Chromosomal evolution in parrots, lorikeets and cockatoos (Aves: Psittaciformes)

L. CHRISTIDIS[1], D. D. SHAW[2] and R. SCHODDE[3]

[1] *Department of Ornithology, Division of Natural History, Museum of Victoria, Melbourne, Victoria, Australia 3000*
[2] *Division of Wildlife and Ecology, CSIRO, Gunghalin, Canberra, Australia 2605*
[3] *Molecular and Population Genetics Group, Research School of Biological Sciences, Australian National University, Canberra, ACT, Australia 2601*

The karyotypes of 9 species of parrot (Psittacidae), lorikeet (Loriidae) and cockatoo (Cacatuidae) are presented together with C-band data on 5 of the species. All cockatoos possess a similar karyotype, which is very distinct from those observed in lorikeets and parrots. Even though there is considerable karyotypic diversity within the parrots (Psittacidae) an ancestral karyotype can still be deduced. This ancestral karyotype appears to be shared with the lorikeets (Loriidae), indicating that parrots and lorikeets are closely related. C-band variation is greatest within the cockatoos (Cacatuidae) and involves both centromeric and interstitial bands. The pattern of C-band distribution on the Z-chromosomes is also distinctive in both Cacatuidae and Psittacidae; its possiblle significance is discussed.

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

The parrot order Psittaciformes comprises some 330 to 350 species, grouped by the most widely used classifications (FORSHAW 1973; MORONY et al. 1975) into three families: Cacatuidae (cockatoos), Loriidae (lorikeets) and Psittacidae (parrots). Cockatoos and lorikeets are confined to the Australasian and South Pacific regions while parrots are more widespread, ranging from central and South America to Australasia and the South Pacific, southern Asia and Africa.

Even though many species are kept in captivity, few have been karyotyped. Those that have are 13 species from central and South America, 5 from the Afro-Asian region and 9 from Australasia, comprising three parrots and six cockatoos (summarized in VAN DONGEN and DE BOER 1984; SCHMUTZ and PRUS 1987). Despite the few species studied, the available data indicate considerable karyotypic variability within the order. To add to the karyotypic information for the order we describe here the karyotypes of three cockatoos, three parrots and two lorikeets from Australasia, together with that of one African parrot. C-banded karyotypes are also presented for five of these species. The patterns of chromosomal evolution in the Psittaciformes are summarized and discussed.

Material and methods

The following members from the three currently recognized psittaciform families were examined karyotypically (the second number refers to individuals C-banded), *Cacatua roseicapilla,* Galah (3, 2 males, 2, 2 females), *C. galerita,* Sulphur-crested Cockatoo (1, 1 male) and *Nymphicus hollandicus,* Cockatiel (1, 1 male), all Cacatuidae (Cockatoos); *Alisterus scapularis,* Australian King Parrot (4, 3 females), *Platycercus elegans,* Crimson Rosella (3, 2 males, 1 female), *Psephotus varius,* Mulga Parrot (1 male, 1 female) and *Agapornis roseicollis,* Peach-faced Lovebird (1 male), all Psittacidae (parrots); *Trichoglossus haematodus,* Rainbow Lorikeet (1 male, 1 female) and *Lorius hypoinochrous,* Western Lory (1 male) both Loriidae (lorikeets). Apart from *Nymphicus* and *Agapornis* both of aviary origin, all species were collected in the wild; their
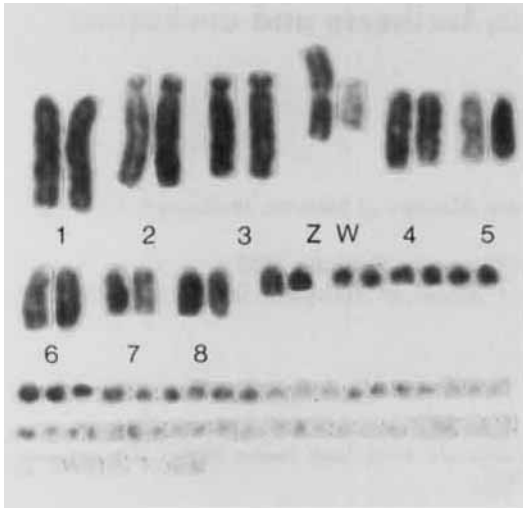
Fig. 1. Karyotype of female Galah (*Cacatua roseicapilla*).

Fig. 2. Karyotype of male Sulphur-crested Cockatoo (*Cacatua galerita*).

locality data are available from the authors on request. Nomenclature follows MORONY et al. (1975).

