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A miscellaneous collection of bird karyotypes

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Abstract

In the framework of a project on bird sexing for zoos, orcein stained karyotypes were studied of 16 species belonging to 7 avian orders, viz. *Tinamus solitarius* (Tinamiformes), *Scopus umbretta*, *Jabiru mycteria, Mycteria cinerea, Ciconia* (=*Dissoura*) (*episcopus*) *stormi* and *C.* (=*D.*) *e. episcopus* (Ciconiiformes), *Aburria pipile cumanensis, A. p. grayi, Penelope purpurascens, Lagopus lagopus* and *Arborophila orientalis* (Galliformes), *Phalcoboenus megalopterus* (Falconiformes), *Burhinus magnirostris* (Charadriiformes), *Carpococcyx renauldi* (Cuculiformes), and *Ceratogymna* (=*Bycanistes*) *subcylindricus* and *C.* (=*B.*) *bucinator* (Coraciiformes). With the exception of *Ciconia* (=*Dissoura*) *e. episcopus*, all these karyotypes are new to cytology. They are briefly described and compared to karyotypes of the respective families and orders known from the literature. Cytotaxonomic implications are briefly discussed. The karyotypes of *Burhinus magnirostris* (2n=42), *Ceratogymna subcylindricus* (2n=44) and *C. bucinator* (2n=40) exhibit the lowest diploid chromosome numbers hitherto found in birds. Of these, the two *Ceratogymna* species almost completely lack microchromosomes.

Introduction

A list of references on avian karyology was published by one of us (L. de B.) in this journal in 1984. It included literature on the karyotypes of 521 species of birds that had been studied with advanced chromosome preparation techniques since approximately 1960. More recently, Bian *et al.* (1988) extended this list to cover 671 species. In spite of this considerable increase, to date still less than 10% of the extant species of the Class Aves have been studied karyologically. The new data collected during the past few years, however, doubtlessly indicate that avian karyology is a most interesting field of study, revealing important information on the evolution of karyotypes in general, as well as on the taxonomy of various individual bird groups. The more birds are studied karyologically, the more intriguing this field becomes, since many of the avian taxa have proved to be more heterogeneous karyologically than was previously believed.

The present authors have been studying avian karyotypes for many years. In doing so, however, their interest has not been purely scientific. Rather, they have used karyology as an applied technique to identify the gender of birds of sexually monomorphic species, mainly in the framework of breeding programmes for rare and endangered animal species in zoos and related institutions. Since most birds can easily be sexed on the basis of chromosomes that are routinely stained with orcein, and because of pressure constraints (there are more applications for sexing birds than can be honoured), individual karyotypes are only rarely studied in more detail, for instance by using specific chromosome banding techniques. Thus, the scientific standard of this type of avian chromosome work generally remains rather low.

Nevertheless, when sexing birds for breeding programmes, species are regularly studied whose karyotypes have not been investigated before. It is important that such new data are recorded in the

scientific literature, as despite of the relative superficiality of these studies, they may indicate which avian taxa warrant further studies, involving more detail and scientific thoroughness. These more in depth studies can then be more effectively directed, and would probably reveal fascinating results.

With this reasoning in mind, we present here the karyotypes of 15 hitherto unstudied species and subspecies of birds belonging to various orders and families.

Material and methods

Peripheral blood samples were obtained from the following birds: *Tinamus solitarius* (1 male, 1 female), *Scopus umbretta* (2 males, 2 females), *Jabiru mycteria* (2 males, 4 females), *Mycteria cinerea* (3 males, 8 females), *Ciconia* (=*Dissoura*) (*episcopus*) *stormi* (2 males), *C.* (=*D.*) *e. episcopus* (2 males, 2 females), *Aburria pipile cumanensis* (6 males, 3 females), *A. p. grayi* (10 males, 6 females), *Penelope purpurascens* (2 males, 2 females), *Lagopus lagopus* (2 males, 1 female), *Arborophila orientalis* (1 male), *Phalcoboenus megalopterus* (1 female), *Burhinus magnirostris* (1 female), *Carpococcyx renauldi* (4 males), *Ceratogymna* (= *Bycanistes*) *subcylindricus* (1 male, 3 females) and *C.* (=*B.*) *bucinator* (1 female).

All animals were resident in collections of zoological gardens and private collections in several European countries (see Acknowledgements). They were identified taxonomically by experienced bird curators. Their sex was identified or confirmed on the basis of their karyotypes.

Blood cultures and chromosome preparations were performed according to the techniques extensively described by Belterman and De Boer (1984). Chromosome pairs in the karyotypes are generally arranged in accordance to the arrangements used for the respective families and orders in earlier publications (e.g. De Boer & Van Brink, 1982; Belterman & De Boer, 1984). Magnification of chromosomes in all illustrations is 3000×.

Results and cytotaxonomic comparisons

Results are presented below per order. Cytotaxonomic comparisons between present findings and karyotypic data known from the literature are included, addressing each order separately. This section is followed by a brief discussion on general aspects of avian karyology.

Tinamiformes

The karyotype of *Tinamus solitarius* (Fig. 1) has a diploid chromosome number of approximately 80. The first three pairs of autosomes are large and of a characteristic size and shape. Pairs 4 and 5 are acrocentrics of medium size and indistinguishable from the Z chromosome. The remaining chromosomes, including the W (which is tentatively chosen in Fig. 1) are acrocentric microchromosomes.

Studies of tinamou karyotypes have been limited to date. The only clear illustration available in the literature is that of *Eudromia elegans* in Sasaki *et al.* (1980) (unfortunately, the illustrations of two tinamous published by De Lucca, 1974, and De Lucca and Chamma, 1977, do not present enough detail for proper comparison, while the publication of De Lucca, 1985, with karyotypes of two additional members of the order, was not accessible to us). In its

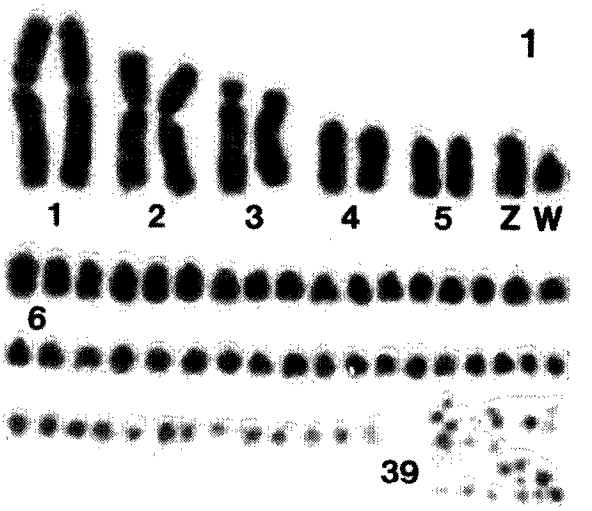


Fig. 1. Representative karyogramme of female *Tinamus solitarius* (2n=80) (Tinamiformes: Tinamidae). W chromosome chosen tentatively.

overall structure the karyotype of *E. elegans* is similar to that of *T. solitarius* presented here. Sasaki *et al.*, however, mention the presence of subcentromeric secondary constrictions in the chromosomes of pairs 3 and 4, which are absent in our material. In addition Sasaki *et al.* found small short arms in pair 5, which are apparently lacking in *T. solitarius*. Conversely, *T. solitarius* exhibits small but distinct short arms in pair 3, which are clearly lacking in Sasaki *et al.*'s illustration.

