The Condor 93:302–317
© The Cooper Ornithological Society 1991

RELATIONSHIPS AMONG THE AUSTRALO-PAPUAN PARROTS, LORIKEETS, AND COCKATOOS (AVES: PSITTACIFORMES): PROTEIN EVIDENCE[1]

L. CHRISTIDIS
Department of Ornithology, Division of Natural History, Museum of Victoria, Melbourne, Victoria, Australia 3000

R. SCHODDE
Australian National Wildlife Collection, Division of Wildlife and Ecology, CSIRO, Gunghalin, Canberra, Australia 2602

D. D. SHAW AND S. F. MAYNES
Molecular and Population Genetics Group, Research School of Biological Sciences, Australian National University, Canberra, ACT, Australia 2601

Abstract. Allozyme variation at 21 presumptive protein loci was examined by electrophoresis and used to assess relationships among Australo-Papuan parrots, lorikeets and cockatoos. Hypotheses of relationships were generated from the data by phenetic and cladistic analyses. The results, when taken into account with other biochemical, chromosomal and morphological data, demonstrate that cockatoos form a monophyletic lineage distant from the other Australo-Papuan parrots and lorikeets. The lorikeets are also monophyletic, but are clustered among other parrots. A core of Australian broad-tailed (platycercine) parrots is defined by the rosellas and ringnecks (*Platycercus, Barnardius*), Bluebonnet (*Northiella*), Red-capped Parrot (*Purpureicephalus*), Swift Parrot (*Lathamus*) and grass parrots (*Psephotus*). New Guinean *Psittacella* also appears to be a member of this assemblage, to which the polytelitine parrots (*Alisterus-Polytelis*) may be linked as well. Other "conventional" platycercine parrots—the Ground Parrot (*Pezoporus*), Budgerigar (*Melopsittacus*), Red-fronted Parakeet (*Cyanoramphus*), and Blue-winged and Bourke's Parrots (*Neophema*)—are still more distant and of disparate affinity; the two latter species are polyphyletic among the platycercines. Of psittacine parrots, Eclectus (*Eclectus*) and Red-cheeked Parrots (*Geoffroyus*) are closely related but their links to other psittacine genera are not clear. Similarly, the relationships of the fig-parrots (*Cyclopsitta*), pygmy-parrots (*Micropsitta*), lovebirds (*Agapornis*) and ring-necked parakeets (*Psittacula*) are ambiguous. Biogeographical implications of these results are canvassed in the discussion.

Key words: *Parrots; protein electrophoresis; Psittacidae; systematics; Australo-Papuan.*

INTRODUCTION

The order Psittaciformes comprises some 330–350 species of parrots, lorikeets and cockatoos which occur naturally in Central and South America, Australasia and the South Pacific, Africa and southern Asia. There are two major radiations, one in Australasia and the other in South America. Although the order is well-defined morphologically, the primary evolutionary lineages within it are not so clear-cut (cf. Glenny 1957, Sibley 1960, Brereton 1963, Boetticher 1964, Sibley and Ahlquist 1972, Smith 1975, Homberger 1980). Two discrete assemblages have been recognized in all studies: the cockatoos and brush-tongued lorikeets, both of which are confined to the Australasian and South Pacific regions. The arine parrots, comprising the entire New World complement, also appear to form a monophyletic radiation, judged by their wide biochemical distance from other parrots (Mainardi 1962, Gysels 1964) and their several unique pigmentary, ontogenetic and copulatory traits (Smith 1975).

Most controversy centers on the only other large group, the Australasian seed-eating psittacine parrots. Up to eight tribes and subfamilies have been distinguished among them (Smith 1975, Homberger 1980), and there is considerable dispute over their composition and relationships to the cockatoos and lorikeets (see Smith 1975 and Table 1 this study). Towards resolving some of these questions, we employed multilocus

[1] Received 28 June 1990. Final acceptance 6 November 1990.

protein electrophoresis to examine relationships among 36 species of Psittaciformes, covering six of the tribes recognized by Smith (1975). The survey is limited to the Australasian region, and focussed on the principal loriine and psittacine assemblages.

MATERIALS AND METHODS

Protein electrophoresis was performed on 80 individuals of 36 species (Table 2) representing 16 of the 22 genera of Australo-Papuan psittacine parrots, seven of the 10 genera of lorikeets, and two of the five genera of cockatoos (Condon 1975, Beehler and Finch 1985), as well as one Pacific species (Norfolk Island Red-fronted Parakeet, *Cyanoramphus*) and two Afro-Asian psittacine genera (*Psittacula, Agapornis*). Locality data for the material collected are available from the authors on request.

Electrophoresis was carried out on liver and breast muscle samples which had been stored in liquid nitrogen. Separate homogenates of the two tissues were prepared by grinding a cubic millimeter of each in 300 μl buffer (0.1 M Tris, 1.0 mM EDTA, 0.5 μl/ml 2–mercaptoethanol, 0.05 mM NADP; pH 7.0). The homogenates were then spun in an Eppendorf centrifuge for 3 min and the supernatant screened for 25 enzyme systems representing 32 presumptive loci (Table 3).

Enzymes were stained according to the recipes in Harris and Hopkinson (1976) except GOT (Table 3), for which the procedure of Shaw and Prasad (1970) was followed. All systems were run in a cellulose acetate matrix on a paper support (Cellogel, Chemetron, Italy). Where two loci represented a single enzyme, the most anodal was designated −1, and the other −2. Individual alleles were given alphabetical designations in sequence from the anode, beginning with "a."

Of the 32 loci screened, the following 10 were excluded from analysis because they could not be scored consistently across all species: GPT, GLUD, TPI, ACON-1, ACON-2, EST-1, MDH-2, GDA, NP, and PGM-2. Variation at LDH-1 and LDH-2 could not be distinguished unambiguously because of differential expression of the polymer bands. Accordingly, their variation was scored on pattern alone and treated as a single locus.

From allelic frequencies at the 21 loci remaining (Table 2), Rogers' (1972) and Nei's (1978) genetic distances were calculated between taxa (Table 4). UPGMA (Sneath and Sokal 1972) and distance-Wagner (Farris 1972, Swofford 1981) dendrograms were then constructed with the BIOSYS-1 program (Swofford and Selander 1981). The distance-Wagner dendrogram was rooted by both mid-point and out-group procedures, the cockatoos being used as the outgroup for psittacine and loriine lineages because of the morphological (Smith 1975, Homberger 1980), biochemical (Adams et al. 1984, Ovenden et al. 1987) and chromosomal (Christidis et al., in press) evidence that they are a distinctive sister lineage of the other Psittaciformes.

A cladistic analysis was also performed by treating the loci as characters and their constituent alleles as character states. Where loci were

TABLE 1. Recent classifications of the genera examined in the present study.

Homberger 1980	Smith 1975	Peters 1937
Cacatuinae[a]	Platycercinae Cacatuini[a]	Kakatoeinae[a]
Psittacinae Platycercini	Platycercinae Platycercini	Psittacinae
Melopsittacus	*Melopsittacus*	*Melopsittacus*
Neophema	*Neophema*	*Neophema*
Psephotus	*Psephotus*	*Psephotus*
Northiella	*Northiella*	*Northiella*
Purpureicephalus	*Purpureicephalus*	*Purpureicephalus*
Platycercus	*Platycercus*	*Platycercus*
Barnardius	*Barnadius*	*Barnardius*
Lathamus	*Lathamus*	
Cyanoramphus	*Cyanoramphus*	*Cyanoramphus*
	Pezoporus	*Pezoporus*
Psittacinae Psittaculini	Loriinae Psittaculini	Psittacinae
Geoffroyus	*Geoffroyus*	*Geoffroyus*
Eclectus	*Eclectus*	*Eclectus*
	Psittacella	*Psittacella*
Alisterus	*Alisterus*	*Alisterus*
Polytelis	*Polytelis*	*Polytelis*
Agapornis	*Agapornis*	*Agapornis*
Psittacula	*Psittacula*	*Psittacula*
Loriinae[b]	Loriinae Loriini[b]	Loriinae[b]
		incl. *Lathamus* *Cyclopsitta*
Not examined	Loriinae Psittaculirostrini	not recognized
	Cyclopsitta	
Not examined	Loriinae Micropsittini	Micropsittinae
	Micropsitta	*Micropsitta*

[a] Includes the 2 genera listed under Cacatuidae in Table 2.
[b] Includes the 7 genera listed under Loriidae in Table 2.

TABLE 2. Species examined, sample sizes and allelic constitutions. Asterisks signify species excluded from PAUP analysis. Species codes refer to Table 4.

