Chromosome studies of 8 species of parrots of the families Cacatuidae and Psittacidae (Aves: Psittaciformes)

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Abstract

The karyotypes of 7 species of Psittaciformes new to cytology are described: Cacatua galerita, Calyptorhynchus magnificus and Probosciger aterrimus of the Cacatuidae, and Ara macao, A. ararauna, Amazona viridigenalis and Psittrichas fulgidens of the Psittacidae. For reasons of comparison the karyotype of Melopsittacus undulatus is also described. These karyotypes are compared to 8 psittaciform karyotypes previously recorded. There is a remarkable heterogeneity of karyotypes in the Psittaciformes. Nevertheless, it seems possible to recognize Cacatua, Calyptorhynchus and probably also Probosciger (Cacatuidae) by their karyotypes as a clearly related group. The karyotypes of these cacatuids also bear some resemblance to that of Loriculus (Psittacidae). The psittacid genera Amazona, Ara, Nestor, Melopsittacus, Psittacula, Psittacus and Psittrichas are karyologically heterogeneous, but their karyotypes show certain relationships. The karyotype of Brotogeris is very different from those of other psittacids.

Introduction

Although parrots are easily recognizable, and although there is no doubt as to which species belong within the Psittaciformes, there are many different opinions with regard to the classification within the order. Not only in their anatomy and morphology but also in their molecular biology do the parrots form a rather heterogeneous group. Sibley (1960) found extensive variation in the eggwhite protein patterns of six genera. Mainardi (1962) compared red-cell antigens and observed great diversity, just as Gysels (1964) who studied eye-lens and muscle proteins.

This heterogeneity gave rise to widely diverging classifications. Verheyen (1956) assumed five families of Psittaciformes. Glenny (1957), basing his classification on the variation in the structure of the carotid artery, concluded to the existence of only one family with nine subfamilies. Von Boetticher (1964) also recognized a single family, but described only seven subfamilies. The latter classification was adopted by Kolar and Koehler (1975) who, however, remarked that the position of several forms, such as *Nymphicus hollandicus*, is still rather uncertain. The classification used by the American Museum of Natural History (Morony *et al.*, 1975), which is followed here, includes three families with six subfamilies.

In contrast to several other avian orders in which very uniform karyotypes are found, the Psittaciformes exhibit a rather heterogeneous karyotypic morphology. The karyotypes of nine species of the order have been previously studied in some detail, viz. Melopsittacus undulatus (Van Brink, 1959; Rothfels et al., 1963; Ohno et al., 1964; De Lucca, 1977), Psittacula krameri, P. cyanocephala and P. alexandri (Ray-Chaudhuri et al., 1969; the latter species also by Kaul & Ansari, 1983), Nestor notabilis, Amazona ochrocephala and Psittacus erithacus (De Boer & Belterman, 1980) and Brotogeris sanctithomae (De Lucca, 1974). In addition, De Lucca (1981) studied five species of *Aratinga* and one of *Forpus*, but reported no details of karyotypic structure.

Generally, where structural differences in karyotypes exist between various species of an order it is possible to draw hypotheses as to their phylogenetic relationships. The psittaciform species studied to date have demonstrated that clear karyotypic differences exist in the order. However, since the number of species whose karyotype has been analysed is very small, the present authors believed it of importance to extend the basic karyological knowledge of the parrots. In this context they describe the somatic chromosome complements of seven new species: Cacatua galerita, Calyptorhynchus magnificus and Probosciger aterrimus of the family Cacatuidae and Amazona viridigenalis, Ara ararauna, A. macao and Psittrichas fulgidens of the family Psittacidae. For reasons of comparison the karyotype of Melopsittacus undulatus is added to this series. On the basis of this material and previously described karyotypes, the karyological relationships of the Psittaciformes are discussed.