In fact, the karyotype of *T. solitarius*, as presented here, is identical to the karyotypes of the ratite birds which probably represent the most basic karyotypes found in the avian class (e.g. Belterman & De Boer, 1984). The presence of distinct short arms in chromosome pair 3 is especially of interest. This pair carries similar short arms in the ratites, as well as in the basic karyotypes of several orders of Carinatae. None of the galliform species studied so far exhibit such short arms however, as their pair 3 is acrocentric. Therefore an acrocentric number 3 is considered as a shared apomorphic characteristic of all Galliformes (Belterman & De Boer, 1984). The finding of an acrocentric chromosome 3 in *E. elegans* by Sasaki *et al.* (1980) could indicate a possible relationship of the tinamous with the gallinaceous birds, a relationship suggested by several taxonomists (e.g. Sibley & Ahlquist, 1972). Yet the presence of distinct short arms in the number 3 of *T. solitarius*, contradicts this and most probably shows that the resemblance of pair 3 of *E. elegans* and the gallinaceous birds is not indicative of a Galliform-Tinamiform relationship.

Ciconiiformes

Scopus umbretta (Fig. 2) has a diploid chromosome number of 66. Its karyotype consists of three pairs of large macrochromosomes (pairs 1-3, which are of the shape and size characteristic for many birds), three pairs of medium-sized metacentric to submetacentric macrochromosomes (pairs 4-6), seven pairs of small metacentrics (pairs 7-12 + 14), one pair of small acrocentrics (pair 13) and 36 small to minute microchromosomes. The Z is a medium-sized submetacentric chromosome, the W a small submetacentric element.

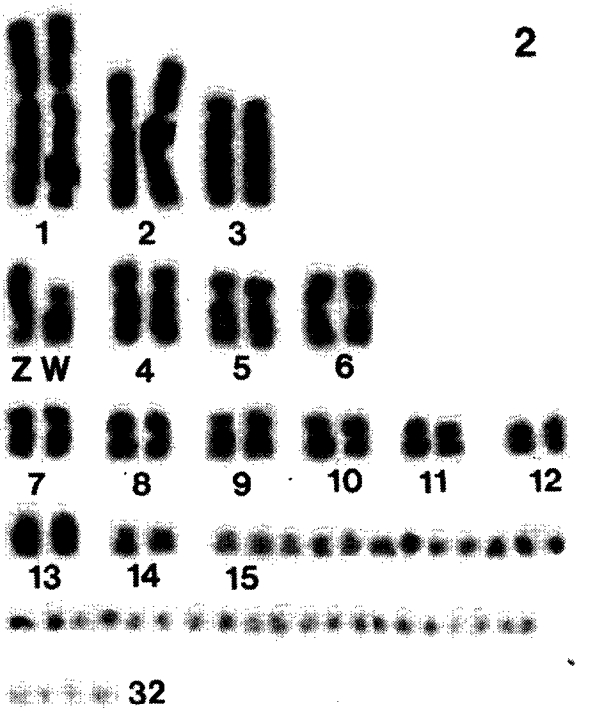


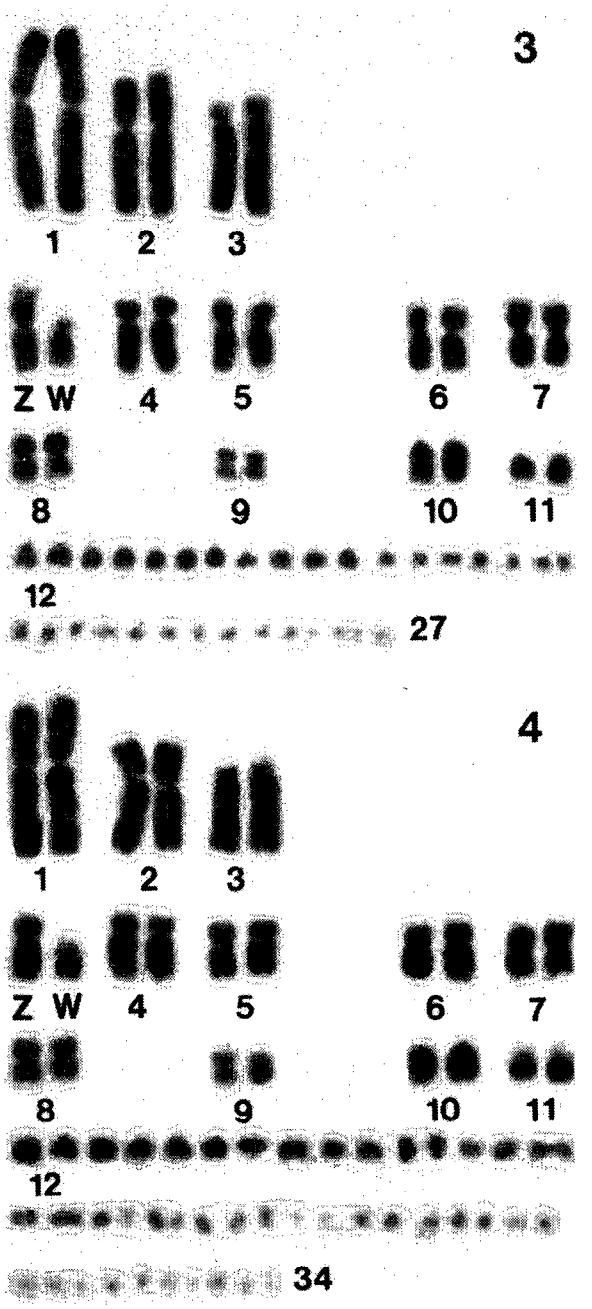
Fig. 2. Representative karyogramme of female *Scopus umbretta* (Ciconiiformes: Scopidae) (2n=66).

The systematic position of *Scopus* has always been a matter of discussion. It is placed in a monotypic family, Scopidae, by most experts on ciconiiform taxonomy; sometimes it is even placed in a superfamily of its own. The karyotype of *Scopus* certainly is not allied with those of the family Ardeidae, all of which (including *Cochlearius*) are characterized by a submetacentric pair 3 (which is to be considered an apomorphic characteristic of this group; see De Boer & Van Brink, 1982; Belterman & De Boer, 1984). Nor does it resemble the karyotypes of the members of the Threskiornitidae, all of which are characterized by a fissioned pair 1 (an apomorphic trait as well; same references). The remaining two ciconiiform families, Ciconiidae and Balaenicipitidae, have the same structure of the macrochromosome pairs 1-3 as *Scopus*. However, this structure must be regarded as plesiomorphic, since it is found in many bird orders as an original characteristic. *Scopus* most closely resembles *Balaeniceps rex*, the sole representative of Balaenicipitidae, with respect to the structure of the remaining macrochromosomes. These two forms have the same number and structure of medium-sized meta- to

submetacentric chromosomes (pairs 4-6), as well as the same number and structure of small metacentric elements (pairs 7-12). The only difference is the presence of satellites attached to the acrocentrics of pair 13, a trait found polymorphically in *Balaeniceps* (De Boer & Van Brink, 1982). This polymorphic system, however, also involves the occurrence of the normal, acrocentric type of chromosome 13 as seen in *Scopus*. In the Ciconiidae on the other hand, there are always at least four pairs of medium-sized metacentric to submetacentric chromosomes (three pairs in *Scopus* and *Balaeniceps*), and mostly two, but never more than four pairs of small metacentrics (seven in *Scopus* and *Balaeniceps*). Such comparisons on the basis of orcein-stained, non-banded chromosomes, necessarily remain somewhat superficial however. It would be most interesting to study a possible *Balaeniceps/-Scopus* relationship in much more detail using sophisticated chromosome banding techniques. Such studies would need to focus on the medium-sized and small macrochromosomes, and consequently would require investigation of elongated prophase chromosomal material.