Species	Common name	No.	Code	Locus			
				PGM-1	6PGD	GOT-1	GOT-2
Cacatuidae							
Calyptorhynchus funereus	Yellow-tailed Black Cockatoo	3	CFU	c	c	c	c
Cacatua roseicapilla	Galah	2	CRO	a	e (0.17) f (0.83)	d	c
*Cacatua galerita**	Sulphur-crested Cockatoo	2	CGA	a	f	d	c
Loriidae							
*Trichoglossus haematodus**	Rainbow Lorikeet	3	THA	a	j (0.83) k (0.17)	e	c
Glossopsitta concinna	Musk Lorikeet	3	GCO	a	j	e	c
*Psitteuteles versicolor**	Varied Lorikeet	1	PVE	a	j	e	c
*Neopsittacus musschenbroekii**	Yellow-billed Lorikeet	1	NMU	a	j	e	c
*Neopsittacus pullicauda**	Orange-billed Lorikeet	2	NPU	a	j	e	c
*Lorius lory**	Western Black-capped Lory	1	LLO	a	j	e	c
*Charmosyna papou**	Papuan Lorikeet	3	CPA	a	g (0.50) l (0.50)	e	c
*Oreopsittacus arfaki**	Plum-faced Lorikeet	1	OAR	a	j	e	c
Psittacidae							
Alisterus scapularis	Australian King-Parrot	3	ASC	b	j	a (0.34) e (0.66)	c
*Polytelis swainsonii**	Superb Parrot	3	PSW	b	d (0.17) j (0.83)	e	c
Platycercus elegans	Crimson Rosella	3	PEL	a	d	e	b
*Platycercus eximius**	Eastern Rosella	3	PEX	a	d (0.83) f (0.17)	b (0.17) e (0.83)	b
Barnardius zonarius	Ringneck	3	BBA	a	d	e	b
Purpureicephalus spurius	Red-capped Parrot	1	PSP	a	d	e	–
Pezoporus wallicus	Ground Parrot	2	PWA	a	h	e	c
Melopsittacus undulatus	Budgerigar	4	MUN	a	j	e	c
Cyanoramphus novaezelandiae	Red-fronted Parakeet	1	CNO	b	j	e	–
Neophema bourkii	Bourke's Parrot	3	NBO	b	i (0.17) j (0.83)	e	c
Neophema chrysostoma	Blue-winged Parrot	3	NCH	b	j (0.83) l (0.17)	e	c
Psephotus haematonotus	Red-rumped Parrot	3	PHA	b	d	e	c
Northiella haematogaster	Blue Bonnet	3	NHA	a	j	e	b
Lathamus discolor	Swift Parrot	3	LDI	a	a (0.17) d (0.66) j (0.17)	e	b
Geoffroyus geoffroyi	Red-cheeked Parrot	3	GGE	b	j	e	c
*Geoffroyus simplex**	Blue-collared Parrot	1	GSI	b	j	e	c
Eclectus roratus	Eclectus Parrot	1	ERO	b	d (0.50) j (0.50)	e	c
Cyclopsitta gulielmiterti	Orange-breasted Fig-Parrot	3	CGU	a	j	e	d
Psittacella brehmii	Brehm's Tiger-Parrot	1	PBR	a	b (0.50) j (0.50)	e	c
*Psittacella picta**	Painted Tiger-Parrot	1	PPI	a	b (0.50) j (0.50)	e	c
Micropsitta bruijnii	Red-breasted Pygmy-Parrot	1	MBR	b	j	e	c
*Micropsitta pusio**	Buff-faced Pygmy-Parrot	2	MPU	b	j	e	c
Psittacula himalayana	Slaty-headed Parakeet	1	PHI	a	j	e	c
Psittacula derbiana	Derbyan Parakeet	1	PDE	a	j	e	a
Agapornis roseicollis	Peach-faced Lovebird	2	ARO	b	f	e	c

TABLE 2. Continued.

Species	Locus									
	IDH-1		IDH-2		GPI		GPD		ALD	
Cacatuidae										
Calyptorhynchus funereus	c		d		c (0.17)	g (0.83)	a (0.17)	d (0.83)	c	
Cacatua roseicapilla	c		d		a		j		c	
*Cacatua galerita**	c		d		a		g (0.50)	j (0.50)	c	
Loriidae										
*Trichoglossus haematodus**	g		e		e		l		c	
Glossopsitta concinna	g		e		e		l		c	
*Psitteuteles versicolor**	g		e		e		l		c	
*Neopsittacus musschenbroekii**	g		e		e		m		c	
*Neopsittacus pullicauda**	g		e		e		m		c	
*Lorius lory**	g		g		e		l		c	
*Charmosyna papou**	f (0.17)	g (0.83)	e		e		l		c	
*Oreopsittacus arfaki**	g		e (0.50)	g (0.50)	f		l		c	
Psittacidae										
Alisterus scapularis	c		d		i		j		c	
*Polytelis swainsonii**	c		d		d (0.17)	i (0.83)	j		c	
Platycercus elegans	c		d		e		c (0.17)	e (0.83)	c	
*Platycercus eximius**	c		d		e		c (0.17)	e (0.83)	c	
Barnardius zonarius	c		d		e		i		c	
Purpureicephalus spurius	c		d		e		i		c	
Pezoporus wallicus	c		d		e		i		c	
Melopsittacus undulatus	e		a		h		k		b (0.83)	d (0.17)
Cyanoramphus novaezelandiae	c		d		b		i		c	
Neophema bourkii	c (0.83)	d (0.17)	b (0.17)	c (0.83)	e		i		e	
Neophema chrysostoma	i		d		e		i		c	
Psephotus haematonotus	c		d		e		i		c	
Northiella haematogaster	c		d		e		h (0.34)	i (0.66)	c	
Lathamus discolor	c		d		e		i		c	
Geoffroyus geoffroyi	c		d		i		b		c	
*Geoffroyus simplex**	c		d		i		b		c	
Eclectus roratus	c		d		e		n		c	
Cyclopsitta gulielmiterti	h		d		e		b		c	
Psittacella brehmii	c		d		e		i		c	
*Psittacella picta**	c		d		e		i		c	
Micropsitta bruijnii	b		f		e		d		c	
*Micropsitta pusio**	a		f		e		c		c	
Psittacula himalayana	c		d		e		i		c	
Psittacula derbiana	c		d		i		i		c	
Agapornis roseicollis	i		c		j		f		a	

TABLE 2. Continued.

Species	Locus													
	CK	AK	PK	ENOL	LDH	PGK	GA3PD	FUM	MDH-1	MPI		EST-2		GP
Cacatuidae														
Calyptorhynchus funereus	a	a	b	b	g	—	a	c	a	e (0.83)	f (0.17)	e		a
Cacatua roseicapilla	b	b	b	d	g	—	a	a	a	e		e		a
*Cacatua galerita**	b	b	b	b	g	—	a	a	a	e		e		a
Loriidae														
*Trichoglossus haematodus**	a	a	d	b	c	b	a	b	a	e		a		b
Glossopsitta concinna	a	a	d	b	c	b	a	b	a	e		a		b
*Psitteuteles versicolor**	a	a	d	b	c	b	a	b	a	e		a		b
*Neopsittacus musschenbroekii**	a	a	d	b	c	b	a	b	a	e		a		b
*Neopsittacus pullicauda**	a	a	d	b	c	b	a	b	a	e		a		b
*Lorius lory**	a	a	d	b	c	b	a	b	a	d (0.50)	e (0.50)	a		b
*Charmosyna papou**	a	a	d	b	c	b	a	b	a	d (0.17)	e (0.83)	a (0.83)	b (0.17)	b
*Oreopsittacus arfaki**	a	a	d	b	c	b	a	b	a	e		a		b
Psittacidae														
Alisterus scapularis	a	c	f	b	h	b	a	b	a	a (0.83)	b (0.17)	e		d
*Polytelis swainsonii**	a	c	f	b	h	b	a	b	a	e		e		d
Platycercus elegans	a	c	h	c	a	b	a	b	a	e		e		d
*Platycercus eximius**	a	c	h	c	a	b	a	b	a	e		e		d
Barnardius zonarius	a	c	h	c	a	b	a	b	a	e		e		d
Purpureicephalus spurius	a	c	h	e	a	b	a	b	a	e		e		d
Pezoporus wallicus	a	a	d	g	i	b	a	b	a	e		f		b
Melopsittacus undulatus	a	a	k	a	b	b	a	b	a	e		e		b
Cyanoramphus novaezelandiae	a	—	h	b	e	b	a	b	a	c		e		c
Neophema bourkii	a	a	h	c	a	c	b	b	a	g (0.17)	h (0.83)	e		b
Neophema chrysostoma	a	a	h	f	b	b	a	b	a	e		a		b
Psephotus haematonotus	a	c	h	c	a	b	a	b	a	b		e		d
Northiella haematogaster	a	c	h	c	a	b	a	b	a	e		d (0.34)	e (0.66)	d
Lathamus discolor	a	c	h	b	d	b	a	b	a	e		e		d
Geoffroyus geoffroyi	c	a	g	b	a	a	a	b	a	b		e		b
*Geoffroyus simplex**	c	a	g	b	a	a	a	b	a	b		e		b
Eclectus roratus	c	a	a	b	a	b	a	b	a	e		e		b
Cyclopsitta gulielmiterti	a	a	c	b	a	b	a	b	a	b (0.17)	e (0.83)	g		b
Psittacella brehmii	a	a	j	e	a	b	a	b	b	e		e		c
*Psittacella picta**	a	a	j	e	a	b	a	b	b	e		e		c
Micropsitta bruijnii	a	a	i	b	j	b	a	b	a	e		h		b
*Micropsitta pusio**	a	a	i	b	j	b	a	b	a	e		i		b
Psittacula himalayana	a	a	e	b	f	a	a	b	a	b		c		b
Psittacula derbiana	a	a	e	b	f	a	a	b	a	b		e		b
Agapornis roseicollis	a	a	l	b	a	b	a	b	a	e		e		b