Material and methods

Chromosome studies were carried out on the following animals: 3 male and 1 female scarlet macaws (Ara macao), 1 female blue-and-yellow macaw (Ara ararauna), 2 male and 1 female sulphur-crested cockatoos (Cacatua galerita), 1 female black cockatoo (Calyptorhynchus magnificus), 2 male palm cockatoos (Probosciger aterrimus), 1 female vulturine parrot (Psittrichas fulgidens), 2 female blunt-tailed parrots (Amazona viridigenalis) and 1 female budgerigar (Melopsittacus undulatus). The animals were obtained from the Rotterdam Zoological and Botanical Gardens except the blunttailed parrots, which came from a private collection. All except the budgerigar were wild-caught.

Chromosome preparations were obtained from whole-blood cultures according to slightly modified techniques of De Boer and Belterman (1980). Cultures were prepared from 0.5 ml heparinized venous blood, 5.0 ml of RPMI 1640 culture medium and 1.0 ml of bovine serum (calf). Usually no antibiotics were added. Whenever possible more than one culture was prepared from each animal, varying several factors in the culture mixture, particularly the addition of either phytohaemagglutinin (0.10 ml per culture), pokeweed mitogen (0.15 ml)per culture), or both. In most cases the results of phytohaemagglutinin as a mitotic stimulator were better than those with pokeweed mitogen, provided that no excessive agglutination took place.

Results

Results are given per species below. In several parrots there is no sharply demarcated boundary between macrochromosomes and microchromosomes. In the karyotypes presented here the chromosome pairs are generally arranged in the following groups: biarmed macrochromosomes, acrocentric macrochromosomes, small-to-minute biarmed chromosomes and small-to-minute acrocentrics (including all elements of which the centromeric position cannot be discerned because of their minute size). When appropriate, arm ratios (A.R., length of long arm divided by that of the short arm) of individual chromosome pairs are given.

Amazona viridigenalis (Cassin, 1853) (blunt-tailed parrot; Psittacidae; Fig. 1)

The diploid number of Amazona viridigenalis is approximately 72. The karyotype of Figure 1 does



Fig. 1. Representative karyogram of female Amazona viridigenalis (bar represents $5 \mu m$; all other illustrations same magnification).

not follow the numbering system proposed for A. ochrocephala by De Boer and Belterman (1980), because this would lead to an inconstistency in numbering the chromosomes of other parrots newly described here. Pair 1 consists of two large acrocentrics; it is placed separately from the other acrocentric pairs for reasons given in the discussion. Pairs 2, 3 and 4 are subtelocentric (A.R. 4.0, 4.2 and 4.5). Pairs 5, 6 and 7 are acrocentrics of medium size. Pair 8 consists of the only small metacentric elements in the karyotype (A.R. 1.2). The remaining autosomes (approximately 54; the diploid number is ca 72) are of small to minute size and acrocentric in as far as their centromeric position can be determined. The Z-chromosome is metacentric (A.R. 1.1) and about the size of pair 4. The W-chromosome is metacentric as well (A.R. 1.2) and somewhat larger than the chromosomes of pair 8.

Ara macao (L., 1758) (scarlet macaw; Psittacidae; Fig. 2)

The diploid chromosome number of Ara macao is estimated to be 70. Pair 1 consists of clearly distinguishable large metacentrics (A.R. 1.1). Pair 2 is of almost the same size, but subtelocentric (A.R. 4.0). Pairs 3 and 4 are subtelocentrics (A.R. 3.8 and 6.7). Pairs 5 and 6 are subtelocentrics (A.R. 4.7 and 4.3), clearly smaller than those of pairs 3 and 4. There are three pairs of small biarmed chromosomes: pairs 7, 8 and 9 (A.R. 1.7, 1.3 and



Fig. 2. Representative karyogram of female Ara macao.

1.0). The remaining chromosomes (approximately 50) are small acrocentrics or of uncertain centromeric position. The elements of pair 10 are distinguishable because of their larger size. The Z-chromosome is almost the size of pair 4. It is metacentric (A.R. 1.3) and easily identifiable. The W is a small metacentric (A.R. 1.0) of the size of pair 8.

Ara ararauna (L., 1758) (blue-and-yellow macaw; Psittacidae)

In as far as detectable the karyotype of Ara ararauna is identical to that of A. macao.