Chromosomal preparations were made from short term bone marrow cell cultures as outlined in CHRISTIDIS (1985). C-bands were obtained through a modification of the $Ba(OH)_2$ method of SUMNER (1972) in which the 2×SSC treatment is reduced to 50 min at 65°C. Both banded and unbanded slides were stained with 3 % Giemsa in phosphate buffer (pH 7.2) for 5 min.

Results

Cacatua roseicapilla (Fig. 1). — The diploid karyotype comprises 76 chromosomes in which eight pairs of autosomal macrochromosomes can be recognized. Autosomes 2 and 3 are acrocentric while the remainder, including the microchromosomes, are telocentric. The Z-chromosome is metacentric and fourth in order of size, while the acrocentric W-chromosome is equivalent to autosomes 7 and 8. Autosomes 1–3 are similar in size as are 4–6 and 7–8. C-banding (Fig. 6b) reveals both a centromeric and a proximal interstitial band on each of the telocentric autosomal macrochromosomes. The interstitial band is generally the more prominent. Acrocentric autosomes 2 and 3 have faint centromeric bands as does the Z-chromosome. The W-chromosome is differentially banded with two large bands on the long arm; one is distal and the other proximal. One pair of large microchromosomes and

several smaller ones are largely C-positive while the remainder have a centromeric C-band.

Cacatua galerita (Fig. 2). — This karyotype differs from that of the previous cockatoo insofar as autosomes 2 and 3 are telocentric rather than acrocentric and the diploid number is 80. Furthermore, autosomes 2 and 3 are noticeably smaller than 1. A female was not examined but VAN DONGEN and DE BOER (1984) identified the W-chromosome as a metacentric element similar in size to autosomes 7 and 8 in this species. The Z-chromosome is second in order of size overall. C-banding (Fig. 6d) reveals a contrasting pattern to *C. roseicapilla* in that the centromeric C-bands are much more prominent than the interstitial ones. Autosomes 1 to 7 have both interstitial and centromeric C-bands although the former are not always clear in both homologues. Autosome 8 lacks an interstitial C-band. In our male examined, both Z-chromosomes display a centromeric C-band and one of them also has a prominent interstitial C-band. The distribution of heterochromatin amongst the microchromosomes is similar to that in *Cacatua roseicapilla*.

Nymphicus hollandicus (Fig. 3). — The diploid number of 72 includes only seven pairs of autosomal macrochromosomes, which show a progressive decrease in size. Autosomes 1 to 3 are acrocentric, 4 is submetacentric and the remaining three are telocentric. The metacentric Z-chromosome is equivalent in size to autosome 1. C-bands

Fig. 3. Karyotype of male Cockatiel (*Nymphicus hollandicus*).

Fig. 4. Karyotype of female Australian King Parrot (*Alisterus scapularis*).

(Fig. 6c) are not very pronounced in this species. Autosome 1 has both a centromeric and a proximal interstitial C-band while 2, 3 and the Z-chromosome lack any obvious bands. Only one of the autosome 4 homologues has an obvious centromeric band. Autosomes 5 to 7 have distinct proximal and fainter centromeric C-bands. Few of the microchromosomes possess clear C-bands.

Alisterus scapularis (Fig. 4). — The distinctive karyotype of this species comprises 76 chromosomes with eight pairs of medium-sized autosomal macrochromosomes. Apart from pair 8, which has minute short arms, the remaining macrochromosomes range from acrocentrics to metacentrics. The Z-chromosome is third in size and submetacentric as is the slightly smaller W-chromosome. Prominent C-bands (Fig. 5) are centromeric on all the autosomal macrochromosomes and on many of the microchromosomes. No bands are apparent on the Z-chromosome but the W-chromosome has three distinct bands, one near the centromere and one near each of the telomeres.

Platycercus elegans (Fig. 7). — Its diploid number of 68 comprises six pairs of autosomal macrochromosomes, the sex-chromosomes, and 54 telocentric microchromosomes. Autosomes 1, 4, 5, and 6 are acrocentric while 2 and 3 are metacentric. Chromosomes 1 to 3 are similar in size, as are 4 to 6. In this species, the submetacentric Z-chromosome is fifth or sixth in size and the W-chromosome is a telocentric microchromosome. Most chromosomes possess centromeric C-bands (Fig. 6a). The Z-chromosome, however, lacks any obvious C-band, while autosomes 4 and 5 have additional distal C-bands on their long arms.
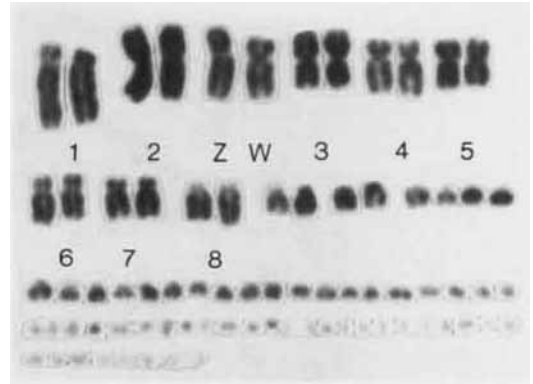
Psephotus varius (Fig. 8). — Apart from its lower diploid number of 66, the karyotype of this species is very similar to that of the rosella, *Platycercus elegans*. Autosome 6 displays a proximal secondary constriction on the long arm which is not apparent in the rosella. The W-chromosome here is a telocentric medium-sized element.