TABLE 3. Enzymes examined, buffers used, and tissue distribution of each enzyme.

Enzyme (E.C. No.)	Abbreviation	No. of loci	Tissue	Running buffer[a]	Running time (hr)[b]
Aconitase (4.2.1.3)	ACON	2	Liver, muscle	F	3
Adenylate kinase (2.7.4.3)	AK	1	Muscle	A	3
Aldolase (4.1.2.13)	ALD	1	Muscle	D	3
Creatine kinase (2.7.3.2)	CK	2	Muscle	A	3
Enolase (4.2.1.11)	ENOL	1	Liver	A	3
Esterase[c] (3.1.1.1)	EST	2	Muscle	A	1.5
Fumerase (4.2.1.2)	FUM	1	Liver	F	2.5
General protein[d]	GP	1	Muscle	A	3
Glucose-phosphate isomerase (5.3.1.9)	GPI	1	Liver	E	3
Glutamate dehydrogenase (1.4.1.3)	GLUD	1	Muscle	A	3
Glutamate oxaloacetate transaminase (2.6.1.1)	GOT	2	Liver	F	3
Glutamate pyruvate transaminase (2.6.1.2)	GPT	1	Liver	F	2.5
Glyceraldehyde-3-phosphate dehydrogenase (1.2.1.12)	GA3PD	1	Liver	D	3
Glycerophosphate dehydrogenase (1.1.1.8)	GPD	1	Liver	F	3
Guanine deaminase (3.5.4.3)	GDA	1	Liver	C	1
Isocitrate dehydrogenase (1.1.1.42)	IDH	2	Liver	F	3
Lactate dehydrogenase (1.1.1.27)	LDH	2	Muscle	A, D	3
Malate dehydrogenase (1.1.37)	MDH	2	Muscle	A	1.5
Mannose phosphate isomerase (5.3.1.8)	MP1	1	Muscle	C	1.5
Phosphoglucomutase (2.7.5.1)	PGM	2	Liver	A	3
6-Phosphogluconate dehydrogenase (1.1.1.44)	6PGD	1	Liver	C	2.5
Phosphoglycerate kinase (2.7.23)	PGK	1	Liver	A	3
Purine nucleoside phosphorylase (2.4.2.1)	NP	1	Liver	F	1.5
Pyruvate kinase (2.7.1.40)	PK	1	Muscle	B	2
Triose-phoshpate isomerase (5.3.1.1)	TPI	1	Liver	D	3

[a] A = 50 mM TEM, B = 15 mM TEB, C = 50 mM TEM + NADP, D = 50 mM TEM + NAD, E = 25 mM TEB, F = 0.1 M Tris-citrate. Recipes for 1 liter of above buffers. A: 6.06 g Tris, 1.86 g Na EDTA, 0.20 g anhydrous MgCl, pH to 7.8 with Maleic acid. B: 1.82 g Tris, 1.86 g Na EDTA, 0.20 g anhydrous MgCl, pH to 8.0 with boric acid. C: as for A but add 10 mg NADP. D: as for A but add 10 mg NAD. E: 3.06 g Tris, 1.86 g Na EDTA, 0.20 g anhydrous MgCl, pH to 8.0 with boric acid. F: 12.11 g Tris, pH to 7.8 with citric acid.

[b] At 7 mA per 12 cm gel (except B and E buffers; 5 mA).

[c] By method A in Harris & Hopkinson (1976) with 4-methyl-umbelliferyl-acetate.

[d] Stained with amido black.

TABLE 4. Genetic distance measures. Upper matrix, Nei (1978) unbiased genetic distance; lower matrix, Rogers (1972) genetic distance. For species code refer to Table 2.

Species code	CFU	CRO	CGA	THA	GCO	PVE	NMU	NPU	LLO	CPA	OAR	ASC	PSW	PEL	PEX	BBA	PSP	PWA
CFU	—	0.549	0.468	0.954	0.962	0.962	0.962	0.962	1.004	0.949	0.950	0.802	0.718	0.950	0.933	0.962	0.842	0.842
CRO	0.430	—	0.049	1.245	1.253	1.253	1.253	1.253	1.328	1.250	1.241	0.944	0.831	0.953	0.916	0.965	0.847	0.965
CGA	0.382	0.048	—	1.091	1.099	1.099	1.099	1.099	1.161	1.092	1.087	0.826	0.726	0.953	0.916	0.965	0.847	0.965
THA	0.617	0.711	0.663	—	0.000	0.000	0.049	0.049	0.063	0.026	0.063	0.764	0.651	0.722	0.722	0.734	0.639	0.397
GCO	0.620	0.714	0.667	0.008	—	0.000	0.049	0.049	0.062	0.034	0.062	0.755	0.646	0.730	0.730	0.742	0.647	0.405
PVE	0.620	0.714	0.667	0.008	0.000	—	0.049	0.049	0.062	0.034	0.062	0.755	0.646	0.730	0.730	0.742	0.647	0.405
NMU	0.620	0.714	0.667	0.056	0.048	0.048	—	0.000	0.115	0.087	0.115	0.755	0.646	0.730	0.730	0.742	0.647	0.405
NPU	0.620	0.714	0.667	0.056	0.048	0.048	0.000	—	0.115	0.087	0.115	0.755	0.646	0.730	0.730	0.742	0.647	0.405
LLO	0.633	0.738	0.690	0.079	0.071	0.071	0.119	0.119	—	0.093	0.076	0.743	0.681	0.769	0.770	0.781	0.681	0.430
CPA	0.610	0.712	0.665	0.053	0.057	0.057	0.105	0.105	0.113	—	0.102	0.833	0.712	0.716	0.716	0.728	0.631	0.386
OAR	0.614	0.708	0.660	0.079	0.071	0.071	0.119	0.119	0.095	0.129	—	0.743	0.634	0.823	0.825	0.835	0.730	0.468
ASC	0.557	0.610	0.562	0.544	0.536	0.536	0.536	0.536	0.529	0.570	0.530	—	0.045	0.535	0.548	0.567	0.484	0.755
PSW	0.518	0.565	0.517	0.481	0.481	0.481	0.481	0.481	0.505	0.514	0.471	0.076	—	0.439	0.437	0.451	0.378	0.630
PEL	0.615	0.614	0.614	0.516	0.519	0.519	0.519	0.519	0.543	0.517	0.560	0.436	0.365	—	0.000	0.037	0.142	0.548
PEX	0.608	0.603	0.603	0.520	0.524	0.524	0.524	0.524	0.547	0.521	0.565	0.431	0.370	0.016	—	0.037	0.144	0.545
BBA	0.620	0.619	0.619	0.520	0.524	0.524	0.524	0.524	0.548	0.522	0.565	0.441	0.370	0.043	0.059	—	0.100	0.480
PSP	0.573	0.571	0.571	0.473	0.176	0.476	0.476	0.476	0.500	0.474	0.517	0.393	0.322	0.138	0.154	0.095	—	0.405
PWA	0.573	0.619	0.619	0.330	0.333	0.333	0.333	0.333	0.357	0.331	0.375	0.536	0.469	0.424	0.428	0.381	0.333	—
MUN	0.665	0.712	0.712	0.434	0.426	0.426	0.426	0.426	0.450	0.472	0.420	0.581	0.526	0.564	0.569	0.569	0.521	0.474
CNO	0.514	0.667	0.619	0.484	0.476	0.476	0.476	0.476	0.470	0.511	0.470	0.346	0.338	0.471	0.476	0.429	0.381	0.429
NBO	0.701	0.807	0.807	0.569	0.569	0.569	0.569	0.569	0.562	0.591	0.610	0.593	0.577	0.517	0.521	0.474	0.474	0.521
NCH	0.617	0.711	0.711	0.341	0.341	0.341	0.341	0.341	0.365	0.384	0.383	0.497	0.433	0.468	0.472	0.425	0.378	0.330
PHA	0.609	0.667	0.667	0.568	0.571	0.571	0.571	0.571	0.565	0.558	0.613	0.341	0.322	0.186	0.202	0.143	0.143	0.429
NHA	0.630	0.629	0.629	0.473	0.465	0.465	0.465	0.465	0.489	0.510	0.506	0.404	0.348	0.100	0.105	0.079	0.175	0.391
LDI	0.566	0.613	0.565	0.461	0.465	0.465	0.465	0.465	0.489	0.467	0.506	0.382	0.311	0.152	0.157	0.109	0.157	0.375
GGE	0.561	0.667	0.619	0.532	0.524	0.524	0.524	0.524	0.517	0.558	0.517	0.389	0.397	0.567	0.571	0.571	0.524	0.524
GSI	0.561	0.667	0.619	0.532	0.524	0.524	0.524	0.524	0.517	0.558	0.517	0.389	0.397	0.567	0.571	0.571	0.524	0.524
ERO	0.519	0.613	0.565	0.402	0.405	0.405	0.405	0.405	0.429	0.419	0.446	0.417	0.346	0.400	0.405	0.405	0.357	0.375
CGU	0.620	0.722	0.675	0.349	0.341	0.341	0.341	0.341	0.354	0.379	0.383	0.532	0.489	0.432	0.436	0.437	0.437	0.389
PBR	0.566	0.613	0.613	0.450	0.452	0.452	0.452	0.452	0.476	0.467	0.494	0.512	0.446	0.370	0.374	0.327	0.232	0.327
PPI	0.566	0.613	0.613	0.450	0.452	0.452	0.452	0.452	0.476	0.467	0.494	0.512	0.446	0.370	0.374	0.327	0.232	0.327
MBR	0.584	0.762	0.714	0.341	0.333	0.333	0.333	0.333	0.357	0.379	0.375	0.489	0.433	0.567	0.571	0.571	0.524	0.429
MPU	0.620	0.762	0.714	0.341	0.333	0.333	0.333	0.333	0.357	0.379	0.375	0.489	0.433	0.560	0.564	0.571	0.524	0.429
PHI	0.561	0.667	0.619	0.389	0.381	0.381	0.381	0.381	0.375	0.415	0.422	0.484	0.481	0.519	0.524	0.476	0.429	0.333
PDE	0.561	0.667	0.619	0.484	0.476	0.476	0.476	0.476	0.470	0.511	0.470	0.437	0.444	0.519	0.524	0.476	0.476	0.429
ARO	0.620	0.714	0.667	0.473	0.476	0.476	0.476	0.476	0.500	0.474	0.470	0.536	0.469	0.567	0.567	0.571	0.524	0.524

