ZOOLOGICAL SCIENCE **23**: 191–198 (2006)

Phylogenetic Relationships Within Parrots (Psittacidae) Inferred from Mitochondrial Cytochrome-*b* Gene Sequences

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Blood and tissue samples of 40 individuals including 27 parrot species (15 genera; 3 subfamilies) were collected in Indonesia. Their phylogenetic relationships were inferred from 907 bp of the mitochondrial cytochrome-*b* gene, using the maximum-parsimony method, the maximum-likelihood method and the neighbor-joining method with Kimura two-parameter distance. The phylogenetic analysis revealed that (1) cockatoos (subfamily Cacatuinae) form a monophyletic sister group to other parrot groups; (2) within the genus *Cacatua*, *C. goffini* and *C. sanguinea* form a sister group to a clade containing other congeners; (3) subfamily Psittacinae emerged as paraphyletic, consisting of three clades, with a clade of *Psittaculirostris* grouping with subfamily Loriinae rather than with other Psittacinae; (4) lories and lorikeets (subfamily Loriinae) emerged as monophyletic, with *Charmosyna placentis* a basal sister group to other Loriinae, which comprised the subclades *Lorius*; *Trichoglossus*+*Eos*; and *Chalcopsitta*+*Pseudeos*.

Key words: phylogeny, parrots, Psittacidae, mitochondrial, cytochrome-*b*

INTRODUCTION

The bird group of parrots (Order Psittaciformes) comprises approximately 350 species in 83 genera (Smith, 1975; Forshaw, 1989; Sibley and Ahlquist, 1995; Juniper and Parr, 1998). Although most taxonomists of parrots believe the order Pittaciformes to be monophyletic, and some studies based on morphological, biochemical, chromosomal, and allozyme data have been conducted (Smith, 1975; Adams *et al*., 1984; Van Dongen and De Boer, 1984; Christidist, 1991a), the within-order phylogeny is still controversial.

Smith (1975) classified parrots morphologically into a single family Psittacidae consisting of four subfamilies: Psittacinae (1 tribe; Psitticini), Arinae (1 tribe; Arini), Loriinae (5 tribes; Loriini, Micropsittini, Psittaculini, Psittaculirostrini, and Psittrichasini) and Platycercinae (4 tribes; Cacatuini, Nestorini, Platycercini, and Strigopini). However, Forshaw (1989) suggested that the tribes Loriini and Cacatuini are independent from other tribes, and established a single family Psittacidae composed of three subfamilies: Cacatuinae (cockatoos), Loriinae (lories and lorikeets), and Psittacinae. Since the analyses of allozyme (Christidist, 1991a) and chromosome (Christidist *et al*., 1991b) data suggested that cockatoos are distinct from lorikeets and other parrots, which seem to be closely related to one another, del Hoyo *et al*. (1997) upgraded cockatoos into an independent family, Cacatuidae. Further morphological and molecular analyses at the family and subfamily levels, as well as at the species and genus levels will be necessary to resolve parrot phylogeny.

We selected the mitochondrial cytochrome-*b* gene for our study, since sequences of this gene have been used to reconstruct phylogeny within and among a number of bird families (Edwards *et al*., 1991; Morita *et al*., 1992; Krajewski and Fetzner, 1994; Lanyon and Hall, 1994; Nunn *et al*., 1996; Griffiths, 1997; Sheldon *et al*., 1999; de los Monteros, 2000; Sheldon *et al*., 2000; Veron and Winney, 2000; Salzburger *et al*., 2002; Weibel and Moore, 2002), and also among parrot species (Birt *et al*., 1992; Leeton *et al*., 1994; Miyaki *et al*., 1998). Birt *et al*. (1992) sequenced 307 bp of the cytochrome-*b* gene to obtain a phylogeny of 12 parrot species, but suggested that information from several unlinked genes is required for reconstructing phylogenetic relationships among parrots. Leeton *et al*. (1994) sequenced 924 bp of the mitochondrial cytochrome-*b* gene from eight Australasian parrots and determined the phylogenetic relationship among them. Miyaki *et al*. (1998) sequenced 885 bp of the cytochrome-*b* gene from six Neotropical parrot genera to reconstruct their phylogeny and compared the sequence data with those of Leeton *et al*. (1994) from Australasian parrots. All of these studies suggest the utility of the cytochrome-*b* gene for the reconstruction of parrot phylogeny.

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doi:10.2108/zsj.23.191

In our study, we inferred the phylogenetic relationships of some parrots from Indonesia based on 907 bp of mitochondrial cytochrome-*b* gene sequences. The goals of our study were to examine 1) the phylogenetic relationships among parrots at the subfamily level (Cacatuinae, Loriinae, and Psittacinae), 2) whether cockatoos (Cacatuinae) are monophyletic and distinct from other parrots, 3) whether lories and lorikeets (Loriinae) are monophyletic, 4) the phylogenetic relationships among some genera of Loriinae.