If such studies would be undertaken, another most intriguing question regards the karyological relationship between Pelicaniformes on the one hand (specifically the pelicans s.s.), and *Scopus* and *Balaeniceps* on the other. When the karyotypes of the latter two forms (this report and De Boer & Van Brink, 1982, respectively) are compared to those of the pelicans (e.g. Belterman & De Boer, 1984), there appears to be a striking resemblance in the overall structure. It remains to be determined whether or not this resemblance is superficial, but keeping in mind that several taxonomists have suggested relationships of especially *Balaeniceps* with taxa outside the order Ciconiiformes (for a review see Sibley & Ahlquist, 1972) - and have placed them with the pelicans amongst others - this question requires further clarification.

The other four ciconiiform species studied karyologically belong to the family Ciconiidae. The karyotype of *Mycteria cinerea* (2n=70) (Fig. 4), reported here for the first time, is identical to the karyotypes of *Ciconia ciconia* [incl. *C.* (*c.*) *boyciana*] *C.* (=*Euxenura*) *maguari, Ephipiorhynchus senegalensis, E.* (=*Xenorhynchus*) *asiaticus* and *Leptoptilos javanicus* (e.g. De Boer & Van Brink, 1982; Belterman & De Boer, 1984). This karyotype, with a relatively high diploid number (66-72), the characteristic pairs 1-3, four pairs of medium-sized metacentric to submetacentric chromosomes (4-7), two pairs of small metacentrics (8 and 9) and one pair of small acrocentrics (10), probably is original in the family. With respect to its macro-



Figs. 3-4. Representative karyogrammes of female *Jabiru mycteria* (2n=56) (3) and female *Mycteria cinerea* (2n=70) (4) (Ciconiiformes: Ciconiidae). Arrangement and numbering of chromosome pairs according to Belterman and De Boer, 1984.

chromosomes, the karyotype of *Jabiru mycteria* (Fig. 3) is identical to that of *Mycteria cinerea* and the supposed ancestral ciconiiform karyotype. Its chromosome number (56), however, is considerably lower because of the unexplained absence of some 14 minute microchromosomes.

The karyotypes of *Ciconia* (=*Dissoura*) (*episcopus*) *stormi* (Fig. 5a) and *C.* (=*D.*) *e. episcopus* (Fig. 5b) are identical to each other, and differ from the above, supposedly original ciconiid karyotype in several respects: the lower diploid number (56 and 58 or 60 respectively), the absence of the acrocentric pair 10, and the presence of an additional pair of medium-sized metacentric macrochromosomes (designated pair 10/11, since supposedly this pair evolved from a fusion between the original pairs 10 and 11; see De Boer & Van Brink, 1982, and Belterman & De Boer, 1984). The karyological similarity between both forms seems to confirm their close relationship. Their karyotypes also closely resemble that of *C. nigra* (see Belterman & De Boer, 1984), which, however, has a somewhat lower number of small microchromosomes (2n=52).

According to Kahl (1972) the Ciconiidae should be arranged in three tribes, Mycteriini, Ciconiini and Leptoptilini, a view that is supported by several other taxonomists (e.g. Wood, 1973). In that case, the supposed original ciconiid karyotype (see above) is found in all of these tribes (*Mycteria* in Mycteriini; *Ephippiorhynchus* and *Ciconia maguari* and *C. ciconia* in Ciconiini; *Leptoptilos javanicus* in Leptoptilini). Karyological changes would then have taken place within *Ciconia* of Ciconiini, leading to the possibly common lineage of *C. episcopus* and *C. nigra*. Within *Leptoptilos* of Leptoptilini important karyological changes must have taken place as well, leading to the karyotype of *L. crumeniferus* (De Boer & Van Brink, 1982; Belterman & De Boer, 1984). As stated by Belterman and De Boer, this karyotype bears some resemblance to that of *C. nigra*, e.g. with respect to the low diploid number (2n=52 in both). Since all taxonomists agree that the genus *Leptoptilos* forms a closed natural group (see Kahl, 1972), it must be concluded that this resemblance is either superficial or due to convergence.