TABLE 4. Continued.

Species code	MUN	CNO	NBO	NCH	PHA	NHA	LDI	GGE	GSI	ERO	CGU	PBR	PPI	MBR	MPU	PHI	PDE	ARO
CFU	1.092	0.718	1.224	0.954	0.941	0.979	0.827	0.823	0.823	0.722	0.972	0.830	0.830	0.861	0.962	0.823	0.823	0.962
CRO	1.247	1.099	1.668	1.245	1.099	0.982	0.951	1.099	1.099	0.953	1.273	0.953	0.953	1.435	1.435	1.099	1.099	1.253
CGA	1.247	0.965	1.668	1.245	1.099	0.982	0.833	1.965	0.965	0.835	1.115	0.953	0.953	1.253	1.253	0.965	0.965	1.099
THA	0.560	0.654	0.841	0.412	0.839	0.628	0.612	0.751	0.751	0.505	0.414	0.589	0.589	0.409	0.409	0.484	0.654	0.639
GCO	0.554	0.647	0.833	0.409	0.847	0.621	0.617	0.742	0.742	0.507	0.409	0.590	0.590	0.405	0.405	0.480	0.647	0.647
PVE	0.554	0.647	0.833	0.409	0.847	0.621	0.617	0.742	0.742	0.507	0.409	0.590	0.590	0.405	0.405	0.480	0.647	0.647
NMU	0.554	0.647	0.833	0.409	0.847	0.621	0.617	0.742	0.742	0.507	0.409	0.590	0.590	0.405	0.405	0.480	0.647	0.647
NPU	0.554	0.647	0.833	0.409	0.847	0.621	0.617	0.742	0.742	0.507	0.409	0.590	0.590	0.405	0.405	0.480	0.647	0.647
LLO	0.584	0.635	0.821	0.434	0.835	0.655	0.651	0.730	0.730	0.536	0.428	0.623	0.623	0.430	0.430	0.468	0.635	0.681
CPA	0.625	0.711	0.901	0.460	0.816	0.702	0.616	0.816	0.816	0.530	0.464	0.619	0.619	0.461	0.461	0.529	0.711	0.631
OAR	0.542	0.635	0.941	0.472	0.953	0.704	0.699	0.730	0.730	0.578	0.472	0.669	0.669	0.468	0.468	0.548	0.635	0.635
ASC	0.858	0.408	0.870	0.664	0.396	0.485	0.457	0.471	0.471	0.513	0.744	0.692	0.692	0.656	0.655	0.641	0.553	0.755
PSW	0.737	0.401	0.852	0.561	0.378	0.400	0.357	0.489	0.489	0.414	0.653	0.581	0.581	0.557	0.557	0.646	0.572	0.630
PEL	0.829	0.635	0.714	0.627	0.199	0.080	0.146	0.835	0.835	0.495	0.554	0.455	0.455	0.835	0.808	0.730	0.730	0.835
PEX	0.831	0.633	0.714	0.625	0.203	0.072	0.146	0.837	0.837	0.498	0.551	0.452	0.452	0.837	0.810	0.730	0.730	0.819
BBA	0.841	0.560	0.629	0.552	0.154	0.057	0.103	0.847	0.847	0.507	0.566	0.393	0.393	0.847	0.847	0.647	0.647	0.847
PSP	0.736	0.480	0.629	0.472	0.154	0.166	0.158	0.742	0.742	0.430	0.566	0.260	0.260	0.742	0.742	0.560	0.647	0.742
PWA	0.641	0.560	0.726	0.397	0.560	0.479	0.465	0.742	0.742	0.468	0.484	0.393	0.393	0.560	0.560	0.405	0.560	0.742
MUN	—	0.736	0.827	0.560	0.959	0.744	0.808	0.841	0.841	0.675	0.648	0.675	0.675	0.641	0.641	0.736	0.736	0.641
CNO	0.521	—	0.555	0.409	0.405	0.506	0.452	0.480	0.480	0.430	0.639	0.430	0.430	0.560	0.560	0.480	0.480	0.647
NBO	0.566	0.438	—	0.545	0.460	0.588	0.803	0.645	0.645	0.579	0.825	0.672	0.672	0.726	0.726	0.645	0.743	0.629
NCH	0.434	0.341	0.426	—	0.472	0.485	0.526	0.654	0.654	0.428	0.490	0.505	0.505	0.409	0.409	0.484	0.654	0.552
PHA	0.616	0.333	0.379	0.378	—	0.225	0.278	0.560	0.560	0.430	0.717	0.468	0.468	0.742	0.742	0.560	0.647	0.742
NHA	0.531	0.413	0.469	0.399	0.222	—	0.142	0.750	0.750	0.508	0.458	0.379	0.379	0.716	0.716	0.562	0.591	0.839
LDI	0.557	0.370	0.558	0.414	0.252	0.163	—	0.814	0.814	0.499	0.537	0.447	0.447	0.711	0.711	0.531	0.531	0.833
GGE	0.569	0.381	0.485	0.484	0.429	0.534	0.560	—	0.000	0.292	0.538	0.681	0.681	0.647	0.647	0.405	0.336	0.647
GSI	0.569	0.381	0.485	0.484	0.429	0.534	0.560	0.000	—	0.292	0.538	0.681	0.681	0.647	0.647	0.405	0.336	0.647
ERO	0.497	0.357	0.451	0.354	0.357	0.415	0.395	0.262	0.262	—	0.434	0.436	0.436	0.430	0.430	0.507	0.590	0.468
CGU	0.481	0.473	0.565	0.397	0.516	0.378	0.425	0.421	0.421	0.365	—	0.512	0.512	0.484	0.484	0.459	0.538	0.654
PBR	0.497	0.357	0.498	0.402	0.375	0.341	0.364	0.500	0.500	0.357	0.413	—	0.000	0.681	0.681	0.507	0.590	0.730
PPI	0.497	0.357	0.498	0.402	0.375	0.341	0.364	0.500	0.500	0.357	0.413	0.000	—	0.681	0.681	0.507	0.590	0.730
MBR	0.474	0.429	0.521	0.341	0.524	0.513	0.513	0.476	0.476	0.357	0.389	0.500	0.500	—	0.154	0.560	0.742	0.560
MPU	0.474	0.429	0.521	0.311	0.524	0.513	0.513	0.476	0.476	0.357	0.389	0.500	0.500	0.143	—	0.560	0.742	0.560
PHI	0.521	0.381	0.485	0.389	0.429	0.439	0.417	0.333	0.333	0.405	0.373	0.405	0.405	0.429	0.429	—	0.154	0.847
PDE	0.521	0.381	0.533	0.484	0.476	0.460	0.417	0.286	0.286	0.452	0.421	0.452	0.452	0.524	0.524	0.143	—	0.847
ARO	0.474	0.476	0.474	0.425	0.524	0.582	0.565	0.476	0.476	0.375	0.484	0.517	0.517	0.429	0.429	0.571	0.571	—