MATERIALS AND METHODS

Sampling of DNA

A total of 40 individuals of 27 parrot species (15 genera) from Indonesia were used for the study (Table 1). Blood or liver tissues of these species were collected from each individual bird in zoos, bird parks or wild habitats in Indonesia, and preserved in 99% ethanol.

DNA extraction, PCR, and DNA sequencing

DNA was extracted from 5–20 mg blood or liver tissue from each bird, using a Qiagen DNA Isolation Kit following the manufacturer's protocol. The mitochondrial cytochrome-*b* gene was amplified by polymerase chain reaction (PCR) as two fragments (approximately 740 and 370 base pairs) using two internal primer pairs: L14841 (Kocher *et al.,* 1989) / H15547 (Edwards *et al.*, 1991) and L15424/H15767 (Edwards *et al.*, 1991). The primer sequences are as follows: L14841, 5'-CCATCTCCGGTTTACAATGAC-3'; H15547, 5'-AATAGGAAGT ATCATTCGGGTTTGATG-3'; L15424, 5'-ATCCCATTCCACCAT ACTACTC-3'; and H15767, 5'-ATGAAGGGATGTTCTACTGGTTG-3'. The two fragments were overlapping, and the total length of the combined sequences, exclusive of the outer primers, was around 935–957 bp.

PCR reactions .were performed in 20 µl volumes that contained 5 pmol of each primer, 1 mM each dNTP, 1.5 mM $MgCl_2$, 1 × buffer, and 0.1U of Taq DNA polymerase (Applied Biosystems).

Tabel 1. Parrots used in this study

Species*	Number of samples	DDBJ Accession numbers	Origin
Subfamily Cacatuinae			
Cacatua alba	1	AB177973	Moluccas
Cacatua galerita	1	AB177977	Irian Jaya
Cacatua goffini	2	AB177974, AB177975	Tanimbar islands
Cacatua moluccensis	2	AB177979, AB177980	Moluccas
Cacatua sanguinea	1	AB17782	Irian Jaya
Cacatua sulphurea	1	AB177976	Sulawesi
Probosciger aterrimus	2	AB177953, AB177981	Irian Jaya
Subfamily Loriinae			
Chalcopsitta atra	1	AB177956	Irian Jaya
Chalcopsitta duivenbodei	2	AB177957, AB177969	Irian Jaya, North New Guinea
Chalcopsitta scintilata	1	AB177955	Irian Jaya, West New Guinea
Charmosyna placentis	2	AB177954, AB177968	Irian Jaya or Moluccas
Eos bornea	1	AB177947	Moluccas
Eos squamata	1	AB177946	Irian Jaya
Lorius garrulus	1	AB177951	Moluccas
Lorius lory	1	AB177952	Irian Jaya, West Papuan island
Pseudeos fuscata	2	AB177945, AB177964	Irian Jaya, West Papuan island
Trichoglossus euteles	2	AB177943, AB177963	Lesser Sunda Islands
Trichoglossus haematodus	1	AB177942	Irian Jaya, West New Guinea
Subfamily Psittacinae			
Aprosmictus erythropterus	1	AB177959	Irian Jaya
Eclectus roratus	2	AB177948, AB177965	Moluccas
Loriculus galgulus	2	AB177950, AB177967	Sumatra Island
Loriculus pusillus	2	AB177949, AB177966	Java Island
Psitrichas fulgidus	1	AB177944	Irian Jaya
Psittaculirosris desmarestii	1	AB177960	Irian Jaya
Psittaculirostris desmarestii	2	AB177961, AB1774971	Irian Jaya
Psittacula alexandri	2	AB177958, AB177970	Java island
Tanygnathus sumatranus	2	AB177962, AB177972	Sulawesi

Amplification of each gene fragment was conducted under the following PCR conditions: one cycle of denaturation at 94°C for 8 min, followed by 35 cycles, with each cycle consisting of denaturation at 92°C for 1 min, annealing at 52°C for 1 min, and extension at 72°C for 1 min. These cycles were followed by final extension at 72°C for 10 min.

Table 2. Nucleotide composition, variable sites and informative sites in the 907 bp area of the cytochrome-*b* gene examined. A total of 42 individuals were analyzed, including 27 parrot species and two outgroup species (*A. striatus and C. livia*).