Cacatua galerita (Latham, 1790) (sulphur-crested cockatoo; Cacatuidae; Fig. 3)

The diploid chromosome number of *Cacatua* galerita is considerably higher than those of the above species: approximately 82. Apart from the sex chromosomes the karyotype exclusively consists of acrocentrics. The first 8 pairs of autosomes are clearly larger than the remaining ca 64 small to minute chromosomes. The Z-chromosome is easily identifiable, metacentric (A.R. 1.0) and only slightly smaller than the largest autosomes. The W is metacentric as well (A.R. 1.2 and about the size of the eighth pair of autosomes.



Fig. 3. Representative karyogram of female Cacatua galerita.

Calyptorhynchus magnificus (Shaw, 1790) (black cockatoo; Cacatuidae; Fig. 4)

The karyotype of Calyptorhynchus magnificus shows clear similarities with that of Cacatua galerita. The diploid number of the karyogram shown (Fig. 4) is somewhat lower (72), but in the other metaphase plates counts up to 78 were made. All autosomes are acrocentric and differ only from those of C. galerita in the somewhat smaller size of pair 8. Unlike the situation in C. galerita the Zchromosome is submetacentric (A.R. 2.0). It is almost as large as the largest autosomes. The W is also metacentric (A.R. 1.2).



Fig. 4. Representative karyogram of female Calyptorhynchus magnificus.

Melopsittacus undulatus (Shaw, 1805) (budgerigar; Psittacidae; Fig. 5)

The diploid number of *Melopsittacus undulatus* is low: approximately 62. Of all parrots studied to date it has the highest number of biarmed chromosomes. Pair 1 consists of metacentrics (A.R. 1.1), which are, however, considerably smaller than the metacentrics of pair 1 in many other parrots. Pairs 2, 3 and 4 are subtelocentric (A.R. 5.2, 3.8 and 6.0). Pairs 5 and 6 are clearly smaller and submetacentric (A.R. 1.7) and subtelocentric (A.R. 3.0) respectively. Pair 7 is the only medium-sized pair of acrocent-



Fig. 5. Representative karyogram of female Melopsittacus undulatus.

rics. Pairs 8 to 11 are small to minute metacentrics. Pair 12 consists of small acrocentrics which are clearly distinguishable from the even smaller remaining 34 microchromosomes. The Z-chromosome is a submetacentric (A.R. 1.7) somewhat smaller than pair 4. The W is submetacentric (A.R. 2.0).

Probosciger aterrimus (Gmelin, 1788) (palm cockatoo; Cacatuidae; Fig. 6)

The diploid number of *Probosciger aterrimus* appears to be somewhat lower than that of the other



Fig. 6. Representative karyogram of male Probosciger aterrimus. ZZ-chromosome pair chosen tentatively.

cockatoos: counts of over 74 were not made. Although the gross morphology of the karyotype is similar to that of *Cacatua galerita* and *Calyptorhynchus magnificus*, it differs because of the presence of small but distinct short arms in the larger pairs of autosomes (pairs 1-4; A.R. 4.0, 5.0, 5.0 and 9.0). As far as centromeric positions can be identified, the remaining autosomes are acrocentric. Although no female specimens could be studied, in Figure 6 a pair of metacentric elements (A.R. 1.2) is tentatively chosen as the Z-chromosome pair since all other parrots studied to date possess metacentric or submetacentric Z-chromosomes of comparable size (intermediate in length between pairs 3 and 4).

Psittrichas fulgidens (Lesson, 1830) (vulturine parrot; Psittacidae; Fig. 7)

The diploid number of *Psittrichas fulgidens* is approximately 72. Pair 1 consists of large meta-



Fig. 7. Representative karyogram of female Psittrichas fulgidens.

centrics (A.R. 1.1) of the same size as pair 2. Pairs 2, 3 and 4 are subtelocentric (A.R. 5.2, 3.8 and 6.0). Pairs 5, 6 and 7 are smaller subtelocentrics. There are no medium-sized acrocentrics. Only one pair of small chromosomes is biarmed (pair 8; A.R. 1.0). The remaining 64 chromosomes are of small to minute size, acrocentric or of uncertain centromeric position. The Z-chromosome is submetacentric (A.R. 1.8) and of the same size as pair 4. The W is a small metacentric chromosome indistinguishable from pair 8.