Agapornis roseicollis (Fig. 9). — The unusual karyotype of this species comprises only 46 chromosomes, of which 22 are macrochromosomes. Although pair 5 resembles the Z-chromosome in the previous four species, the sex pair cannot be identified because only a male was examined. Chromosomes 1 to 7 are biarmed, while 8 to 11 and the microchromosomes are telocentric.

Trichoglossus haematodus (Fig. 10). — This species has a low diploid number of only 58, with seven pairs of autosomal macrochromosomes and a metacentric microchromosome pair intermediate in size between macro- and microchromosomes. Autosomes 1, 2, 4, 5, 6 and the Z-chromosome display a similar morphology to their counterparts in *Psephotus varius* and *Platycercus elegans*. Autosome 3 is acrocentric in *Trichoglossus* and smaller than its metacentric counterpart in *Platycercus* and *Psephotus*. Sub-metacentric macrochromosome 7 has no obvious counterpart in either *Platycercus* or *Psephotus*. The W-chromosome is sub-metacentric and intermediate in size between autosomes 7 and 8.

Lorius hypoinochrous (Fig. 11). — A decrease in the diploid number to 54 and two additional pairs of metacentric microchromosomes are the only features which distinguish the karyotype of this species from that of *Trichoglossus haematodus*.
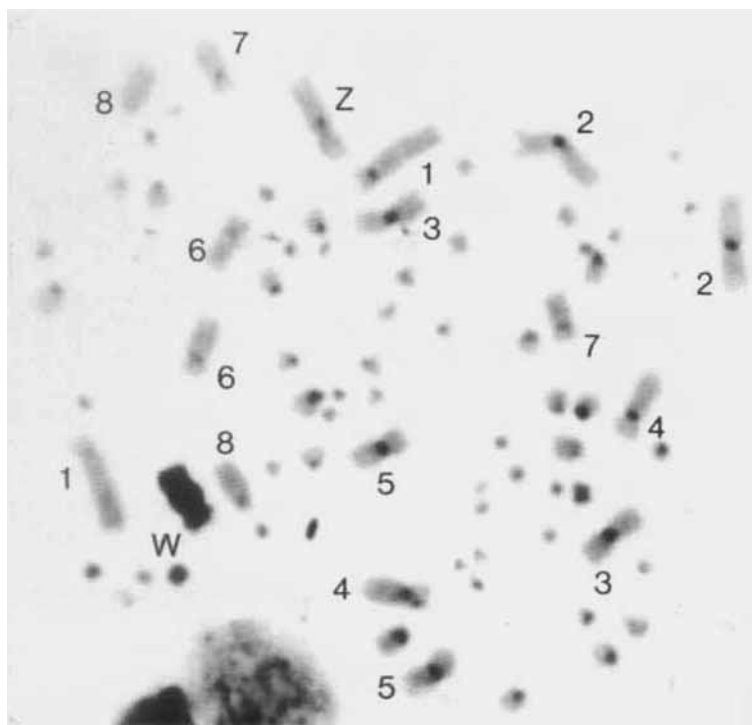
Fig. 5. C-banded metaphase spread of female Australian King Parrot (*Alisterus scapularis*).

Discussion

Sex-chromosomes and heterochromatin variation

Very little is known of the patterns of heterochromatin distribution amongst the Psittaciformes. Outside the present study, C-band information has only been gathered for five species of *Aratinga* (DE LUCCA 1984), *Forpus xanthoptergius* (DE LUCCA 1983; DE LUCCA and DE MARCO 1983), and for the W-chromosome in three species of *Amazona* (MENGDEN 1981), all of which are South American. Nevertheless, the available data indicate that changes in both the quantity and distribution of heterochromatin have played a significant role in chromosomal evolution in this order.