Codon Position	% Nucleotide				No. nucleotides		
	A	C	G	T	Total	Variable sites	Informative sites
All positions	26.8	35.7	13.6	23.9	907	445 (49.1 %)	373
1st position	24.4	30	22.4	23.1	303	303 (22.9 %)	76
2nd position	19.9	28.3	13.9	37.9	302	67 (15.1 %)	44
3rd positions	36	48.8	4.7	10.5	302	276 (62.0 %)	253

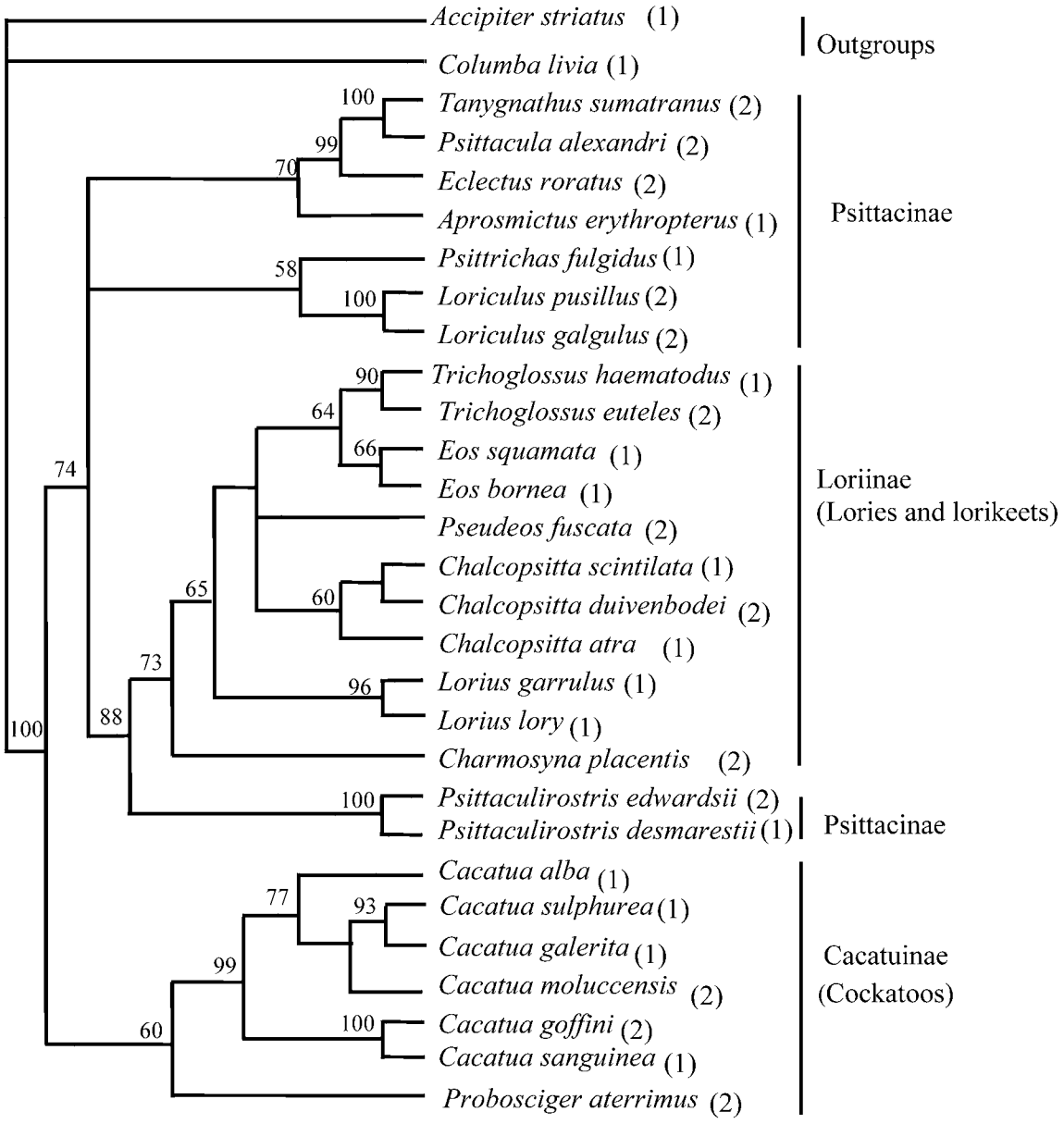

Fig. 1. A strict consensus maximum-parsimony (MP) tree inferred from cytochrome-*b* gene sequences, with *A. striatus* and *C. livia* as outgroups. The numbers above branches refer to bootstrap values calculated from 100 full heuristic search replicates. Unlabelled nodes received <50% bootstrap support. The number of individuals of each species is shown in parentheses.