Discussion

Of the seven newly described parrot karyotypes only one is clearly identical to a previously reported karyotype: that of Amazona viridigenalis, which is indistinguishable from that of A. ochrocephala (De Boer & Belterman, 1980). However, the chromosome complements of Calyptorhynchus magnificus and Cacatua galerita, which except for possible differences in the diploid numbers and in the arm ratios of the Z-chromosomes are identical to each other, very much resemble that of Loriculus vernalis (Ray-Chaudhuri et al., 1969). Like both cockatoos, the latter species was shown to possess a karyotype entirely made up of acrocentrics with the exception of a single pair of metacentrics. In the cockatoos these metacentrics proved to be the Zchromosomes, which are (sub)metacentric and also in all parrots studied to date. Ray-Chaudhuri et al. (1969) studied only a male specimen of Loriculus vernalis and Ray-Chaudhuri (1973) suggested one of the medium-sized pairs of acrocentrics to represent the Z-chromosomes, a suggestion followed by De Boer and Belterman (1980). Nevertheless it also seems possible that the only pair of metacentrics are the Z-chromosomes, although in L. vernalis these are somewhat larger than the Zs of the other parrot species. In that case the karyotypes of Loriculus vernalis (Psittacidae) and Calyptorhynchus magnificus and Cacatua galerita (both Cacatuidae) would be almost identical. The karyotype of Probosciger aterrimus (Cacatuidae) is similar to those of the other two cockatoos, except for the presence of minute short arms in the first four pairs of autosomes. Thus, the possible homology between these subtelocentrics and the largest acrocentrics of Calyptorhynchus and Cacatua needs to be confirmed. Karyotypes with a morphology comparable to those of both species of Ara (arauna and macao) and Psittrichas fulgidens have not been reported so far. The karyotype of Melopsittacus undulatus described here is identical to those recorded for this species earlier (Van Brink, 1959; Rothfels et al., 1963; Ohno et al., 1964; De Lucca, 1977).

Five additional different types of chromosome complements have been described in the literature, those of *Psittacula krameri* and *P. alexandri* (identical to each other; Ray-Chaudhuri *et al.*, 1969), *Psittacula cyanocephala* (Ray-Chaudhuri *et al.*, 1969), *Nestor notabilis* (De Boer & Belterman,



1980), Brotogeris sanctithomae (De Lucca, 1974) and Psittacus erithacus (De Boer & Belterman, 1980). Thus, among the 16 parrot species studied to date at least 10 different karyotypes are found, indicating a remarkable karyological heterogeneity in the Psittaciformes (in these figures the data of five species of *Aratinga* and one of *Forpus* studied by de Lucca, 1981, are not included since neither karyotypic descriptions nor illustrations of these are available).

In Figure 8 an attempt is made to summarize the karyology of the parrots. As indicated above the

karyotypes of the three species of Cacatuidae (Calyptorhynchus magnificus, Cacatua galerita and Probosciger aterrimus) are probably closely related and there is a possibility that Loriculus vernalis also has affinities to them. In spite of their heterogeneity, some common characteristics can be found within the karyotypes of all Psittacidae studied except Loriculus and Brotogeris. All of them possess three pairs of large subtelocentric chromosomes (pairs 2, 3 and 4). In addition, in all except the two species of Amazona, the first pair is made up of large metacentrics. These metacentrics are of the same size or slightly smaller than the elements of pair 2. Only in Melopsittacus undulatus are they significantly smaller so that at most partial homology with pair 1 of the others exists. In Amazona ochrocephala and A. viridigenalis the metacentrics of pair 1 are absent. Instead an additional pair of acrocentrics of somewhat shorter length is found. Possible (partial) homology between these acrocentrics and the metacentrics of the others need to be confirmed. A pair of small metacentric chromosomes (pair 8) is found in Amazona (ochrocephala and viridigenalis), Nestor notabilis, Melopsittacus undulatus, Ara (ararauna and macao) and Psittrichas fulgidens. In the illustrations of Psittacula (krameri, alexandri and cyanocephala) of Ray-Chaudhuri et al. (1969) this pair is not detectable. This however, may be an effect of the quality of their material. In Psittacus erithacus this pair with certainty is absent.