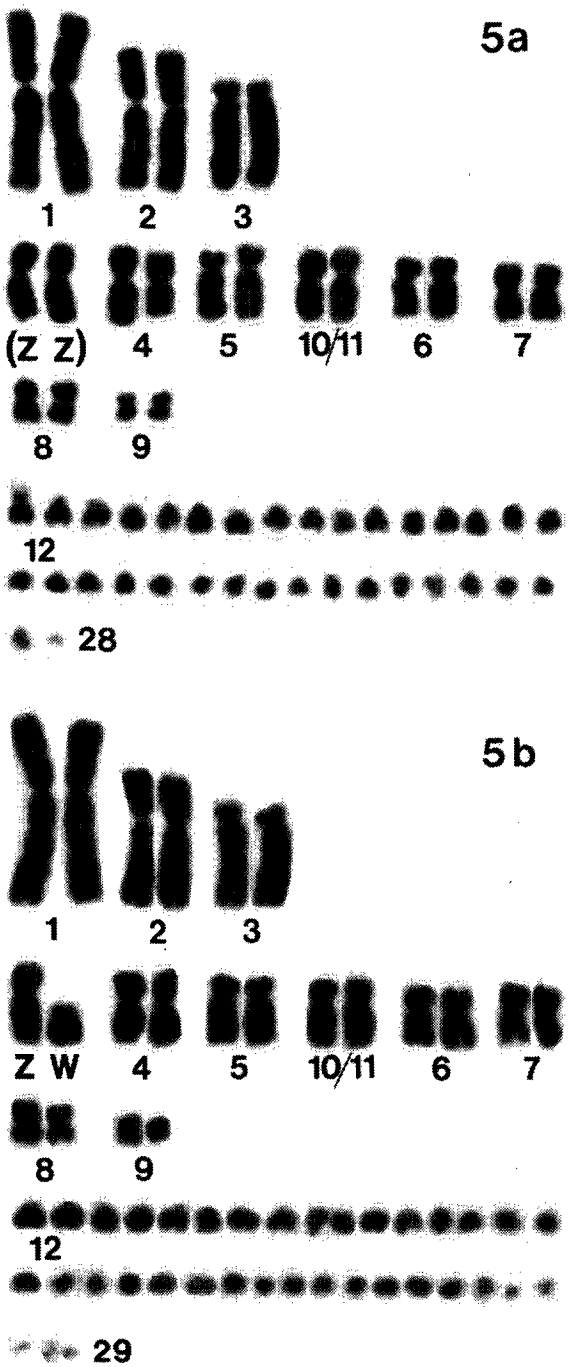
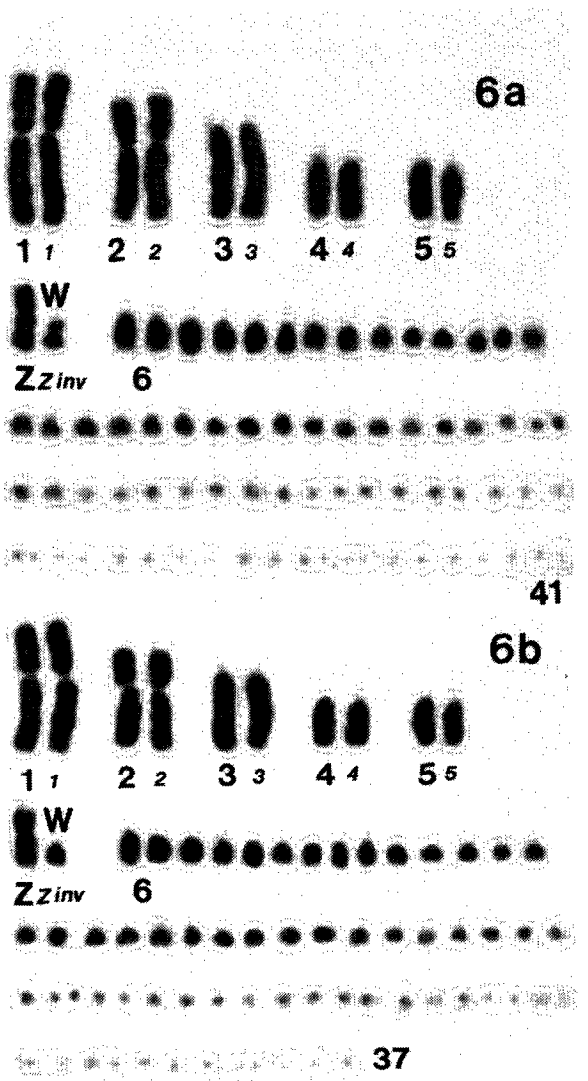
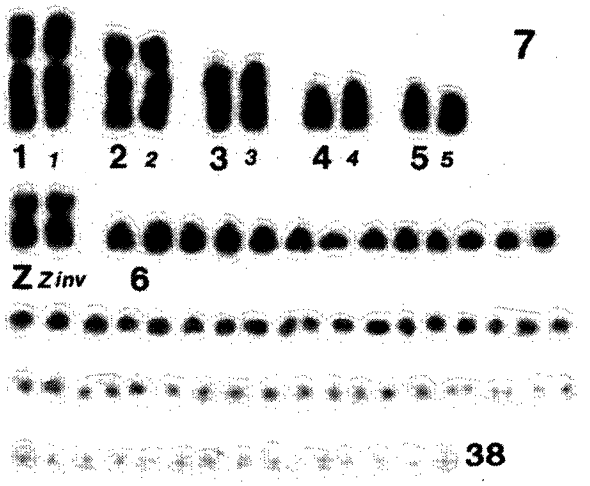


Fig. 5. Representative karyogrammes of *Ciconia* (=*Dissoura*) (*episcopus*) *stormi* (5a), and *C.* (=*D.*) *e. episcopus* (2n=58 or 60) (5b) (Ciconiiformes: Ciconiidae). Numbering and arrangement of chromosome pairs according to Belterman and De Boer, 1984 (pair '10/11' supposedly evolved from a fusion between the original ciconiiform pairs 10 and 11). Z chromosomes of *C.* (=*D.*) (*episcopus*) *stormi* chosen tentatively on the basis of comparison with *C.* (=*D.*) *episcopus episcopus*.

Galliformes

The karyotypes of the three members of the family Cracidae, viz. *Aburria pipile cumanensis* (Fig. 6a), *A. p. grayi* (Fig. 6b) and *Penelope purpurascens* (Fig. 7) presented here (2n approximately 84, 76 and 78 respectively), are identical to each other as well as to those of all other cracids hitherto studied (*Crax mitu, Ortalis canicollis, Penelope jacquacu* and *P. superciliaris*; for specific references see De Boer, 1984). Apart from their submetacentric Z chromosome, these karyotypes are supposed to be identical to the ancestral karyotype of all Galliformes (Belterman & De Boer, 1984). Within the Galliformes, only the megapodes possess the supposedly original acrocentric Z chromosome which is also found in tinamous and ratites. All other galliform families have a submetacentric (inverted) Z, or a secondarily derived Z. The structure of pair 3 (acrocentric) found in the cracids, is characteristic of all Galliformes (see the discussion on Timamiformes above).





Figs. 6-7. Representative karyogrammes of Cracidae (Galliformes): female *Aburria pipilae cumanensis* (2n=84) (6a), female *A. p. grayi* (2n=76) (6b) and male *Penelope purpurascens* (2n=78) (7). Small italic numbers refer to chromosome pair numbering system of the supposed ancestral galliform karyotype as proposed by Belterman and De Boer, 1984. Large chromosome numbers are the numbers of pairs in decreasing size order as used in the text (compare also Figs. 8 and 9).

Lagopus lagopus (Fig. 8) is the second member of the family Tetraonidae to be studied using modern tissue culturing techniques. Its karyotype (2n=82) differs in one respect from that published for *Centrocercus urophasianus* by Stock and Bunch (1982), namely in the absence of a medium-sized metacentric pair of macrochromosomes. The presence of this pair (supposedly evolved by fusion of two pairs of microchromosomes) was believed to be characteristic of the Tetraonidae in the scheme on galliform karyotype evolution presented by Belterman and De Boer (1984). Because of the absence of this pair, the karyotype of *L. lagopus* is identical to the karyotype believed to be ancestral to Tetraonidae, Meleagrididae, the pheasants s.s., and the quails of the tribe Odontophorini (*Colinus, Collipepla* and *Lophortyx*). All of these are characterized by a fissioned original pair 2, resulting in the presence of two additional pairs of acrocentric macrochromosomes (designated '*2p*' and '*2q*' in Fig.

8). In fact, the karyotype of *L. lagopus* is identical to those of several of the above forms. Consequently the presence of a medium sized metacentric macrochromosome in *C. urophasianus* (Stock & Bunch, 1982) is not a family characteristic of the Tetraonidae, but an apomorphic characteristic of this species.