PCR products were purified by the PEG (polyethylene glycol) method and used as templates for cycle sequencing with a Dye terminator Cycle Sequencing Ready Reaction Kit with Ampli *Taq* DNA Polymerase FS. The sequencing reactions were performed in 20 µl volumes according to the manufacturer's (Applied Biosystems) recommendations. Each reaction contained 4 µl Dye Terminator reaction solution, 3–5 µl PCR product, 0.5 µl (around 3.5 pmol) primer, and mili-Q water. Reaction conditions were 35 cycles of denaturation at 96°C for 10 min, annealing at 50°C for 5 min, and extention at 60°C for 4 min. After the sequencing reactions were carried out, the products were purified by ethanol precipitation following the manufacturer's protocol, and the purified products were separated by an ABI Prism 310 DNA Sequencer. The nucleotide sequence data reported in this paper will appear in the DDBJ/EMBL/GenBank nucleotide sequence databases with the accession numbers AB177942–AB177981 (Table 1). As outgroups for constructing rooted phylogenetic trees, the cytochrome-*b* gene sequences of *Accipiter striatus* (ASU83305) and *Columba livia* (AF182694) were obtained from GeneBank.

Cytochrome-*b* gene sequence analyses

The cytochrome-*b* sequences were aligned using DNASIS version 2.0, and each 907 bp sequence was translated to the amino acid sequence to confirm the absence of nuclear pseudogenes.