Within the cockatoos, *Cacatua roseicapilla* and *C. galerita* display contrasting patterns in the prominence of centromeric and interstitial C-bands on the macrochromosomes. In *C. galerita*, the more prominent bands are centromeric while in *C. roseicapilla* they are interstitial. This pattern is also found on the Z-chromosomes. *Nymphicus hollan-*

dicus differs in having both faint interstitial and centromeric bands. The significance of this variation is not known because no obvious link between C-band pattern and chromosomal morphology could be established. Autosomes 2 and 3 in *C. roseicapilla* are acrocentric and lack the interstitial C-bands found on the remaining telocentric macrochromosomes. It is argued below that these acrocentric chromosomes are the result of macro-microchromosome fusions and so the question arises as to whether the lack of interstitial C-bands predisposed these chromosomes to fusion or if the bands were lost during or after fusion events. Apart from this anomaly, it is of interest that all the macrochromosomes in the three cockatoos display a single-species specific C-banding pattern.

Interstitial C-bands appear to characterize the cacactuine karyotype. In all other psittaciform genera that have been examined — *Alisterus*, *Platycercus* (this study), *Aratinga* (DE LUCCA 1984) and *Forpus* (DE LUCCA 1983; DE LUCCA and DE MARCO 1983) — C-bands are confined to the centromeric regions of the macrochromosomes and microchromosomes.
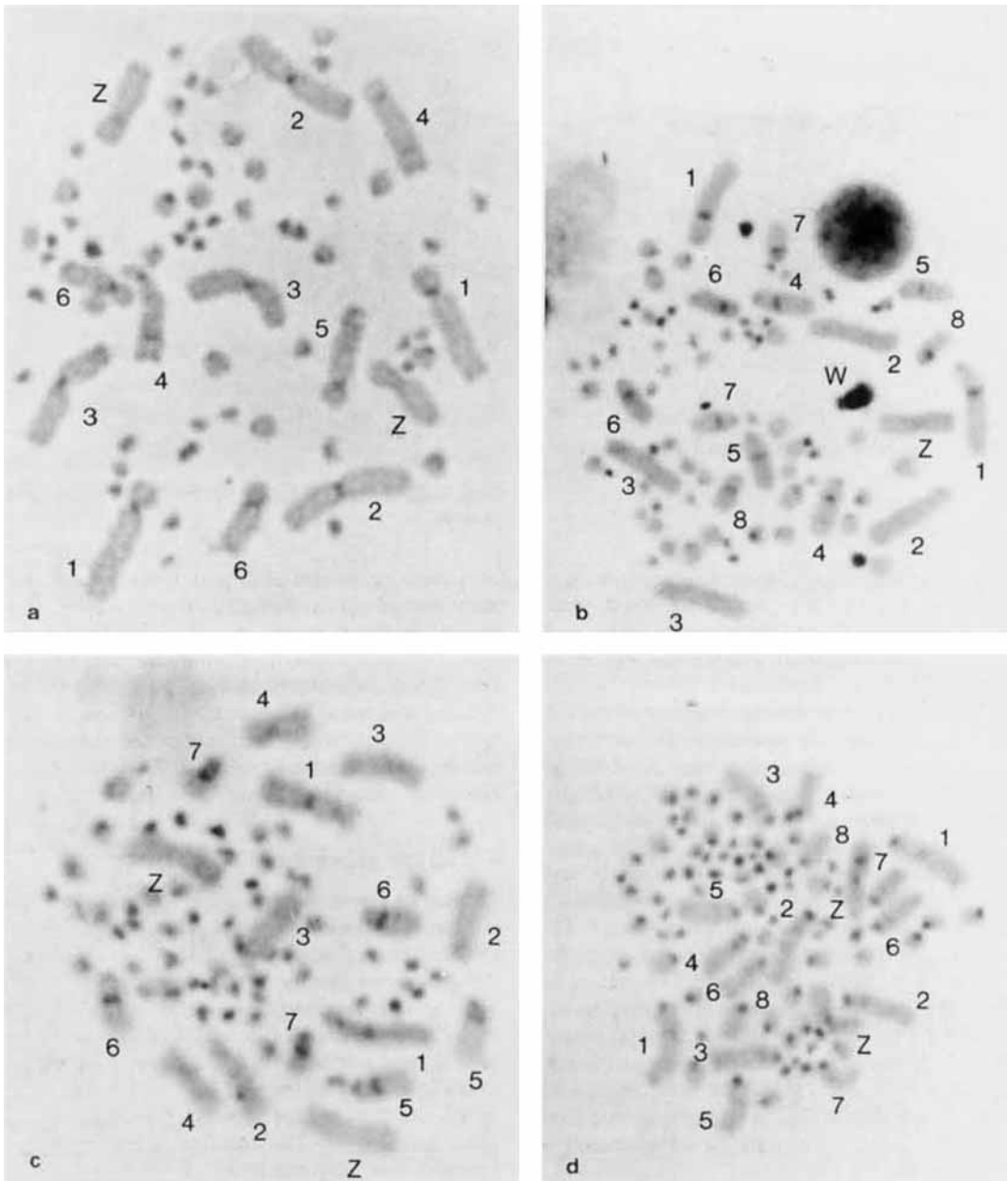
Fig. 6a–d. C-banded metaphase spreads. **a** male Crimson Rosella (*Platycercus elegans*), **b** female Galah (*Cacatua roseicapilla*), **c** male Cockatiel (*Nymphicus hollandicus*), **d** male Sulphur-crested Cockatoo (*Cacatua galerita*). One of the autosome 5 homologues is missing from the cell of the Crimson Rosella.