Arborophila orientalis (Fig. 9), belonging to the quails of the tribe Perdicini, has a karyotype (2n = 76 approximately) that is unique among the galliformes hitherto studied. Compared with the scheme of karyotypic evolution in the Galliformes given by Belterman and De Boer (1984), it has the ancestral type of pair 1 (shared with all galliformes except Megapodidae). Pair 2 also retained the ancestral structure and is shared with the Numididae, *Gallus, Pavo* and *Afropavo*. Cracidae, Tetraonidae, Meleagrididae, the pheasants s.s., and the quails of the tribe Odontophorini all have a fissioned pair 2 (resulting in two acrocentric pairs instead of the large submetacentric original number 2). The quails of the tribe Coturnicini in the scheme of Belterman and De Boer were tentatively placed together with the former group (sharing the original pair 2), but in the two species of this tribe studied (*Coturnix coturnix* and *Excalfactoria chinensis*) an inversion changed this chromosome to become metacentric instead of submetacentric. Pair 3 of *A. orientalis* is submetacentric, whereas in all other galliformes it is acrocentric. Possibly this is due to a unique inversion. Pair 4 of this species possibly is identical to the pair indicated as '*4/m*' in the scheme mentioned, being the result of a fusion between the original pair 4 of galliformes and a pair of microchromosomes. This characteristic pair is also found in Numididae, *Pavo*, *Afropavo* and *Gallus*, while it is absent in Megapodidae, Cracidae, Tetraonidae, Meleagrididae, the pheasants s.s., and the quails of the tribe Odontophorini (all of which possess the original acrocentric pair 4). In the former group (similar as with respect to the structure of pair 2) the quails of the tribe Conturnicini from an exception; their supposed submetacentric pair '*4/m*' became subtelocentric due

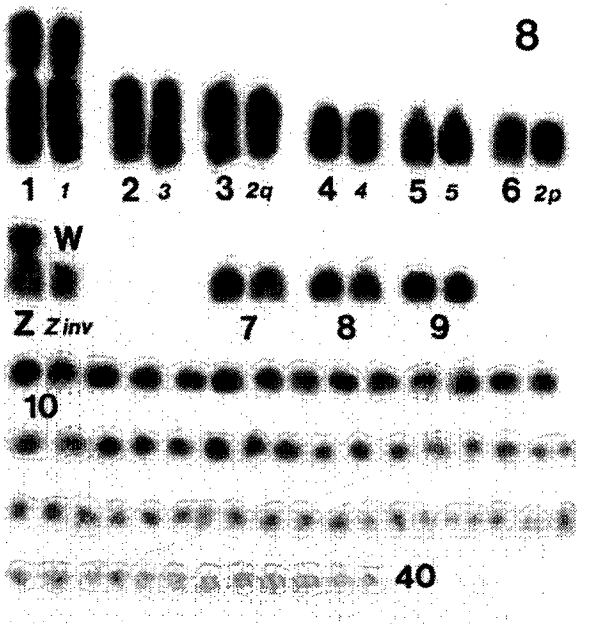


Fig. 8. Representative karyogramme of female *Lagopus lagopus* (2n=82) (Galliformes: Tetraonidae). For explanation of small italic and large chromosome numbers see legend to Figs. 6-7 ('*2q*' and '*2p*' supposedly evolved from fissioning of the original galliform chromosome pair *2*).

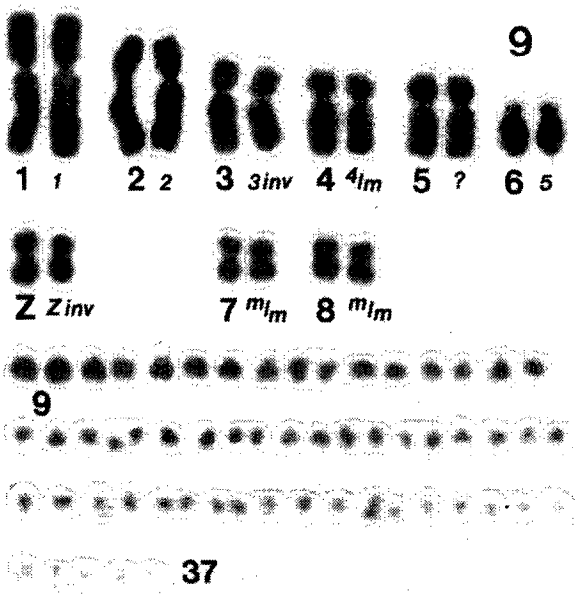


Fig. 9. Representative karyogramme of male *Arborophila orientalis* (2n=76) (Galliformes: Phasianidae). Z chromosomes are chosen tentatively on the basis of comparisions with other galliform species. For explanation of small italic and large chromosome numbers see legend to Figs. 6-7. Pair '*4/m*' supposedly evolved from a fusion between the original pair *4* and a pair of microchromosomes. The '*3inv*' pair is unique in Galliformes. Pair 5 is unique as well, but its homology with chromosomes of the ancestral galliform karyotype is uncertain and thus it is indicated as '?' (it may evolved from fusion between microchromosomes, although its long arms are too large to consist of only one pair of such elements). Pairs 7 and 8 may have evolved from fusions between microchromosomes. Their homology with similar small metacentrics in some other galliform species (indicated as '*m/m1*' to '*m/m4*' in Belterman & De Boer, 1984), however is unclear.

to an inversion. Pair 5 of *A. orientalis* probably is unique among the Galliformes. It is submetacentric and of the same size as pair 4. It might have evolved from a fusion between one of the largest and a smaller pair of microchromosomes. Its long arm, however, seems to be longer than the largest acrocentric microchromosomes in other gallinaceous birds. Thus, its homology with other galliform chromosomes is not clear. Pair 6 of *A. orientalis*, a small subtelocentric, probably is identical to the ancestral pair 5, shared by all extant galliformes. In addition to these six pairs of macrochromosomes, *A. orientalis* possesses two pairs of small metacentric chromosomes. Small metacentric chromosomes – supposedly evolved from fusions between small microchromosomes, or from pericentric inversions of the larger acrocentric microchromosomes – have been found in several galliform groups. Their number never exceeds two pairs (viz. one pair in *Centrocercus urophasianus*, one pair in *Numida meleagris* and *Acryllium vulturinum*, and two pairs in *Pavo cristatus* and *Afropavo congensis*; all of these small metacentrics probably evolved independently). Since only a male individual could be studied, the Z chromosomes of *A. orientalis* could not be identified with certainty. Tentatively a pair of metacentric macrochromosomes was chosen as Z chromosome pair (Fig. 9), similar in size and structure to the Z supposed to be ancestral to all galliformes except Megapodidae (indicated as '*Zinv*' in the scheme of Belterman & De Boer, 1984).

To our knowledge, so far only a single other member of the Perdicini has been studied karyologically, viz. *Francolinus pondicerianus* (Rath *et al.*, 1975). The material presented by these authors (illustrated with drawings of the chromosomes) does not permit good comparison with *Arborophila orientalis*. *A. orientalis* (together with *Gallus, Pavo* and *Afropavo*; sharing also characteristics with Numididae) deviates from the group of the pheasants s.s. and the quails of the tribe Odontophorini (which share characteristics with Meleagrididae and Tetraonidae) particularly with respect to the structure of pairs 2 and 4. The position of the quails of the tribe Coturnicini, in our scheme of 1984 placed along with the former group (*Gallus, Pavo, Afropavo*; Numididae), is not very clear since if it indeed belongs to this group their pairs 1, 2 and 4 secondarily underwent structural rearrangement.