Clear variation exists with respect to the remaining autosomes of the psittacids. In Amazona and Nestor notabilis (De Boer & Belterman, 1980) three pairs of medium-sized acrocentrics are found (pairs 5, 6 and 7). In Psittacula krameri and P. alexandri (Ray-Chaudhuri et al., 1969) there are only two such pairs (6 and 7) and one additional pair of

medium-sized subtelocentrics (pair 5). In P. cyanocephala (Ray-Chaudhuri et al., 1969) pairs 6 and 7 have possibly fused to form a pair of large metacentrics (pair '6/7' in Fig. 8). In Psittacus erithacus (De Boer & Belterman, 1980) there is one pair of medium-sized acrocentrics (pair 7) and two pairs of medium-sized subtelocentrics (pairs 5 and 6). In Melopsittacus undulatus the same situation is found. However, in this species there are three additional pairs of small to minute metacentrics (pairs 9, 10 and 11). Possibly this is a result of a reduction in the diploid number (60 in M. undulatus, 70-72 in most of the others) by fusions of microchromosomes. Ara ararauna and A. macao lack any medium-sized acrocentrics. Instead they possess two pairs of medium-sized subtelocentrics (pairs 5 and 6) like Psittacus erithacus and Melopsittacus undulatus, and one pair of medium-sized submetacentrics (pairs 7). Both species of Ara show an additional pair of small metacentrics (pair 9 of Ara, comparable to pair 11 of Melopsittacus). Psittrichas fulgidens, finally, like Ara has no medium-sized acrocentrics. Instead it possesses three pairs of medium-sized subtelocentrics (pairs 5, 6 and 7). It has no additional small metacentrics.

As shown in Figure 8 it is tempting to suggest a series of pericentric inversions and one fusion (in *Psittacula cyanocephala*) to be responsible for the decrease in the number of medium-sized acrocentrics in the psittacid species mentioned above, while fusions of microchromosomes may have caused the additional small metacentrics in *Melopsittacus* and *Ara*. The deviating structure of pair 1 in *Amazona* may be the result of pericentric inversion; for the smaller pair 1 of *Melopsittacus* presently no explanation can be given. Apart from these differences in macrochromosomes and small biarmed chromo-

Fig. 8. Schematic representation of the karyology of 14 species of Psittaciformes. The karyotypes of 5 species of Aratinga, one of Forpus and one of Brotogeris (De Lucca, 1974, 1981) are not included for reasons given in the text. For the karyotype of Loriculus vernalis see note 2. Solid lines indicate supposed chromosome homologies. Broken lines indicate possible homologies of chromosomes that may have undergone pericentric inversion or fusion. Of the microchromosomes only the largest and the smallest pairs are shown. Notes: (1) In the species marked with an asterisk (*) the chromosome numbering of the original publication has been changed;- (2) Because of the uncertainty about the structure of its sex chromosomes it is not clear whether or not the karyotype of Loriculus vernalis (Ray-Chaudhuri et al., 1969) could be of the same type as that of Cacatua galerita and Calyptorhynchus magnificus. The first sex chromosome pair in the idiogram is that of C. magnificus, the second that of C. galerita;- (3) The ZZ-chromosome pair of Probosciger aterrimus is chosen tentatively;- (4) Apart from the diploid number the main difference between the karyotype of Amazona and the other Psittacidae is the presence of an additional pair of large acrocentrics in the former instead of the metacentric pair 1 in the others. Therefore, these acrocentrics are tentatively placed as possibly (partly) homologous to pair 1 in the other species;- (5) The absence of the small metacentrics of pair 8 in Psittacula krameri, P. alexandri and P. cyanocephala is uncertain; - (6) The metacentrics of pair 1 of Melopsittacus undulatus are clearly smaller than those in the other species. Thus, their classification as possibly (partly) homologous to pair 1 of the others is tentative.

somes it should be mentioned that in Amazona and Nestor the largest microchromosomes are clearly larger than those in Psittacula, Psittacus, Melopsittacus, Ara and Psittrichas. Thus, the boundary between macro- and microchromosomes in the former two is much less clear than in the others. No explanation is found for this phenomenon, nor is there an explanation for the significantly lower diploid number of Nestor (60 instead of 70-72). The structures of the karyotypes suggest that this low chromosome number was derived independently from the lower number in Melopsittacus.