polymorphic within a species, the allele in higher frequency was designated as the state for the taxon. Alternate alleles were equal in frequency in seven instances. Where one or both of the alleles were autapomorphic, an autapomorph was excluded because this would not affect cladistic analysis; where they were not, we made a conservative decision to choose as the state for the taxa concerned that allele which was most frequent and widespread in other parrots.

The data for cladistic analysis were then entered as unordered, without weighting, into the PAUP program (Swofford 1985) which constructs phylogenies according to the principle of maximum parsimony. Mid-point and out-group procedures using the cockatoos were employed again to root the trees. To reduce arbitrary resolution of polychotomies as distinct trees, taxa which shared identical allelic constitutions or differed only by autapomorphies were excluded (Swofford 1985). Those excluded from this analysis are asterisked in Table 2. Also excluded, to improve the efficiency of the program run, were the following loci in which variation was limited to a single genus or species: GA3PD, FUM-1, MDH-1 and ALD. Because many (50) equally parsimonious trees were produced, consensus trees were constructed with the "strict" method (Rohlf 1982).

RESULTS

Phenetic analysis of genetic distance data. Of the 21 loci assessed, none were monomorphic across the range of species examined (Table 2). Rogers' (1972) and Nei's (1978) genetic distances were correlated throughout (Table 4); accordingly, only the latter are evaluated below as they are the most commonly used (Avise and Aquadro 1982).

Genetic distances were greatest between the cockatoos and the remaining parrots, at values ranging between 0.80 to 1.65. Within cockatoos and parrots, distances among morphologically well-separated genera ranged around 0.40 or higher, similar to the distance between lorikeets and other parrots. There were, nevertheless, exceptions. The seven genera of lorikeets were themselves very close, being separated by genetic distances of only 0 to 0.06. Moreover, other genera of Australian broad-tailed parrots (Platycercinae) were separated by distances of 0.20 or less: *Platycercus, Barnardius, Northiella, Lathamus, Purpureicephalus,* and *Psephotus.* Of these, *Platycercus* and *Barnardius* were closest with a Nei $\bar{D}$ of only 0.04. At distances ranging from 0.26 to 0.45, the New Guinean tiger-parrots (*Psittacella*) were also close to this assemblage. Other slight intergenetic distances were recorded between the polytelitine king parrots, *Polytelis* and *Alisterus,* at 0.05, and between the "typical" palaeotropic parrots, *Eclectus* and *Geoffroyus,* at 0.29. Conversely, the two species of platycercine grass parrot, *Neophema bourkii* and *N. chrysostoma,* differed by 0.55.

UPGMA phenograms based on Nei's (1978) and Rogers' (1972) measures were identical but with one exception. Nei's $\bar{D}$ clustered the Blue-winged Parrot (*N. chrysostoma*) with the fig-parrots (*Cyclopsitta*), pygmy-parrots (*Micropsitta*) and lorikeets, while Rogers' $\bar{D}$ grouped it with the Red-fronted Parakeet (*Cyanoramphus*) near the Australian broad-tailed assemblage (*Platycercus* to *Psephotus*). The Rogers based phenogram had a higher cophenetic correlation of 0.921 compared with 0.893 for the Nei phenogram.

Accordingly, the phenogram based on Rogers' (1972) $\bar{D}$ is depicted in Figure 1. In it, the major dichotomy is between the cockatoos and other parrots. The two main cacatuine lineages, the black cockatoos (*Calyptorhynchus*) and white and pink cockatoos (*Cacatua*) are also well differentiated. The first taxon split off among the parrots themselves is Bourke's Parrot, *Neophema bourkii.* The next dichotomy divides the remaining parrots into two major assemblages. One includes all lorikeets, and the fig- and pygmy-parrots (*Cyclopsitta, Micropsitta*) as sister lineages. The Australian Budgerigar (*Melopsittacus*) and African lovebirds (*Agapornis*) are also linked distantly to this group. The other major assemblage comprises two principal clusters. One includes the "typical" palaeotropic parrots: *Geoffroyus* (Red-cheeked and Blue-collared Parrots), *Eclectus* and *Psittacula* (Asian ring-necked parakeets). The second comprises the polytelitine king parrots (*Polytelis, Alisterus*) and core members of the Australian platycercines (Crimson Rosella, *Platycercus,* to Red-rumped Parrot, *Psephotus*). Linked to them are the Red-fronted Parakeet (*Cyanoramphus*), Blue-winged Parrot (*Neophema chrysostoma*), Ground Parrot (*Pezoporus*) and New Guinean tiger-parrots (*Psittacella*).

Phylogenetic analysis of genetic distance data. Both midpoint and outgroup (Fig. 2) rooted distance-Wagner trees had identical topologies and lengths (4.668) with cophenetic correlations of

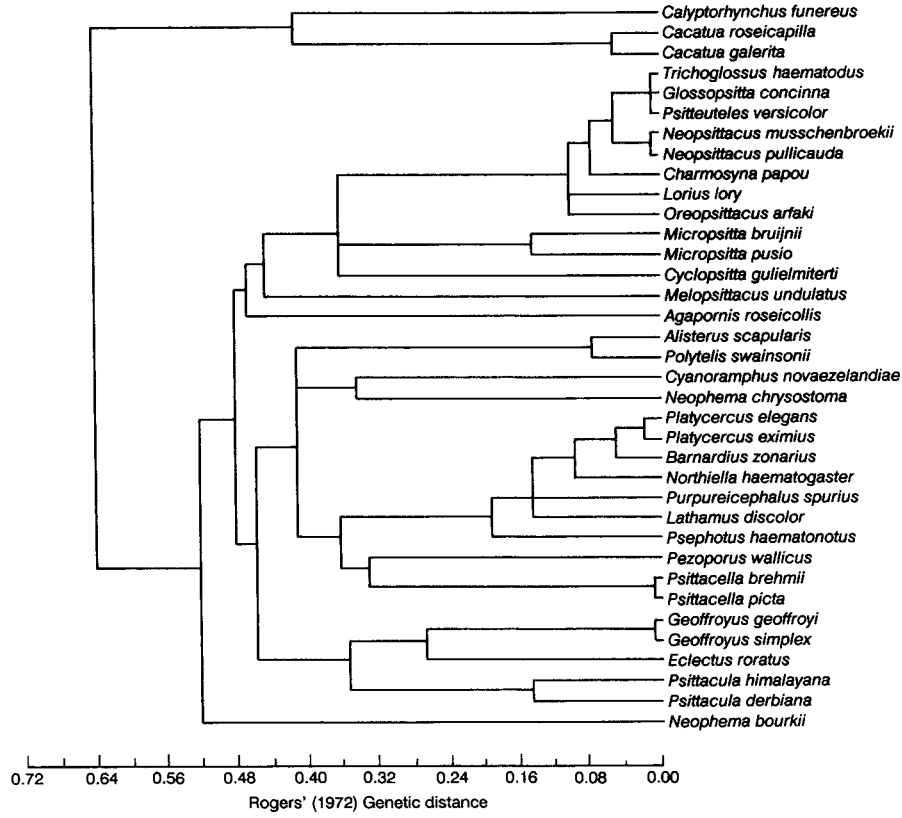

FIGURE 1. UPGMA phenogram for representative Australo-Papuan Psittaciformes based on Rogers' (1972) distance measure.

