i>C.....G.....A.....C.....C.....T.....T.....C.....C.....A.....A.....G.....C.....G.....A.....G.....
<i>Platycercus</i>T.....A.....A.....C.....C.....A.....A.....A.....A.....G.....T.....G.....A.....G.....
<i>Polytelis</i>T.....A.....C.....C.....A.....T.....T.....C.....C.....A.....A.....A.....C.....T.....C.....T.....A.....T.....G.....
<i>Calyptorhynchus</i>C.....G.....A.....C.....C.....T.....T.....C.....C.....A.....A.....A.....G.....T.....C.....T.....A.....T.....G.....
<i>Grus</i>C.....T.....A.....T.....C.....C.....T.....C.....CG.....A.....A.....C.....C.....T.....T.....G.....C.....A.....A.....T.....
<i>Pitta</i>C.....T.....C.....C.....C.....T.....T.....A.....A.....G.....C.....G.....A.....A.....T.....G.....T.....G.....T.....
<i>Geopsittacus</i>	ProThrLeuThrArgPheAlaLeuLeuIleLeuLeuProPheIleValGlyPheAlaProValHisLeuValPheLeuHisGluThrGlySerAsnAsn
<i>Pezoporus</i>	CCCACACTAACCCGATTCTTCGCCCTACTCATCTCCATTTATATCGTGGATTGGTCCCGTCCCATCTAGTTTTCTTCCATGAACACAGGCTCTAACCAAC
<i>Melospittacus</i>T.....C.....T.....T.....A.....T.....A.....T.....A.....A.....C.....A.....T.....T.....AC.....C.....T.....C.....T.....
<i>Strigops</i>T.....T.....T.....T.....A.....C.....A.....T.....T.....A.....CA.....CC.....A.....TTA.....C.....ACC.....T.....A.....A.....
<i>Neophema</i>C.....T.....T.....T.....A.....T.....T.....A.....ACA.....CA.....A.....TCTT.....CT.....ACC.....T.....C.....T.....A.....A.....T.....
<i>Platycercus</i>T.....T.....T.....T.....A.....T.....T.....A.....AC.....C.....A.....TT.....A.....C.....ACC.....T.....A.....G.....T.....A.....A.....T.....
<i>Polytelis</i>T.....T.....T.....T.....A.....T.....T.....A.....C.....ACA.....CC.....A.....TCTT.....C.....TACA.....T.....A.....T.....A.....A.....T.....
<i>Calyptorhynchus</i>A.....T.....T.....T.....A.....T.....T.....A.....C.....CA.....C.....A.....TT.....C.....CACC.....T.....A.....C.....A.....A.....T.....
<i>Grus</i>T.....T.....T.....A.....TT.....A.....T.....T.....C.....A.....A.....A.....CC.....A.....C.....TAA.....T.....C.....CACC.....C.....GT.....C.....A.....
<i>Pitta</i>T.....T.....T.....T.....ATT.....T.....G.....C.....C.....CAA.....CC.....TA.....A.....TTA.....C.....CACC.....T.....C.....C.....A.....
<i>Geopsittacus</i>	ProLeuGlyIleAsnProAspTrpAspLysIleProPheHisProTyrTyrThrIleLysAspIleLeuGlyPheAlaLeuMetLeuLeuLeuLeuThrThrLeu
<i>Pezoporus</i>	CCATTAGGAATCAACCAGACTGAGACAAAATCCATTCACCAGTACTACACAATTAAGATATCCTAGGATTCGCACCTCATCTCTCCTCCTCACCACCCCTT
<i>Melospittacus</i>C.....G.....C.....C.....T.....C.....C.....C.....C.....C.....C.....C.....C.....C.....C.....C.....C.....C.....A.....A.....
<i>Strigops</i>C.....G.....C.....C.....T.....C.....A.....T.....T.....CT.....C.....T.....CT.....A.....A.....A.....A.....T.....
<i>Neophema</i>C.....G.....TC.....CAT.....C.....T.....T.....CT.....C.....C.....C.....G.....T.....A.....
<i>Platycercus</i>C.....G.....ATC.....CA.....C.....C.....T.....T.....C.....C.....A.....T.....G.....A.....A.....AAGT.....A.....A.....
<i>Polytelis</i>C.....G.....AT.....G.....T.....C.....C.....C.....TT.....C.....C.....C.....A.....T.....A.....A.....A.....AGT.....T.....T.....A.....
<i>Calyptorhynchus</i>CC.....C.....TGTAT.....A.....C.....T.....C.....C.....T.....TTCT.....A.....AT.....A.....T.....CA.....TA.....A.....A.....
<i>Grus</i>CC.....G.....TC.....AT.....CA.....T.....C.....C.....T.....TAT.....CTCA.....C.....TAT.....A.....C.....CA.....A.....TA.....A.....
<i>Pitta</i>CC.....G.....TC.....AT.....CA.....T.....C.....C.....T.....TAT.....CTCA.....C.....TAT.....A.....C.....CA.....A.....TA.....A.....