The Z-chromosome appears to be conserved amongst the Psittaciformes as it is similar in size and metacentric in all species examined, except in the hanging parrot, *Loriculus,* where it is telocentric (RAY-CHAUDHURI 1969). Although its morphology may be conserved, its C-band pattern is more variable. In *Cacatua galerita,* for example, the male examined was polymorphic for the presence/ab-
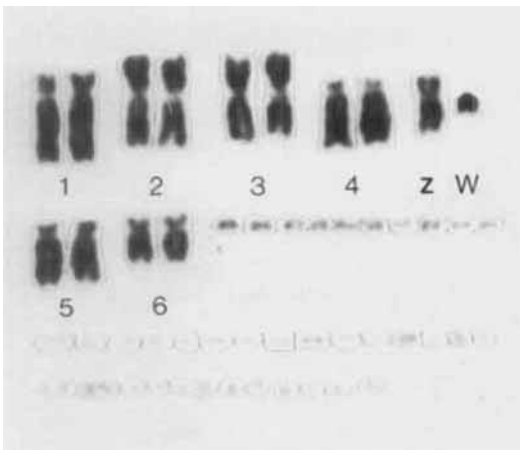
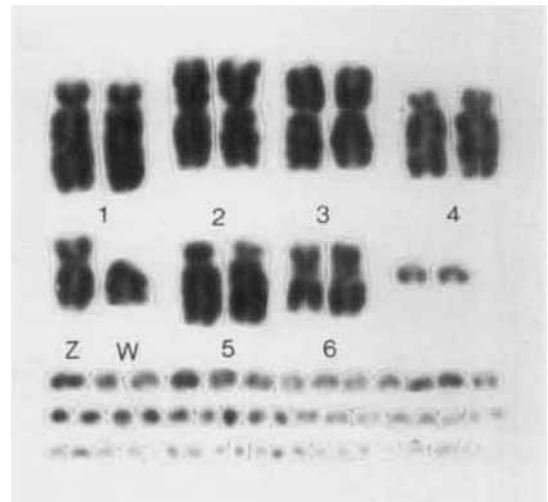**Fig. 7.** Karyotype of female Crimson Rosella (*Platycercus elegans*).

Fig. 8. Karyotype of female Mulga Parrot (*Psephotus varius*).

sence of an interstitial C-band. In other species, the Z-chromosome can also be distinguished readily from the autosomal macrochromosomes by its C-band pattern. In *Alisterus, Platycercus, Forpus* and probably *Aratinga*, centromeric C-bands are missing from the Z-chromosomes whereas, in the macro-autosomes, they are prominent. The situation is more complex in the cockatoos because of the variation in autosomal C-bands, but again, the Z-chromosomes display a C-band pattern that contrasts with that in the macro-autosomes. Similar patterns of Z-chromosome banding are also shown in estrildine finches, Passeridae (CHRISTIDIS 1986a, b). Here, the Z-chromosome usually displays a C-band pattern opposite to that on the macro-autosomes whether they possess centromeric C-bands or not. Given that the W-chromosome is believed to have evolved from the Z-chromosome through amplification of highly repeated DNA sequences (SINGH et al. 1976; MENGDEN 1981), is it possible that this unique behaviour of the Z-chromosome was a precursor for the origin of a highly differentiated W-chromosome?