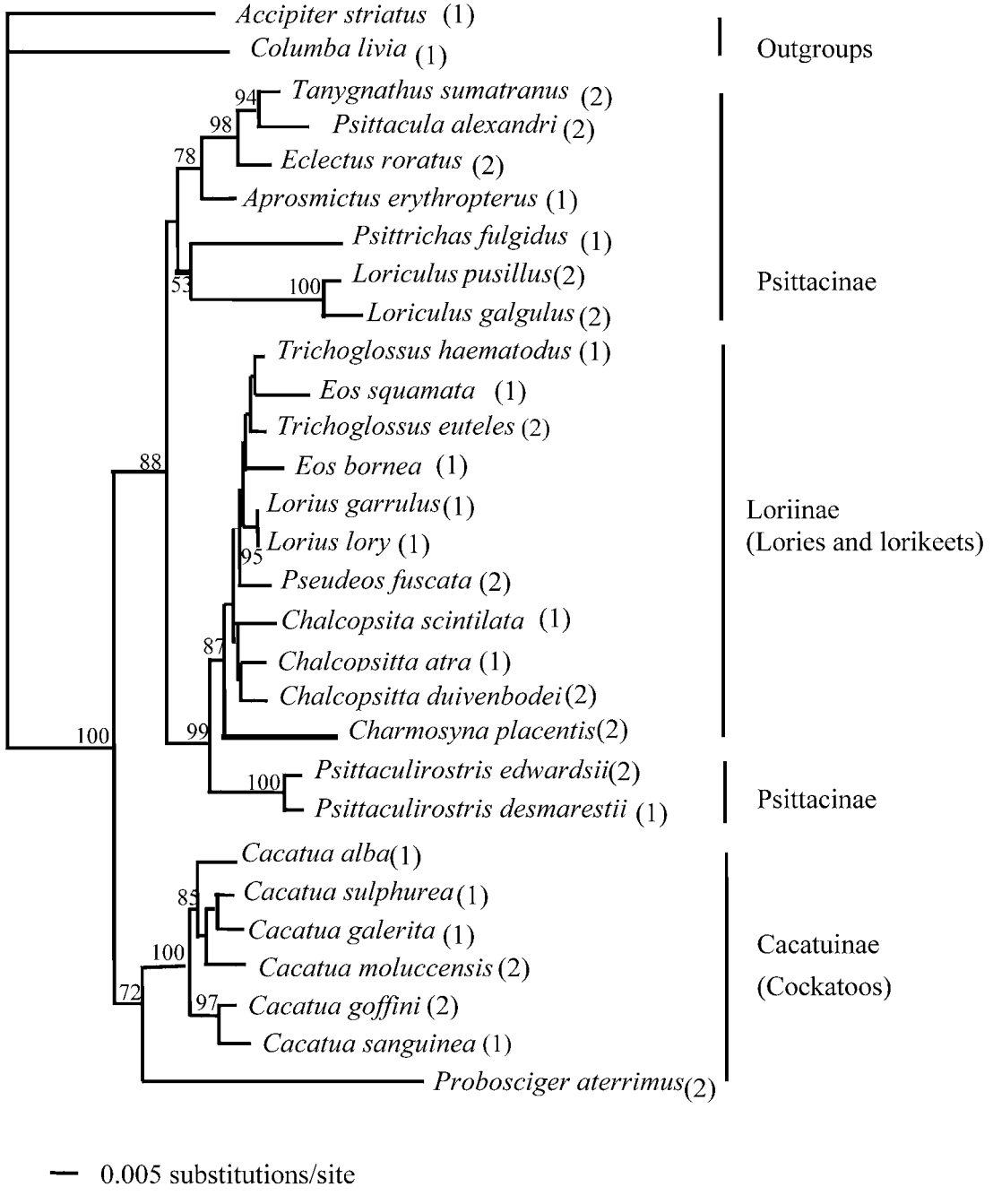

Fig. 2. A neighbor-joining (NJ) tree based on Kimura 2-parameter distances among cytochrome-*b* gene sequences, with *A. striatus* and *C. livia* as outgroups. The numbers above branches refer to bootstrap values calculated from 1000 replicates. Unlabelled nodes received <50% bootstrap support. The number of individuals of each species is shown in parentheses.

Each sequence was also examined by a portion analysis to determine whether or not the sequence involved pseudogene stop codons (Sheldon *et al*., 2000).

In the present study, mtDNA was extracted not only from liver tissue but also from blood samples, and consequently the sequence data might accidentally be contaminated with nuclear pseudogenes. Quinn (1997) suggested that contamination by nuclear pseudogenes in amplifying the mitochondrial cytochrome-*b* gene can be minimized by using mtDNA-rich tissues rather than blood samples, which contain relatively low density of mtDNA copies (Sorenson and Fleischer, 1996). However, across all of 42 individuals examined, there were no insertions and deletions in the 907 base pairs and no stop codons, suggesting that contamination by pseudogenes was absent from the data.

Saturation analyses

The number of transitional substitutions was plotted against the number of transverstional substitutions for all pairwise comparison between species. In our data set, the cytochrome-*b* gene appears to be saturated with transitions in the most divergent pairs of species. Transitional substitutions were also plotted (not shown) against genetic distance for all pairwise comparisons of species, which also demonstrated that the cytochrome-*b* gene became saturated at high genetic distance. The same analyses were conducted separately for each of the first, second, and third codon positions, and it was found that most saturation occurred at third codon position. Based on the saturation effects in the present study and estimation of a 10:1 transition-tranversion in birds (Kocher *et al*., 1990; Nunn and Cracraft, 1996; de los Monteros, 2000), we weighted transitions 10:1 over transversion at each codon position in the MP analysis and included only transversions in the NJ analysis of the complete data set of 29 species. For analyses of subsets of the taxa that included only closely related species (Fig. 3), all informative characters were unweighted.