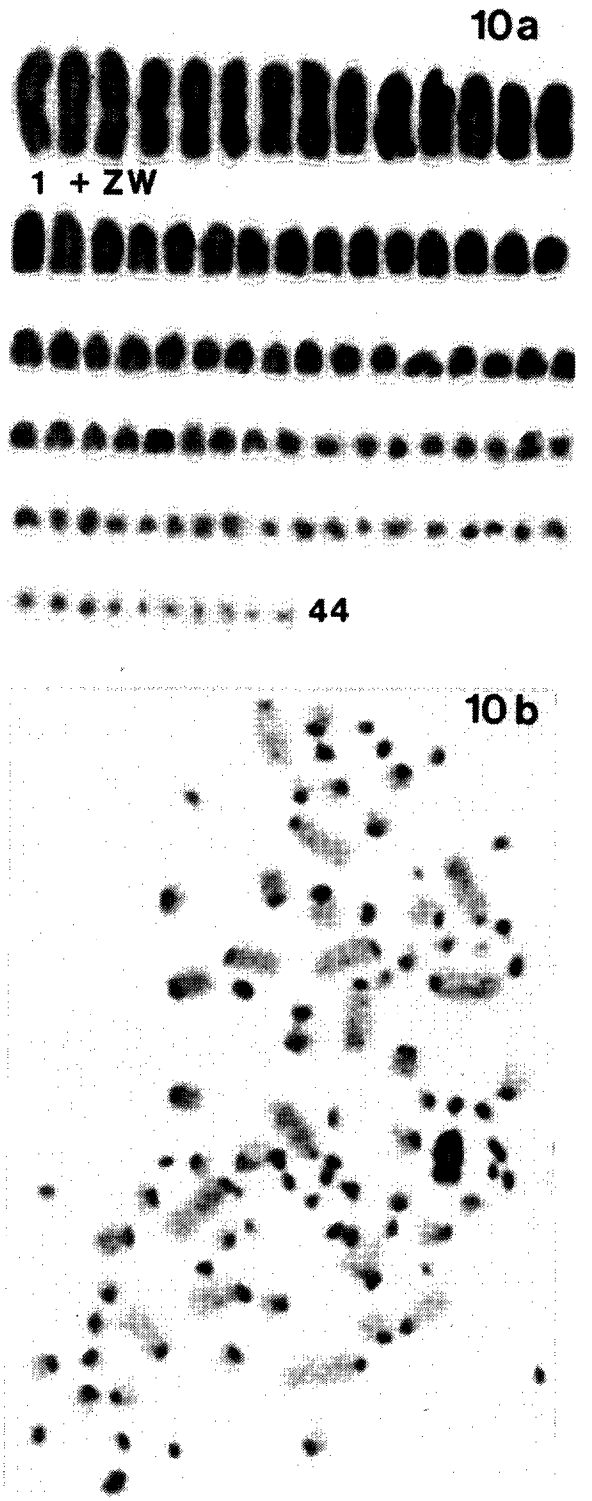


Fig. 10. Representative karyogramme (a) and partial C-banded metaphase plate with W chromosome (b) of female *Phalcoboenas megalopterus* (*2n*=90) (Falconiformes: Falconidae). Chromosomes are not arranged in pairs because of the gradual decrease in size of the exclusively acrocentric chromosomes. The Z chromosome could not be identified.

It is obvious particularly, that the karyotypes of the various tribes of quails deserve further cytologic studies involving detailed banding techniques. The cytotaxonomic position of these tribes within the rather complex chromosomal phylogeny of the galliformes is highly interesting.

Falconiformes

The karyotype of *Phalcoboenus megalopterus* (Fig. 10a) has a diploid chromosome number of approximately 90, and is exclusively made up of acrocentrics, very gradually decreasing in length from the size of medium-sized macrochromosomes to minute microchromosomes. C-banding revealed a relatively large macrochromosome to be the W chromosome (almost entirely C-positive, Fig. 10b). The Z could not be identified with certainty. Relying on the size of most birds' Z chromosomes it is one of the largest acrocentric macrochromosomes.

Phalcoboenus is one of the Neotropical members of the family Falconidae which form a somewhat aberrant group. Three members of this group have been studied karyologically now: *Polyborus plancus* (De Boer, 1975), *Milvago chimachima* (Belterman & De Boer, 1984) and *Phalcoboenus megalopterus* (this report). They all differ from the typical falcons (*Falco*) by their relatively high diploid chromosome number (84 to 90 in the Neotropical forms, 50 to 52 in *Falco* spp). *Polyborus* differs from *Milvago* and *Phalcoboenas* as it has of one pair of medium-sized metacentric macroautosomes which is lacking in the other two genera.

Charadriiformes

The karyotype of *Burhinus magnirostris* (Fig. 11) has an exceptionally low diploid chromosome number, which is among the lowest hitherto found in birds: 42. Bulatova (1977) reported the chromosome number of *B. oedicnemus* to be 40. The karyotypes of both species resemble each other in their overall structure, although the quality of Bulatova's illustration does not permit a detailed comparison.

Twelve pairs of chromosomes are individually

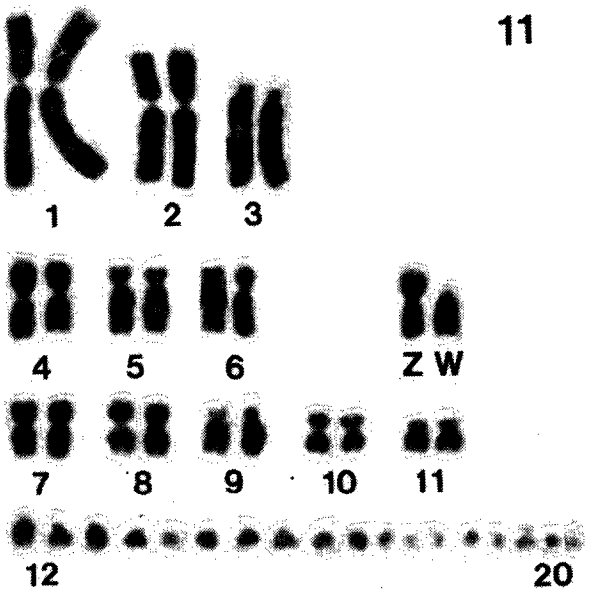


Fig. 11. Representative karyogramme of female *Burhinus magnirostris* (2n=42) (Charadriiformes: Burhinidae).

distinguishable in the karyotype of *B. magnirostris*. Pairs 1 to 3 are large macrochromosomes, similar in structure to the pairs 1-3 of many avian groups. Pairs 4 to 11 are medium-sized to small macrochromosomes with median to submedian centromeric positions. The Z is metacentric, and is slightly larger than the autosomes of pair 4. The W is a distinct acrocentric, somewhat smaller than the autosomes of pair 10. The remaining 18 chromosomes are small to minute microchromosomes.

No other forms of the charadriiform family Burhinidae have ever been studied cytologically. Diploid numbers as low as those of *Burhinus* have not been reported in any of the other families of this order (for lists of references see De Boer, 1984 and Bian *et al.*, 1988). In Jacanidae, Haematopidae, Charadriidae, Scolopacidae, Recurvirostridae and Laridae, the families of which one or more representatives have been studied so far, diploid numbers have been recorded ranging from 68 to approximately 100. The macrochromosome pairs 1-3 of *Burhinus*, which probably retained the ancestral structure of the avian karyotype, are also found in several of the other families. The number of medium to small-sized, biarmed macrochromosomes in the other charadriiformes varies from 3 to 6 pairs. Thus, it can be concluded that, in spite of its low diploid number, compared to other

charadriiformes *Burhinus* neither possesses exceptionally large macrochromosomes, nor has exceptionally high numbers of biarmed medium-sized to small macrochromosomes. Any further comparison between *Burhinus* and other charadriiformes would seem premature at this moment.