In morphology and C-band pattern, the W-chromosome is much more variable within the Psittaciformes. It ranges in size from a macrochromosome to a microchromosome. In *Forpus* (DE LUCCA and DE MARCO 1983) and *Aratinga* (DE LUCCA 1984), the W-chromosome is largely C-positive while MENGDEN (1981) reported light and dark C-bands in the W-chromosomes of three species of *Amazona*. The W-chromosomes of *Cacatua roseicapilla* and *Alisterus scapularis* examined here also display

an alternating pattern of C-positive and intermediately stained bands. Nevertheless, the centromeric regions in these genera are characterized by the lighter bands, whereas in *Amazona* they are the darkest. These preliminary observations indicate that detailed analysis of highly repeated DNA sequences in the Psittaciformes, particularly the cockatoos, will be useful in elucidating the patterns and significance of chromosomal evolution in this order.

Karyotypic changes and relationships

Within the Psittaciformes, there is a sharp distinction between the karyotypic organization of the Cacatuidae (e.g., *Cacatua, Nymphicus* and *Calyptorhynchus*) and that of the Loriidae (e.g., *Lorius, Trichoglossus*) and most Psittacidae (e.g., *Platycercus, Psephotus* and *Psittacula*). Cockatoos have a high diploid number (72–80) composed largely of telocentric chromosomes. Most Psittacidae examined and the Loriidae have, in contrast, lower diploid numbers (60–72) with five to seven pairs of biarmed macrochromosomes. It is a distinction strongly supported by protein electrophoretic data (OVENDEN et al. 1987; CHRISTIDIS et al., submitted). The relationship between the cacatuine karyotype and those of the Psittacidae and Loriidae is difficult to interpret without detailed G-banding data. Therefore, we treat with caution the conclusion of VAN DONGEN and DE BOER (1984) that the karyotypes of the parrot genera *Loriculus* and *Amazona* are closely allied to those of the cockatoos.

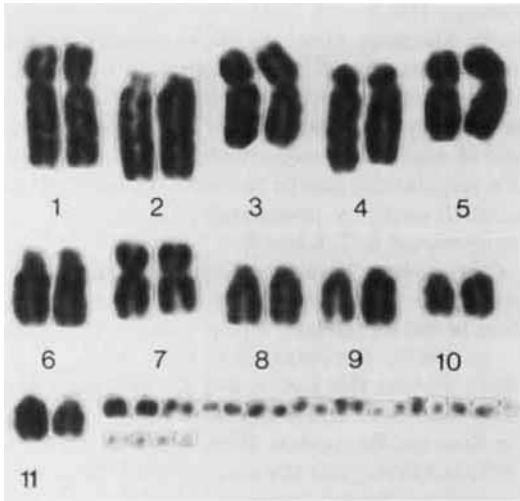Three different karyotypes have now been ob-

Fig. 9. Karyotype of male Peach-faced Lovebird (*Agapornis roseicollis*).

Fig. 10. Karyotype of male Rainbow Lorikeet (*Trichoglossus haematodus*). Inset shows sex-chromosomes of a female.

served in *Cacatua*. *C. galerita* (VAN DONGEN and DE BOER 1984; present study), *C. sanguinea,* and *C. goffini* (SCHMUTZ and PRUS 1987) have a similar karyotype, which lacks any biarmed autosomes. *C. moluccensis* (SCHMUTZ and PRUS 1987) has a single pair of acrocentric macrochromosomes; and *C. roseicapilla* (present study) has two such pairs. There is additional variation in diploid number but in some instances this is probably an artifact of preparation. Nevertheless, *C. roseicapilla* appears to have four fewer microchromosomes than *C. galerita* in both C-banded and unbanded preparations (present study). Taking this into account with the larger size of acrocentric autosomes 2 and 3 in *C. roseicapilla* relative to their telocentric counterparts in *C. galerita* leads us to conclude that micromacrochromosome fusions probably account for the larger acrocentrics in *C. roseicapilla*. In *C. moluccensis* (SCHMUTZ and PRUS 1987) a similar rearrangement has probably occurred between autosome 1 and a microchromosome.

Calyptorhynchus banksii (as *magnificus*) (VAN DONGEN and DE BOER 1984) has no biarmed macrochromosomes and otherwise resembles *C. galerita* in its karyotype; the arm ratio of the Z-chromosome is more submetacentric, however, in *Calyptorhynchus*. Given the large genetic divergence between *Cacutua galerita* and *Calyptorhynchus* (CHRISTIDIS et al. 1991), it is likely that a karyotype lacking biarmed autosomes is ancestral for the Cacatuidae.