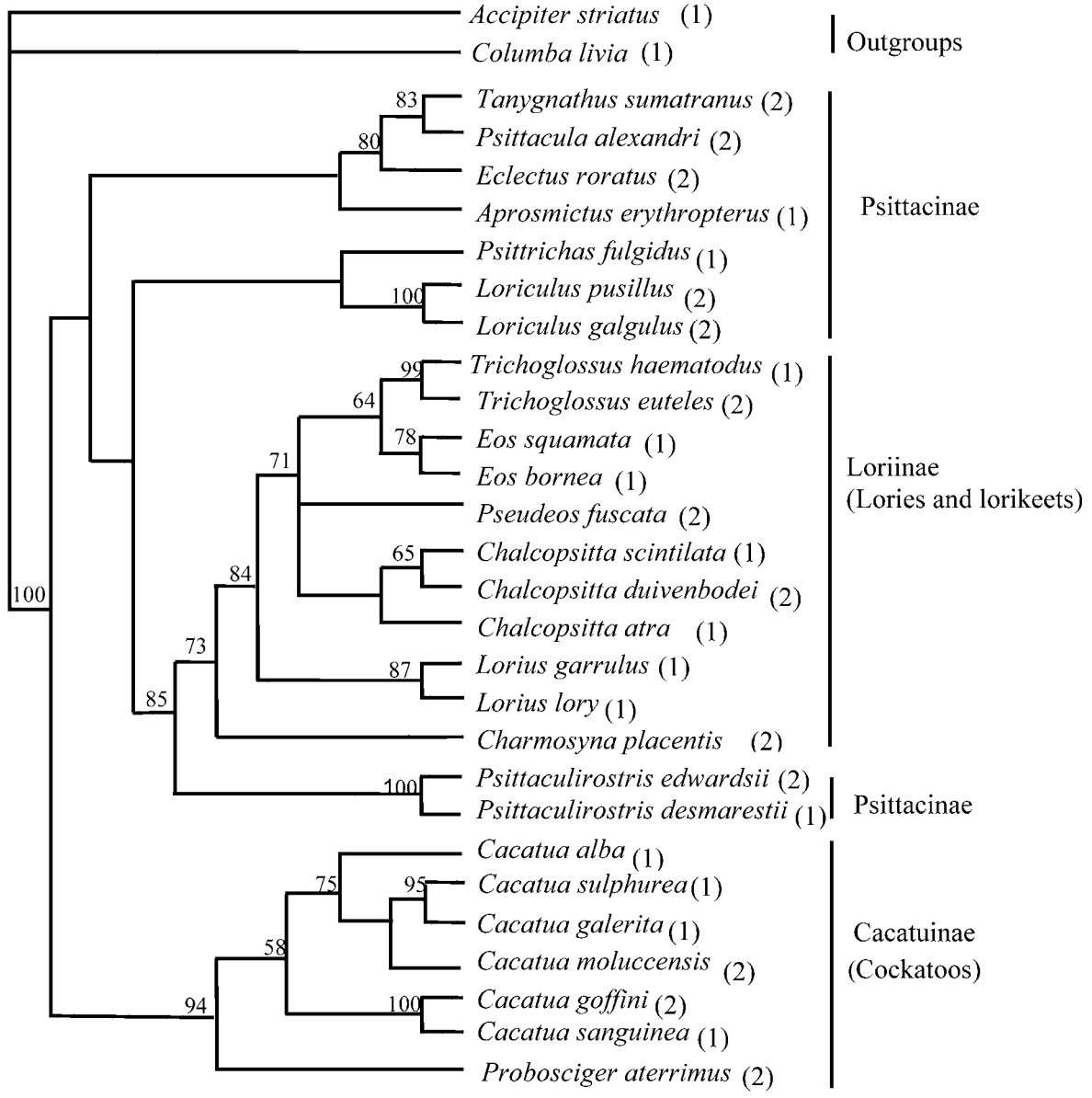

Fig. 3. A maximum-likelihood (ML) tree inferred from cytochrome-*b* gene sequences, with *A. striatus* and *C. livia* as outgroups. The numbers above branches refer to bootstrap values calculated from 100 full heuristic search replicates. Unlabelled nodes received <50% bootstrap support. The number of individuals of each species is shown in parentheses.

Phylogenetic analyses

For the phylogenetic analyses of the cytochrome-*b* sequences, maximum-parsimony (MP), maximum-likelihood (ML) and neighbor-joining (NJ) methods were adopted using PAUP* version 4.0b10 (Swofford, 2000 software). In the MP and ML analyses, we performed 100 and 10 heuristic search replicates, respectively, using random stepwise addition, with tree-bisection-reconnection (TBR) branch-swapping. Non-parametric bootstrap values (Felsenstein, 1985) were determined by heuristic analysis of 100 pseudosamples of the original data set, with replacement. In constructing NJ trees, we used Kimura's two-parameter distances and performed 1000 replicates for bootstrap values.

RESULTS

Characteristics of cytochrome-*b* nucleotide sequences in the parrots examined

The percentage of each nucleotide ranged from 13.6% (guanine) to 35.7% (cytosine), with adenine+thymine (50.7%) nearly equal to cytosine+guanine (49.3%) (Table 2), suggesting the appropriateness of using Kimura's two-parameter model (cf. Nei and Kumar, 2000). However, among the three codon positions, the third position was extremely low in guanine (4.7%) but relatively rich in cytosine (48.8%) and adenine (36.0%). The second position was rich in thymine (37.9%). A Chi-square test performed by PAUP* showed that the sequences did not differ significantly from one another in base composition (Chi-square=35.274804, df= 123, P=1.000000).

Of 907 sites examined, 445 sites were variable and, among these, 373 sites were informative (Table 2). When compared among the three codon positions, the percentage of variable sites was highest at the third position (62.0%) and lowest at the second position (15.1%).

Nucleotide substitutions and genetic distances

The number of transitional substitutions ranged from 13 between closely related *Trichoglossus haematodus* and *T. euteles* to 108 between distantly related *Cacatua sulphurea* and *T. euteles*, while the number of transversional substitutions ranged from 0 between closely related *Lorius garrulus* and *L. lory* to 87 between *Loriculus galgulus* and *Probosciger*