Cuculiformes

Carpococcyx renauldi has a karyotype with 60 chromosomes (Fig. 12). Since only male specimens were studied the sex chromosomes could not be identified. The chromosomes of pair 1 are large submetacentrics, those of pair 2 large subtelocentrics. Pair 3 consists of medium-sized submetacentric chromosomes. Pairs 4-7 consist of biarmed (submetacentric to subtelocentric) elements of medium size, but distinctly smaller than pair 3. Pair 8 consists of small metacentrics and pair 9 of small acrocentrics. The remaining elements (40) are small to minute microchromosomes which are either acrocentric or of unidentifiable centromeric position.

Carpococcyx is a member of the family Cuculidae. In this family most of the karyological studies were done on species of the genus *Cuculus* (e.g. Bian et al., 1988; Roy, 1990). Their karyotypes are quite distinct from that of *C. renauldi*. They possess the pairs 1 and 2 typical of the ancestral bird karyotype, both of which are lacking in *C. renauldi*. On the other hand their pair 3 differs from the ancestral 3 in that it is submetacentric, while in *C. renauldi* the original subtelocentric seems to be present in an unchanged form (pair 2 in Fig. 11). Addittionally, *C. renauldi* has a higher number of medium sized to small biarmed macrochromosomes and a clearly lower diploid number than the *Cuculus* species (whose 2n is approximately 78). *Eudynamys scolopacea*, another cuculiform species studied karyologically (Ray-Chaudhuri, 1967), has a karyotype similar to those of *Cuculus*. The same is probably true for *Guira guira*, studied by De Lucca (1974). The report on the karyotypes of *Crotophaga ani, C. major* and *Piaya cayana* (Waldrigues, 1980), is unfortunately not accessible.

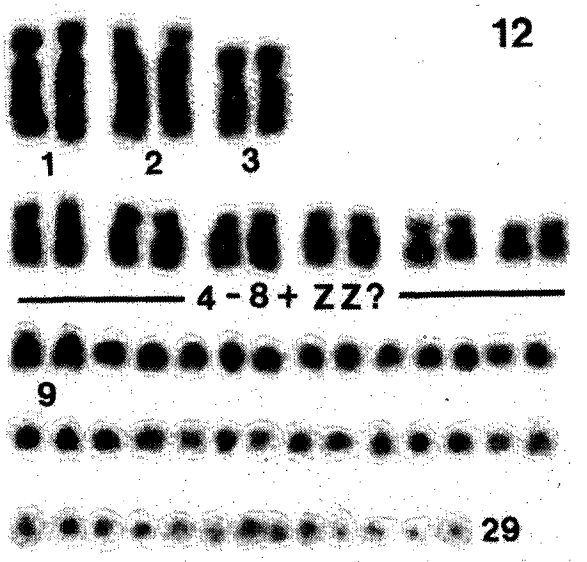


Fig. 12. Representative karyogramme of male *Carpococcyx renauldi* (2n=60) (Cuculiformes: Cuculidae). Z chromosomes could not be identified.

Being very poorly studied, an exhibiting clear karyological diversity, especially expressed by the rather deviating karyotype of *Carpococcyx* reported here, the Cuculidae would seem a rather interesting family for further chromosome investigations.

Coraciiformes

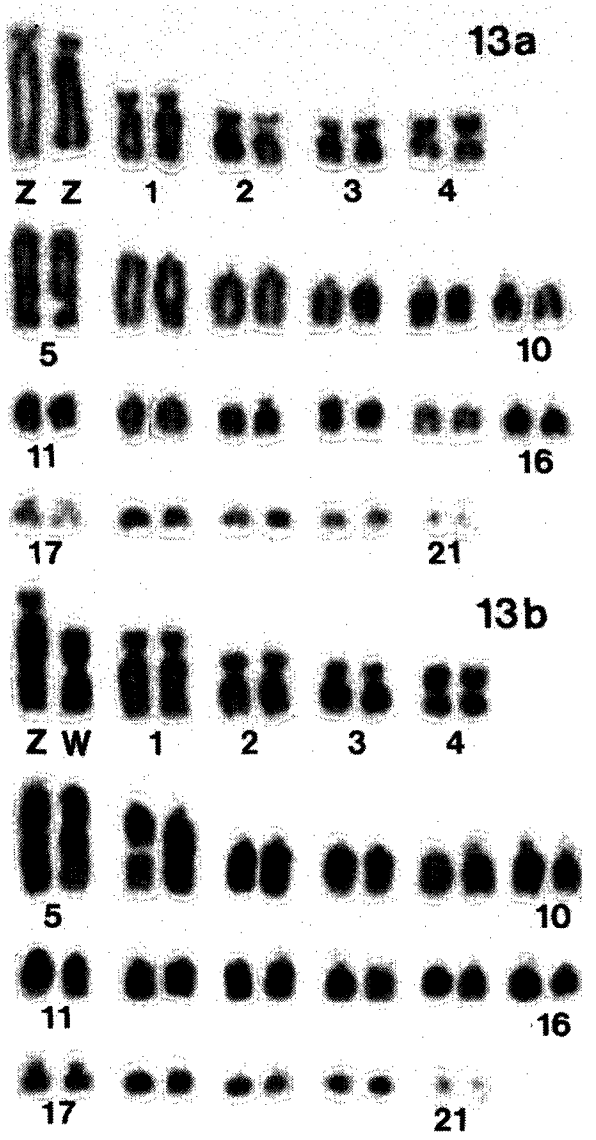
Both *Ceratogymna* (=*Bycanistes*) *subcylindricus* and *C.* (=*B.*) *bucinator (Figs. 13-14)* have very low diploid numbers: 4 and 40 respectively. The karyotype of the first species consists of the following elements: pair 1 of large acrocentrics, pair 2 of medium-sized subtelocentrics, pairs 3-6 of small metacentric to submetacentric elements and pairs 7-21 of medium-sized to minute acrocentrics, the smallest of which can be considered as microchromosomes. The Z chromosome is the largest element in the complement; it is subtelocentric and slightly larger than the chromosomes of pair 1. It is clearly larger than in the karyotypes of most other birds. The W is a metacentric chromosome of medium size.

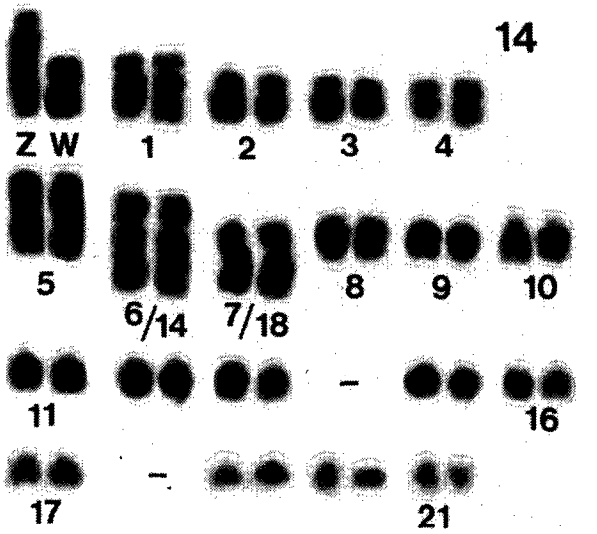
The karyotype of *C. bucinator* is similar to that of *C. subcylindricus*, except for the absence of three pairs of acrocentrics and one pair of microchromosomes. Instead, *C. bucinator* exhibits two additional pairs of submetacentric chromosomes, a large one and one of medium size. Thus, the lower diploid number of this species may possibly be explained as the result of two

fusions involving acrocentric chromosomes. In the absence of chromosome banding data it is impossible to decide exactly which of the *C. subcylindricus* chromosomes were involved; comparing chromosome lengths, probably pairs 6 and 7 fused with smaller acrocentrics, in Figure 14 tentatively indicated as pairs 14 and 18 respectively.