Fusions between macrochromosomes and microchromosomes may also account for the derivation

of the karyotype of the Palm Cockatoo, *Probosciger aterrimus*, which has four pairs of acrocentric macrochromosomes and a lower diploid number than *Calyptorhynchus* (VAN DONGEN and DE BOER 1984). Such fusions in the Cacatuidae have probably been derived independently among the genera. *Nymphicus*, however, may share the same fusions as *C. roseicapilla* in that autosomes 2 and 3 are both acrocentric. In *Nymphicus*, a fusion involving a telocentric in the autosome 4 to 6 size series with another in the autosome 7 to 8 size series could also account for an additional sub-metacentric and lack of two telocentric macrochromosomes. Morphological data (D. HOMBERGER and R. SCHODDE, unpubl.) suggest a link between *Nymphicus* and *C. roseicapilla* and thereby support the karyotypic interpretation. As *C. roseicapilla* is sometimes separated generically in *Eolophus* (FORSHAW 1973), links between *Cacatua, Eolophus* and *Nymphicus* need further investigation.

As recognized by MORONY et al. (1975), the Psittacidae are a much more diverse assemblage than the Cacatuidae and Loriidae and there is doubt as to whether they are monophyletic (SMITH 1975; HOMBERGER 1980). Available chromosomal data certainly reveals significant variation (summarized in CHRISTIDIS 1990). One psittacid pattern comprising at least three karyotypes is particularly widespread, occurring in Australian *Platycercus* and *Psephotus* (present study), African *Psittacus* (DE BOER and BELTERMAN 1980) and Asian *Psittacula* (RAY-CHAUDHURI et al. 1969). *Platycercus, Psephotus* and *Psittacula cyanocephala* possess six
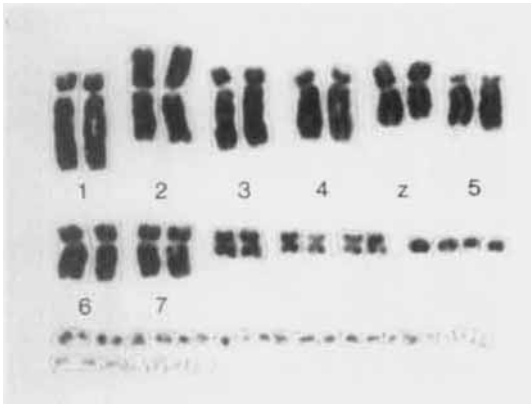
Fig. 11. Karyotype of male Western Lory (*Lorius hypo-inochrous*).

pairs of autosomal macrochromosomes, two of which are metacentric. In *Psittacula alexandri*, *Psittacula krameri* and *Psittacus*, one of the metacentrics is replaced by two telocentric chromosomes. In *Psittacus*, which represents the third karyotype, one of these telocentrics has undergone a further rearrangement to become acrocentric. The karyotypes of the lorikeet genera *Lorius* and *Trichoglossus* have seven pairs of autosomal macrochromosomes, only one pair of which are metacentric. Pairs 6 and 7, however, are acrocentric in comparison to their telocentric form in *Psittacula krameri* and *P. alexandri*. If the similar-shaped chromosomes in these two lorikeets are homologous with their counterparts in *Psittacula*, the ancestral karyotype for all these lineages most likely possessed one metacentric macrochromosome and two pairs of smaller telocentrics in a complement of seven autosomal macrochromosomes.

According to this implicit interpretation, the fused metacentric would have arisen twice: once in *Platycercus-Psephotus*, which are closely related on morphological (HOMBERGER 1980) and biochemical (CHRISTIDIS et al. 1991) criteria, and again independently in *Psittacula cyanocephala*. A diagram illustrating these putative chromosomal changes is given in Fig. 12. Although these conclusions still need to be tested by G-banding, it seems likely the karyotypes shared by *Platycercus-Psephotus*, *Psittacula* and *Psittacus* represent an ancestral condition, given that these genera are unrelated (HOMBERGER 1980; CHRISTIDIS et al 1991).

It is more difficult to relate the known karyotypes of other parrot genera to the presumed ancestral type (see Fig. 12). Two species of *Ara* (VAN DONGEN and DE BOER 1984) and five species of

Aratinga (DE LUCCA 1984)—all members of the South American arine assemblage—share almost identical karyotypes, which appear to bear some similarity to the ancestral type but differ in the morphology of chromosomes 6, 7 and 8. The karyotype of the New Guinean Vulturine Parrot *Psittrichas fulgidus* can also be derived from that of *Psittacula krameri* by postulating rearrangements to chromosomes 6, 7, 8 and 9.