0.906. The outlying lineages among the parrots are the polytelitine king parrots and *Cyanoramphus*. At the next dichotomy, the core members of the Australian broad-tailed parrots, including the New Guinean tiger-parrots, are clustered on one side away from the remaining parrots and lorikeets. *Geoffroyus* and *Eclectus* are again clustered together but distant from *Psittacula* (cf. Fig. 1).

Phylogenetic analysis of allelic states. PAUP analysis with either midpoint or out-group rooting produced 50 equally parsimonious trees each with a length of 95 steps and a consistency index of 0.821. A "strict" consensus tree calculated from them is depicted in Figure 3a. Two major clades are evident. The first comprises the fig-parrots and the palaeotropic parrots, *Eclectus* and *Geoffroyus*, the latter two as sister taxa. The second clade is subdivided into three lineages: (1) the polytelitine king parrots (*Alisterus-Polytelis*), (2) most core members of the Australian broad-tailed parrots (*Platycercus, Barnardius, Purpureicephalus, Northiella* and *Lathamus*), and (3) the Red-rumped Parrot (*Psephotus*). Furthermore, 46 of the initial 50 trees linked the New Guinean tiger-parrots (*Psittacella*) and Red-fronted Parrakeet (*Cyanoramphus*) with the *Alisterus-Platycercus-Psephotus* clade (Fig. 3b).

DISCUSSION

Concordance of lineages among the algorithms. The many discrepancies in the positions of taxa among UPGMA, distance-Wagner and PAUP analyses are due to differing assumptions implicit in these algorithms. In the UPGMA computation (Fig. 1), which assumes a constant rate of evolution among lineages, Bourke's Parrot is separated as a sister group to the remaining parrots. Where differing rates of protein change are taken into account, as in the distance-Wagner procedure (Fig. 2), Bourke's Parrot clusters with other parrots. Moreover, the comparatively low num-

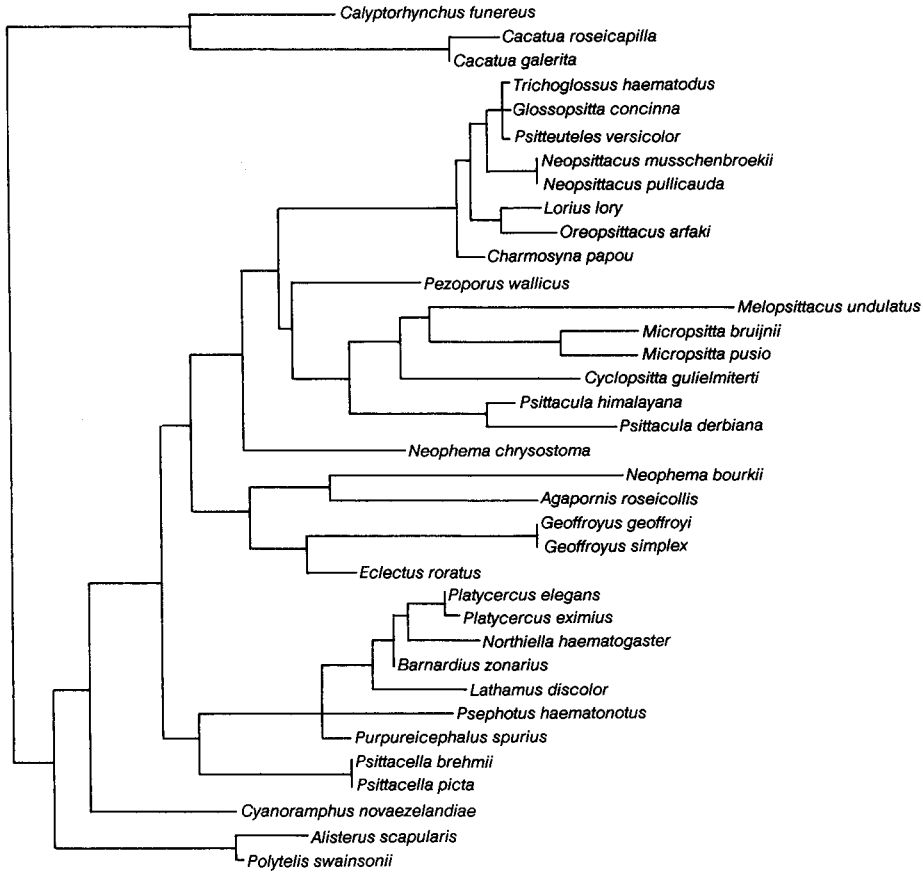

FIGURE 2. Distance Wagner tree for representative Australo-Papuan Psittaciformes based on Rogers' (1972) distance measure, rooted by the cacatuines (cockatoos).

ber of resolved loci may exaggerate inter-locus variance in estimated genetic distances, thereby magnifying apparent heterogeneity in rates of change. In a similar study on passerines, Christidis and Schodde (in press) suggested that confidence could be placed only on assemblages that are grouped consistently by both genetic distance and allelic state data. Accordingly, the following conclusions may be drawn from the data.

(1) The cockatoos form a monophyletic lineage distant from all other Australo-Papuan psittacine parrots.

(2) The lorikeets also form a monophyletic lineage but one that is much more close-knit than the cockatoos and which may fall within the Australo-Papuan psittacid assemblage.

(3) A core of Australian broad-tailed (platycercine) parrots is defined by the rosellas and ringnecks (*Platycercus, Barnardius*), Bluebonnet (*Northiella*), Red-capped Parrot (*Purpureicephalus*), Swift Parrot (*Lathamus*) and grass parrots (*Psephotus*). New Guinean *Psittacella* is also a member of this assemblage.

(4) Other conventional members of the platycercines—the Ground Parrot (*Pezoporus*), Budgerigar (*Melopsittacus*), Red-fronted Parakeet (*Cyanoramphus*), Blue-winged and Bourke's Parrots (*Neophema*)—are much more distant and of disparate affinity in their allozymes.

(5) The polytelitine parrots (*Alisterus-Polytelis*) are a sister group of the platycercine parrots.

(6) The Eclectus (*Eclectus*) and Red-cheeked and Blue-collared Parrots (*Geoffroyus*) are the only palaeotropic genera to cluster consistently. The fig-parrots (*Cyclopsitta*) may also be linked to them.

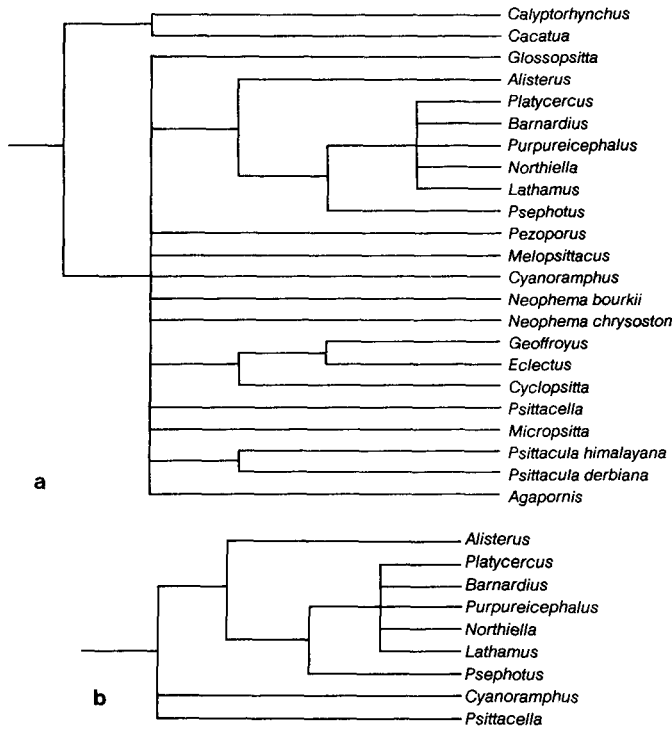

FIGURE 3. a) Strict consensus tree for representative Australo-Papuan Psittaciformes derived from PAUP analysis of the electromorphs using cacatuines as the outgroup. b) relationships within playtycercine assemblage of 3a when 4 outlying PAUP trees are excluded from the consensus tree.