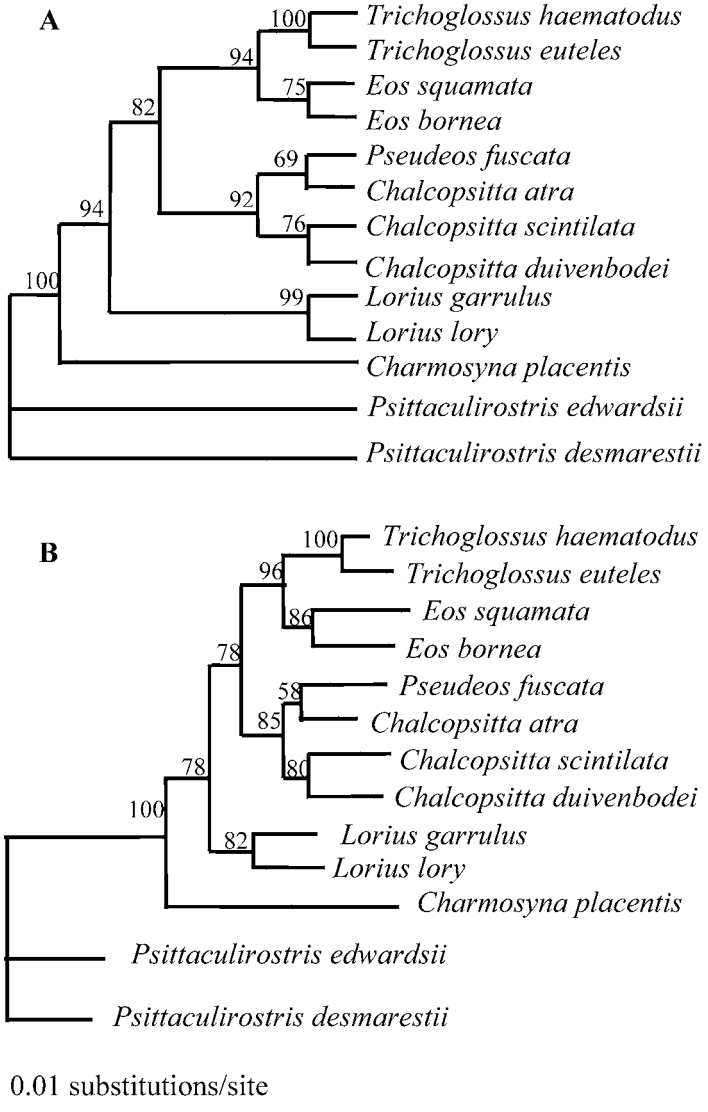

Fig. 4. **A)** Maximum-parsimony and **B)** neighbor-joining trees of Loriinae, inferred from cytochrome-*b* gene sequences, based on all substitutions including transitional ones. *P. desmarestii* and *P. edwardsii* were used as outgroups. The numbers above branches are bootstrap values.

aterrimus. Sequence variation between individuals of the same species ranged from 0 to 17 base changes. Between-species genetic distance calculated from Kimura's two-parameter model based on all substitutions ranged from 0.010 (*Trichoglossus haematodus–T. euteles*) to 0.228 (*Probociger aterrimus–Psittaculirostris edwardsii*), with an average of 0.130, excluding outgroups.

Phylogenetic relationships among parrots examined

The heuristic MP search found four equally optimal trees, and a strict consensus tree (Fig. 1) was quite similar in topology to the NJ tree (Fig. 2). Another heuristic ML search found only one optimal tree which was also similar in topology to the NJ tree (Fig. 3). In all of the trees, conspecific individuals were always most closely related to one another, and the terminal nodes in Figs 1–3 are represented by species names with the numbers of individuals in parentheses. All the trees show *Probosciger aterrimus* and *Cacatua* (subfamily Cacatuinae) to be monophyletic, with *P. aterrimus* comprising a sister group to *Cacatua*. Within the genus *Cacatua*, *C. goffini* and *C. sanguinea* comprise a sister group to the other species. In contrast to the Cacatuinae, species belonging to the Psittacinae appear as paraphyletic, consisting of the following three clades: 1) *Tanygnathus sumatranus*, *Psittacula alexandri*, *Eclectus roratus* and *Aprosmictus erythroptherus*; 2) *Loriculus pusillus*, *L. galgulus* and *Psittrichas fulgidus*; and 3) *Psittaculirostris edwardsii* and *P. desmarestii*. It is intriguing that the clade of *Psittaculirostris edwardsii* and *P. desmarestii* appears closer to the Loriinae than to other clades of Psittacinae.

Although the Loriinae comprise a monophyletic group in all trees (Figs. 1–3), their phylogenetic relationships differed considerably among the trees. Therefore, the phylogenetic relationships within Loriinae were analyzed further by using *Psittaculirostris edwardsii* and *P. desmarestii* as outgroups and all substitutions, including transitional ones, as characters, because in closely related species, the cytochrome-*b* gene is not saturated with transitional substitutions even at the third codon position. The resulting MP (Fig. 4A) and NJ trees (Fig. 4B) show identical topology and indicate that, within Loriinae, *Charmosyna placentis* is basal to a clade comprising the other taxa, in which the genus *Lorius* is itself basal. Other species of Loriinae are divided into two subclades, *Trichoglossus*+*Eos* and *Chalcopsitta*+*Pseudeos*.