Other genera have much more derived karyotypes, each apparently unique to them. These are those of the Budgerigar, *Melopsittacus*, (ROTHFELS et al. 1963), *Loriculus* (RAY-CHAUDHURI et al. 1969), *Forpus* (DE LUCCA and DE MARCO 1983), *Nestor* (DE BOER and BELTERMAN 1980), *Amazona* (DE BOER and BELTERMAN 1980; SCHMUTZ and PRUS 1987) and *Brotogeris* (DE LUCCA 1974). The karyotypes of two further genera reported here are also highly derived and unique. The Australo-Papuan King Parrot, *Alisterus*, has medium-sized macrochromosomes, which do not appear to have any obvious homologues amongst the karyotypes of *Platycercus* and *Psittacula*. These data do not support the commonly held view that *Psittacula* and *Alisterus* are closely allied (SMITH 1975; HOMBERGER 1980). SMITH and HOMBERGER (11. cc.) also align *Agapornis* with *Alisterus* and *Psittacula*; but on karyotype, these three genera represent the most widely divergent lineages within the Psittacidae. Biochemical data (CHRISTIDIS et al. 1991) suggest a link instead between *Alisterus* and *Platycercus-Psephotus*. Detailed G-band comparisons between their karyotypes are obviously needed to determine how their substantial chromosomal differences have accumulated.

Agapornis is not readily linked to other genera on the basis of its proteins (CHRISTIDIS et al. 1991). Its karyotype is also so distinct as to obscure any clues to possible relationships. The number of macrochromosomes (11 pairs) is higher than that of other Psittaciformes, and there are only 12 pairs of small microchromosomes. This suggests that tandem fusions among the larger microchromosomes has led to an increase in the number of macrochromosomes with concomitant lowering of the diploid number. CHRISTIDIS (1983) reported a similar case in the estrildine finches. The typical estrildine karyotype has a diploid number of 76 with six pairs of autosomal macrochromosomes. That of *Pytilia phoenicoptera*, which has 11 pairs of autosomal macrochromosomes and a diploid number of 56, is thought to have evolved through a series of tandem fusions among microchromosomes.

As indicated above, karyotypes within the lori-
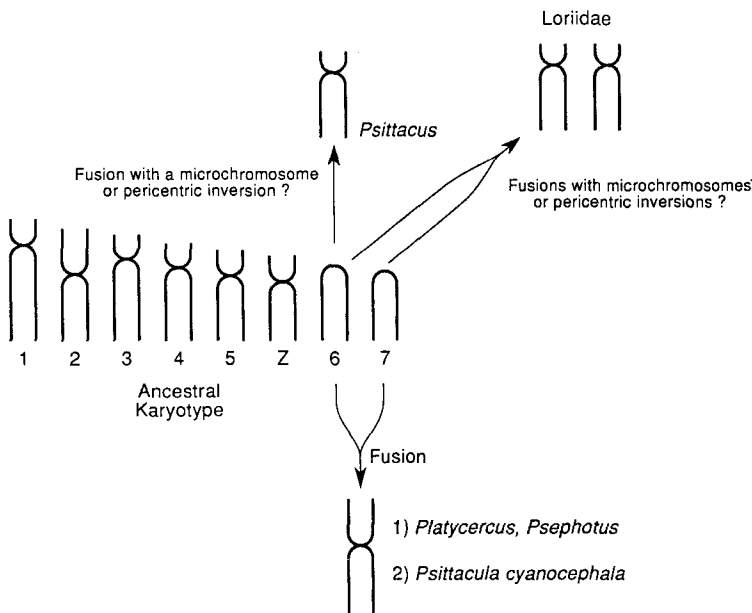
Fig. 12. Presumed chromosomal changes involving autosomes 6 and 7 amongst *Psittacula, Psittacus, Platycercus, Psephotus,* and the lorikeets. It is assumed that the karyotype of *Psittacula alexandri* and *P. krameri* is ancestral for these lineages (see discussion).

keets closely resemble the presumed ancestral type as typified by *Psittacula* (Fig. 12). This is consistent with the conclusions of CHRISTIDIS et al. (1991) that the loriines are of recent derivation from within the psittacid assemblage. The two genera of lorikeets examined here differ in the number of metacentric microchromosomes, *Trichoglossus* having only one pair and *Lorius* three. These differences probably result from fusions among the microchromosomes as *Lorius* has four chromosomes less than *Trichoglossus*.

The results presented here and in other studies quoted indicate that complex fusion-fission changes have played a prominent role in the evolution of karyotypic diversity in the cockatoos, parrots and lorikeets. As more species of birds are examined cytologically, such major karyotypic repatternings may prove to be common. How and why they accumulate is still a matter of speculation but an understanding of them is essential to formulating theories on the significance of chromosomal evolution.

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