The structure of the karyotype of *Brotogeris* sanctithomae appears to be very different from the other psittacids studied. Therefore, and since De Lucca's (1974) illustration of the karyotype is of a very low magnification, currently no appropriate comparison with other species is possible.

Figure 9 shows one of the possible phylogenetic trees of the Psittaciformes based on the karyological data currently available. It should be stressed clearly that this tree is constructed on the basis of karyological data only, and that these data are extremely limited. The limitations concern not only the small number of species studied to date, but also the absence of sound information on interspecific chromosome homology. On the other hand, this preliminary tree clearly demonstrates the heterogeneity of the order, and the promising possibilities of reconstructing evolutionary pathways in the Psittaciformes on the basis of chromosomal data. To do this, however, detailed analyses of interspecific homologies on the basis of chromosome banding studies in many species are needed. Many of the uncertainties in the tree of Figure 9 may be elucidated by further investigations involving more sophisticated chromosome staining methods.

One of the most striking karyological findings to date is the possible relationship between Cacatua and Calyptorhynchus on the one hand (both of which are always classified as Cacatuidae, together with Probosciger and a variable number of the other genera) and Loriculus on the other. The latter has formerly been classified together with a variety of other genera. From the karyological point of view it might be of interest to note that Brereton (1963) allied Loriculus with Micropsitta, while Mudge (1902) included Micropsitta in his Cacatuinae. Although never expressed directly in a classification, this may point at a possible relationship between Loriculus and the cockatoos. This finding underlines the importance of collecting more karyological data on parrots, the taxonomy of which suffers greatly from a lack of conclusive informa-



Fig. 9. Possible phylogenetic relationships between the psittaciform species studied cytologically. In this tree the exact possition of *Psittacus erithacus* (either more closely related to *Melopsittacus* or to *Psittrichas*) cannot be determined. This tree is exclusively based on karyological data. In addition, it should be stated that it is not the only possible tree on the basis of the chromosome findings. Karyotypic changes in the various branches are indicated (st 2,3,4,5,6,7, sm 7, m 1,8,11 and m 6/7 indicate the origin of subtelocentric pairs 2,3,4,5,6,7, submetacentric pair 7, metacentric pairs 1,8,11 and metacentric pair 6/7 respectively; compare Fig. 8).

tion. In their historical review of psittaciform taxonomy, Sibley and Ahlquist (1972) concluded that: '... on the arrangement of groups within the parrots there is little agreement. Some groups, such as the cockatoos, seem to be natural, but their nearest relatives among the parrots are obscure. The parrots have had a complex evolutionary history and their inter-relationships need further study'. From their own studies of egg-white proteins Sibley and Ahlquist declined to draw any conclusions on possible relationships within the order, pending the acquisition of data from many more genera. This picture of wide variability and complex patterns of evolution is confirmed by the karyology. Keeping in mind the above reflections, it is to be expected that in the future karyology will contribute significantly to elucidating the obscure phylogeny of the parrots.

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Addendum

After this paper was prepared it came to the authors' knowledge that three additional papers on karyotypes of parrots by De Lucca currently are in press. These are:

- De Lucca, E. J., 1983. A comparative study of the chromosomes in five species of birds of the genus Aratinga (Psittaciformes: Aves). Cytologia. (Dealing with Aratinga aurea, A. cactorum, A. leucophthalmus, A. solstitialis and A. auricapilla.)
- De Lucca, E. J., 1983. Chromosomal polymorphism in Forpus xanthopterygius (Psittaciformes: Aves). Carylogia.
- De Lucca, E. J., 1983. The somatic chromosomes of Brotogeris sanctithomae and Brotogeris versicolorus (Psittaciformes: Aves). Genética ibérica.