(7) The pygmy-parrots (*Micropsitta*) and the Afro-Asian genera *Psittacula* and *Agapornis* have no obvious links with other taxa screened here.

Concordance of lineages with other biochemical, chromosomal and morphological data. Comparison of these results with other recent protein (Adams et al. 1984, Ovenden et al. 1987) and chromosomal (Van Dongen and De Boer 1984, Schmutz and Prus 1987, Christidis et al., in press) studies, and with the contemporary morphological reviews of Smith (1975) and Homberger (1980), sheds further light on relationships among the Australo-Papuan Psittaciformes (cf. Table 1).

Adams et al. (1984) also concluded that the cockatoos are a distinct lineage among the order, distant from all other groups in the Australo-Papuan region. There are no links with the platycercine broadtails (cf. Smith 1975). Genetic distances between major lineages of the cockatoos are as great as between tribal groupings in other parrots, suggesting, by implication in the distance-Wagner analysis (Fig. 2), that the lineages are ancient rather than rapidly evolving in their alleles. Karyotypes further stress the schism between the cockatoos (represented by *Cacatua, Leptolophus* = *Nymphicus* and *Calyptorhynchus*) and other parrots. Whereas nearly all parrots and the the lorikeets have a diploid complement of 60–72 chromosomes, including usually five to seven pairs of bi-armed macrochromosomes, the cockatoos have a higher diploid number (72–80) composed largely of single-armed elements (Christidis et al., in press). When taken into account with the many morphological and behavioral differences between the cockatoos and other parrots (Smith 1975, Homberger 1980, Adams et al. 1984), these data lend support for recognizing the cockatoos as a family.

The lorikeets also cluster as a monophyletic group on morphological and behavioral characters (Smith 1975, Homberger 1980) and are linked with the psittacine parrot assemblage on karyotype morphology (Christidis et al., in press). Although none of these studies clarify their clos-

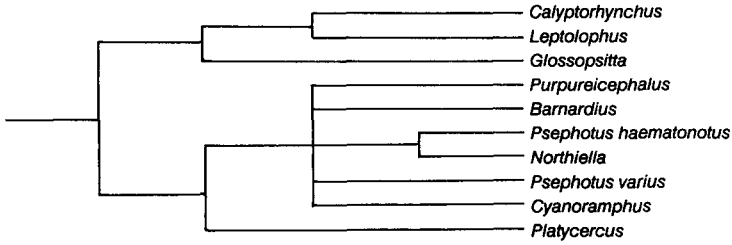

FIGURE 4. Strict consensus tree for Australian Psittaciformes. Computed from the data of Ovenden (1984), using PAUP with mid-point rooting.

est relatives, the lorikeets were perceived by Immelmann (1966) and Holyoak (1973) as springing from the Australo-Papuan platycercine parrots. Indeed, from a single UPGMA computation, Ovenden et al. (1987) reported that *Platycercus* itself was not a member of the "broad-tail" assemblage but aligned with the lorikeet *Glossopsitta* instead. Such a relationship is so at variance with all other findings, including ours, that we reanalysed Ovenden's (1984) raw electrophoretic data with the PAUP procedure. Rooted by the mid-point method, it produced 17 equally parsimonious trees (length 45.0, consistency index 0.821), none of which associated *Platycercus* with *Glossopsitta*. From them a "strict" consensus tree was derived and is depicted in Figure 4. In it, *Platycercus* is aligned with other broad-tailed parrots (*Barnardius, Psephotus,* etc.), albeit as a distinct sister lineage, while *Glossopsitta* is grouped with the cockatoos. Obviously the single UPGMA phenogram of Ovenden et al. (1987) does not represent the phylogenetic position of *Platycercus* accurately.

Among the remaining Psittacidae, other studies have singled out the same Australian platycercine cluster as here, but with differing composition and internal relationships (cf. Table 1). There is consensus only over the inclusion of *Platycercus, Barnardius, Purpureicephalus, Northiella* and *Psephotus*. Moreover, our protein data corroborate the inclusion of the Swift Parrot (*Lathamus*) in this assemblage. The morphological similarities between *Lathamus* and the lorikeets, including nectar feeding, are evidently convergent (Smith 1975, Homberger 1980).

Several other genera conventionally included among the platycercines are placed ambiguously or excluded by our study. They are the Red-fronted Parakeet (*Cyanoramphus*), Ground Parrot (*Pezoporus*), Budgerigar (*Melopsittacus*) and Bourke's and Blue-winged Parrots (*Neophema*) cf. Table 1. If these genera are broadtails, then they are widely divergent elements, as is evident also in their morphology. Unlike other platycercines which have a type A-2 carotid formula, *Melopsittacus* and *Neophema* possess the ancestral type A-1 (Glenny 1957). Moreover, *Pezoporus* and *Melopsittacus* lack the characteristic platycercine nape spot. The great genetic distance between *Neophema bourkii* and *N. chrysostoma,* and their disparate separation in all algorithmic analyses (Figs. 1, 2, 3a), implies that they are generically distinct. This result corroborates the morphological and behavioral conclusions of Immelmann (1966) and Homberger (1980).

Two other lineages linked here to the Australian platycercines are not corroborated in contemporary morphological studies. They are New Guinean *Psittacella* and the Australian polytelitine parrots, *Alisterus* and *Polytelis. Psittacella* has only been reviewed recently by Smith (1975) who no doubt included it among psittaculine parrots because of its stout, short-tailed form and lack of a platycercine wing stripe and nape spot. Nevertheless, *Psittacella* has the pale grey platycercine bill and the barred plumage, colored rump and blue cheeks (*P. picta*) found in some broad-tailed parrots; its undertail coverts are also red, contrasting with the belly as in *Platycercus, Purpureicephalus, Northiella* and *Psephotus.*

The polytelitine parrots have been grouped consistently with palaeotropic psittacine or psittaculine parrots by all current morphological reviews except those of Thompson (1899) and Verheyen (1956) which linked them, as here, to the platycercines. Smith (1975) and Homberger (1980) grouped the polytelitines with *Geoffroyus, Eclectus, Psittacula* and *Agapornis* in the tribe

Psittaculini. Our data corroborate a close relationship between *Geoffroyus* and *Eclectus* but suggest, however, that the Psittaculini are polyphyletic. This is reflected in chromosomal data (Christidis et al., in press) which reveal that *Agapornis, Psittacula* and *Alisterus* have significantly different karyotypes. The morphological and behavioral characters supporting the monophyly of the Psittaculini need to be examined carefully to determine their nature, whether convergent, ancestral or derived. Certainly the phylogenetic significance of the carotenoid bill, which apparently unites the Psittaculini (Smith 1975), has to be re-assessed as it is also present in most lorikeets.

Biogeographical and phylogenetic correlations. It is likely that the primary lineages of Australo-Papuan parrots and cockatoos arose on the Australian continental plate or were co-inherited from Gondwana (Cracraft 1973, Smith 1975, Rich 1975), but without necessarily any "immigration." Cockatoos, lorikeets and broad-tailed platycercine parrots are the dominant groups and all three are centered today in the Australo-Papuan region. The cockatoos are probably one of the oldest lineages of the order. The genera of lorikeets, in contrast, are little differentiated and probably radiated recently. The three in Australia—*Trichoglossus, Psitteuteles* and *Glossopsitta*—have identical allelic constitutions in proteins scored (Table 2). They could be considered derivatives of a single lineage which entered Australia only recently from New Guinea. This is unlikely to have happened before Miocene-Oligocene times, 20–30 million years BP, because significant New Guinean land forms cut off from the Australian continental plate by the Aure trough had not developed before then (Doutch 1972, Dow 1977, Pieters 1982).

Concerning *Psittacella,* the occurrence of this evident platycercine with ancestral morphological traits (type A-1 carotid formula, barred plumage and no wing bar or nape spot) in the montane rainforests of New Guinea is significant. These forests and their vicariant biotas along the east coast of Australia hold a "Tumbunan" avifauna that appears to comprise the surviving elements of the Australian Tertiary rainforest and representatives of ancestral stocks from which many arid-adapted taxa have been derived (Schodde and Calaby 1972).