DISCUSSION

In many birds hitherto studied, the cytochrome-*b* gene is rich in cytosine and adenine (Sheldon, 1999; Miyaki *et al*., 1998; Salzburger *et al*., 2002), especially in the third codon position (Desjardins and Morais, 1990; Edward *et al*., 1991; Nunn and Cracraft, 1996; Moore and DeFillips, 1997; Slikas, 1997; Sheldon *et al*., 1999), whereas the third codon position is poor in guanine and the second codon position is rich in thymine (Desjardins and Morais, 1990; Edward *et al*., 1991; McCracken *et al*., 1999; Sheldon *et al*., 1999). For instance, Edwards *et al*. (1991) analyzed the cytochrome-*b* gene of passerine birds and found that the nucleotide composition at the third codon position was 40% adenine, 40% cytosine, 15% thymine and 5% guanine and that thymine constitutes 40% at the second codon position. Overall, these results are similar to those of the present study.

Whereas Smith (1975) suggested on the basis of morphology that Platycercinae including Cacatuini forms a basal clade of parrots, the present study demonstrated the monophyly of cockatoos (Cacatuinae) (Figs. 1–3). The cockatoos are distinguished from other parrots by the presence of an erectile crest and a gall bladder, and also by the absence of a pericyclic iris and dyck texture in their feathers (Smith, 1975; Forshaw, 1989; Juniper and Parr, 1998). In other parrots, the dyck texture makes the plumage blue or green, whereas the feathers of cockatoos are mostly black, white, or gray or occasionally pink. The karyotypic organization of cockatoos is also different from that other parrot groups (Christidis *et al*., 1991b). The monophyly of cockatoos has also been supported by isozyme (Adams *et al*., 1984), chromosomal (Van Dongen and De Boer, 1984), and protein data (Christidis *et al*., 1991a).

In an analysis using mitochondrial 12sRNA, Brown and Toft (1999) found that the genus *Probosciger* is the most basal of all genera in the Cacatuinae and that white cockatoos, *i.e*., genus *Cacatua*, are divided into group A including *C. galerita*, *C. sulphurea*, *C. alba* and *C. moluccensis* and group B including *C. goffini* and *C. sanguinea*, as demonstrated by the present study. Morphologically, the species of group A have a round wing, heavy bill, and prominent colored crest, whereas the species of group B have a slender wing, small bill, and short crest (Forshaw, 1989).

The monophyly of Loriinae has been suggested biochemically (Christidis *et al*., 1991a) and morphologically (Smith, 1975); a brush-tipped tongue (adaptive for extracting nectar) is synapomorphic for the group (Forshaw, 1989). Within Loriinae, the genus *Charmosyna* is characterized by sexual dimorphism and is morphologically distinct from the genera *Trichoglossus*, *Eos*, *Pseudeos*, *Chalcopsitta* and *Lorius*, whose phylogenetic relationships were previously unclear (Smith, 1975). In the present study, the five genera were grouped into three subclades, *i.e*. *Lorius*, *Chalcopsitta*+*Pseudeos* and *Eos*+*Trichoglossus*, with bootstrap values of more than 90%.

In contrast to Cacatuinae and Loriinae, Psittacinae emerged as paraphyletic, consisting of three clades, with *Psittaculirostris* grouping with Loriinae rather than with other clades of Psittacinae. Smith (1975) also pointed out that *Psittaculirostris* is similar to Loriinae in wing stripe, voice, and behavior. From the high bootstrap values of the node connecting these two clades, we conclude that *Psittaculirostris* is phylogenetically close to Loriinae.

The phylogenetic position of *Psittrichas* has also been controversial. For instance, Thomson (1900) mentioned that *Psittrichas* is an isolated form, whereas Smith (1975) suggested that *Psittrichas* is similar to tribe Loriini in skull size and behavior. Forshaw (1989) suggested that *Psittrichas* is probably related to *Eclectus roratus*. Even in the present study based on cytochrome-*b* gene sequences, the phylogenetic position of *Psittrichas* as a sister taxon to *Loriculus* is poorly supported, whereas *Aprosmictus*, *Eclectus*, *Psittacula* and *Tanygnathus* grouped together with moderate to high bootstrap support.

ACKNOWLEDGMENTS

We would like to express our sincere thanks to staff members of the Research Center for Biology, the Indonesian Institute of Sci-

ences, Ragunan Zoo, Surabaya Zoo, Jakarta Bird Park, and Bali Bird Park, all in Indonesia, for their kind help in collecting materials for the present study. Cordial thanks are also due to Prof. T. Iwakuma for his critical reading of manuscript. This study was conducted under the financial support from JICA (Biodiversity and Conservation Project in Indonesia) and the COE fund of Hokkaido University, Japan.

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(Received June 3, 2005 / Accepted November 16, 2005)