The center of platycercine diversity is in Australia where protein data indicate two successive radiations. The first, which may date from the onset of Tertiary aridity in mid Miocene times (Kemp 1981), appears to have been continent-wide and involved the divergence of the ground parrots (*Pezoporus*), Budgerigar (*Melopsittacus*), Bourke's Parrot (*Neophema* = *Neopsephotus bourkii*), typical *Neophema,* the core platycercine group and the polytelitine parrots from one another. Outlying groups, such as ancestral stocks of *Prosopeia, Cyanoramphus* and *Eunymphicus* perhaps spread to Pacific islands over the same period. The second radiation is centered in the eucalypt-dominated "Bassian" biota of southern Australia where the elements of the core platycercine group—*Platycercus, Barnardius, Purpureicephalus, Northiella, Lathamus* and *Psephotus*—then split from one another. Members of some of these genera have since adaptively colonized the arid "Eyrean" and north Australian "Torresian" biotas (*Barnardius, Northiella, Psephotus*); but none has returned to the "Tumbunan" rainforests of the east coast.

The genetic distances among the other presumed Australo-Papuan psittaculines—*Eclectus-Geoffroyus, Cyclopsitta* (fig-parrots) and *Micropsitta* (pygmy-parrots)—and from their supposed Afro-Asian relatives suggest that they too many have arisen independently from as yet unknown ancestral stocks in the Australian region. Their relationships are among the largest gaps still to be resolved in the phylogeny of the Psittaciformes.

ACKNOWLEDGMENTS

For permission to collect material for this study, we are deeply indebted to the Papua New Guinea Department of Environment and Conservation and to the Australian State National Parks and Wildlife Services in Victoria, Queensland, New South Wales, South Australia, Tasmania and Western Australia, as well as the Conservation Commission of the Northern Territory. Individual help was given by K. Kisokau, L. Seri, G. Kula, G. Maynes, P. Christian, A. Christidis, and I. Schodde in Papua New Guinea, and by J. Bourne, C. Corben, F. Crome, R. H. Green, M. King, L. Moore, G. O'Neill, L. Pedler, J. C. Wombey, H. B. Gill, B. Gillies, J. Pedler, and P. Wilkinson in Australia. We also acknowledge the following for providing tissue material: P. R. Baverstock (South Australian Museum) for *Melopsittacus undulatus, Micropsitta pusio* and *Psitacella picta,* A. Isles for *Psittacula himalayani* and *P. derbiana* and N. Hermes for *Cyanoramphus novaezelandiae.* The figures were prepared by F. Knight, CSIRO Division of Wildlife and Ecology, Canberra, and the manuscript was typed by T. Galariniotis and B.

Gillies, Museum of Victoria, Melbourne. Electrophoresis was carried out in the Department of Population Biology, Australian National University. The work was funded by an ANU-CSIRO collaborative research grant.

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). Aust. J. Zool. 32:363–377.

AVISE, J. C., AND C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates. Patterns and correlations. Evol. Biol. 15: 151–185.

BEEHLER, B., AND B. W. FINCH. 1985. Species-checklist of the birds of New Guinea. Australasian Ornithol. Monogr.

BOETTICHER, H. VON, 1964. Papageien. Wittenberg, A. Ziemsen.

BRERETON, J. LE GAY. 1963. Evolution within the Psittaciformes, p. 499–517. *In* C.G. Sibley [ed.], Proceedings 13th International Ornithological Congress, American Ornithologist Union. Vol. 1. Ithaca, New York.

CHRISTIDIS, L., AND R. SCHODDE. In press. Relationships of Australo-Papuan songbirds (Aves: Passeriformes)—protein evidence. Ibis.

CHRISTIDIS, L., D. D. SHAW, AND R. SCHODDE. In press. Chromosomal evolution in parrots, lorikeets and cockatoos (Aves: Psittaciformes). Hereditas.

CONDON, H. T. 1975. Checklist of the birds of Australia, Part 1. Non-passerines. Royal Australasian Ornithologists Union, Melbourne.

CRACRAFT, J. 1973. Continental drift, paleoclimatology, and the evolution and biogeography of birds. J. Zool. 169:455–545.

DOUTCH, H. F. 1972. The paleogeography of northern Australia and New Guinea and its relevance to the Torres Strait area, p. 1–10. *In* D. Walker [ed.], Bridge and barrier: the natural and cultural history of Torres Strait. Anstralian National Univ. Press, Canberra.

DOW, D. B. 1977. A geological synthesis of Papua New Guinea. Australian Bur. Miner. Resour. Geol. Geophys. Publ., Canberra.

FARRIS, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106:645–668.

GLENNY, F. H. 1957. A revised classification of the Psittaciformes based on the carotid artery arrangement patterns. Ann. Zool. (Agra) 2:47–56.

GYSELS, H. 1964. A biochemical evidence for the heterogeneity of the family Psittacidae. Soc. Roy. Zool. Anvers. Bull. 33:29–41.

HARRIS, H., AND D. A. HOPKINSON. 1976. Handbook of enzyme electrophoresis in human genetics. North Holland Publ., Amsterdam.

HOLYOAK, D. T. 1973. Comments on taxonomy and relationships in the parrot subfamilies Nestorinae, Loriinae and Platycercinae. Emu 73:157–176.

HOMBERGER, D. G. 1980. Funktionell-Morphologische Untersuchungen zur Radiation der Ernahrungs- und Trinkmethoden der Papageien (Psittaci). Bonn. Zool. Monogr. 13:1–192.

IMMELMANN, K. 1966. Die Australische Plattschweifsittiche, 2nd ed. A Ziemsen, Wittemberg.

KEMP, E. M. 1981. Tertiary palaeogeography and the evolution of Australian climate, p. 33–49. *In* A. Keast [ed.], Ecological biogeography of Australia. Junk, The Hague.

MAINARDI, D. 1962. Studio immunogenetico sulla posizione tassonomica di *Melopsittacus undulatus*. Riv. Ital. Ornitol. Ser. 2, 32:136–140.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590.

OVENDEN, J. R. 1984. Investigations into the molecular evolution and phylogeny of Australian rosellas and related parrots. Ph.D. diss., Univ. New South Wales.

OVENDEN, J. R., MACKINLAY, A. G., AND CROZIER, R. H. 1987. Systematics and mitochondrial genome evolution of Australian rosellas (Aves: Platycercidae). Mol. Biol. Evol. 4:526–543.

PETERS, J. L. 1937. Checklist of birds of the world. Vol. 3. Harvard Univ. Press, Cambridge, MA.

PIETERS, P. E. 1982. Geology of New Guinea, p. 15–38. *In* J.L. Gressit [ed.], Biogeography and ecology of New Guinea. Vol 1. Junk, The Hague.

RICH, P. V. 1975. Antarctic dispersal routes, wandering continents and the origin of Australasia's non-passeriform avifauna. Mem. Nat. Mus. Vic. 36:63–126.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics 7. Univ. Texas Publ. 7212:145–153.

ROHLF, F. J. 1982. Consensus indices for comparing classifications. Math. Biosci. 59:131–144.

SCHMUTZ, S. M., AND S. E. PRUS. 1987. A cytogenetic study of four species of cockatoos and Amazon parrots. Genetica 74:69–71.

SCHODDE, R., AND J. H. CALABY. 1972. The biogeography of the Australo- Papuan bird and mammal faunas in relation to Torres Strait, p. 257–300. *In* D. Walker [ed.], Bridge and barrier: the natural and cultural history of Torres Strait. Australian National Univ. Press, Canberra.

SHAW, C. R., AND R. PRASAD. 1970. Starch gel electrophoresis—a compilation of recipes. Biochem. Genet. 4:297–320.

SIBLEY, C. G. 1960. The electrophoretic patterns of avian egg-white proteins as taxonomic characters. Ibis 102:215–284.

SIBLEY, C. G., AND J. E. AHLQUIST. 1972. A comparative study of the egg-white proteins of non-passerine birds. Bull. Peabody Museum Nat. Hist. 39:1–276.

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

SNEATH, P.H.A., AND R. R. SOKAL. 1973. Numerical taxonomy. W.H. Freeman, San Francisco.

SWOFFORD, D. L. 1981. On the utility of the distance Wagner procedure, p. 25–43. *In* V.A. Funk and D.R. Brooks [eds.], Advances in cladistics. Proceedings of the First Meeting of the Willi Hennig Society. New York Botanical Garden, Bronx.

SWOFFORD, D. L. 1985. Phylogenetic analysis using parsimony (PAUP). Illinois Natural History Survey, Champaign.

SWOFFORD, D. L., AND R. K. SELANDER. 1981. A computer program for the analysis of allelic variation in genetics. J. Hered. 72:281–283.

THOMPSON, D'A. W. 1899. On characteristic points in cranial osteology of the parrots. Proc. Zool. Soc. London 1899:9–46.

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

VERHEYEN, R. 1956. Analyse du potentiel morphologique et projet d'un nouvelle classification des Psittaciformes. Bull. Inst. R. Sci. Nat. Belg. 32:1–54.