Five other species of Bucerotidae, the hornbill family to which *Ceratogymna* belongs, have been studied karyologically, all by Belterman and De Boer (1984). All of these have a large Z chromosome comparable in size and shape to that of *Ceratogymna*. It is the largest element in the karyotype in *Aceros undulatus* and *Buceros bicornis*, as in *Ceratogymna*. In the other three, *Bucorvus abyssinicus, B. leadbeateri* and *Tockus fasciatus*, it is second in size because of the presence of a pair of very large metacentric autosomes. Among the five species studied previously, two categories of diploid numbers were found: 2n=68/70 in *Aceros undulatus*, *Buceros bicornis*, and *Tockus fasciatus*, and 2n=86/90 in *Bucorvus abyssinicus* and *B. leadbeateri*. A curious finding was that other than the chromosome number difference, the karyotypes of *Bucorvus* spp. and *Tockus fasciatus* appeared to be identical; no explanation could be found for the absence of some 20 microchromosomes in the latter compared to the former. Nearly all of the *Ceratogymna* chromosomes can in fact be found in the karyotypes of *Buceros* and *Tockus*; thus, between *Tockus* and *Ceratogymna* there is a nearly unexplained difference of some 30 microchromosomes, while between *Ceratogymna* and *Bucorvus* this difference is almost 50 microchromosomes. The Bucerotidae therefore constitute a most fascinating group for further karyological studies.

The karyotypes of the other families of the order Coraciiformes are so different from those of Bucerotidae that comparisons at this moment are not warranted (see Belterman & De Boer, 1984; De Boer, 1984).





Figs. 13-14. Representative karyogrammes of male (13a) and female (13b) *Ceratogymna* (=*Bycanistes*) *subcylindricus* (2n=44) and of female *C.* (=*B.*) *bucinator* (2n=40) (14) (Coraciiformes: Bucerotidae). Chromosome pairs 6/14 and 7/18 in the latter species probably evolved from fusions between pairs 6 and 7 of the former with smaller acrocentrics, possibly numbers 14 and 18 respectively (which can, however, only be confirmed by banding studies).

Discussion

The karyotypes presented here again demonstrate that there is more karyological heterogeneity in the Class Aves than was previously believed. Of the 15 species and subspecies whose karyotypes are described here for the first time, eight exhibit karyotypic structures which are different from those of any other members of their orders or families hitherto reported.

In addition, the above results suggest avian taxa particularly of interest for further detailed, systematic investigations. The Tinamiformes are of interest in view of their intra-order karyological differences, and the unresolved tinamou-Carinatae relationship. The Ciconiiformes are a group of growing karyological interest. The *Balaeniceps-Scopus* relationship, as well as the affinities of these unique birds with either Ciconiidae or extra-order groups (such as the pelicans) require additional karyotypic studies. Within the family Ciconiidae a pattern is becoming clear now; all tribes share the same basic karyotype, while in two of them (Leptoptilini and Ciconiini) considerable karyological changes took place. Further investigation is needed in order to trace evolutionary lineages in these tribes. Within the Galliformes, the Cracidae seem to form a karyologically stable group; all cracids studied to date are karyotypically identical. The remainder of the order, however, exhibits great karyological diversity, and is highly interesting for further investigation. The various tribes of quails – hitherto very poorly studied – and their relationships to each other as well as to the pheasants s.s., and *Gallus, Pavo* and *Afropavo* particularly deserve further detailed study. The situation in Falconidae of Falconiformes has become more clear: the typical falconids all are characterized by karyotypes with low diploid numbers (approximately 50), almost exclusively made up of acrocentrics, while all New World caracaras have similar karyotypic structures but considerably higher chromosome numbers (approximately 90). Within the Charadriiformes, the Burhinidae seem to form a most intriguing group because of their exceptionally low chromosome numbers. Their karyological relationship with the many other charadriiform families has not yet been clarified. The karyotype of *Carpococcyx renauldi* demonstrates that the Cuculidae (Cuculiformes) exhibit much more karyological diversity than was previously known. Therefore, they constitute a highly interesting subject for further study as well. Finally, the Bucerotidae (Coraciiformes), are again an excellent group for further investigations. The eight species studied so far indicate that the family is extremely heterogeneous karyologically, and the finding of karyotypes virtually lacking microchromosomes within *Ceratogymna* is exciting.

The microchromosome problem in general is becoming more and more intriguing. The 'classic' bird karyotype, with a diploid number of 80 to 90, contains some 50 to 60 of such small to minute elements. As they are found in the chromosome complements of both the subclass Carinatae and Ratitae, and in nearly all of their orders, their origin dates back at least a 100 million years ago, which indicates that they must have a very significant evolutionary/adaptive meaning as otherwise they would have disappeared randomly. Nevertheless, as more bird karyotypes are systematically studied, more species or higher taxa are found to exhibit considerable reduction in their number of microchromosomes. In the first group in which this became apparent, the diurnal birds of prey of the falconiform family Accipitridae (e.g. De Boer, 1975; De Boer & Sinoo, 1984), the reduction in the number of microchromosomes could be explained by suggesting recurrent fusions between such elements, resulting in karyotypes with many biarmed, medium-sized to small macrochromosomes and a very low number of remaining microchromosomes. Recently however, more groups have been found in which there is no obvious explanation for the disappearance of microchromosomes: within several groups certain species exhibit a reduction in the number of microchromosomes which is only partly explicable by normal rearrangements. In Ciconiidae three such reductions took place; one within *Leptoptilos* (De Boer & Van Brink, 1982; Belterman & De Boer, 1984) involving some 20 microchromosomes, one within *Ciconia* (leading to *C. episcopus* and *C. nigra*), and one in *Jabiru mycteria* (the latter two involving somewhat less microchromosomes). Within Falconidae, the major difference between the typical falcons and the Neotropical caracaras involves an unexplained reduction of some 40 microchromosomes in the former group. The difference between *Burhinus* (Burhinidae) and the other charadriiform families involves the

unexplained loss of at least 30 microchromosomes. Within Bucerotidae, the situation is most extreme: the only difference between *Bucorvus* and *Tockus* involves the loss of 30 microchromosomes in the latter (Belterman & De Boer, 1984), while the main difference between *Bucorvus* and the karyoptyes of *Ceratogymna* presented here, involves the absence of as many as 50 microchromosomes. In all these, as well as in a number of other cases already described in the literature, a most fascinating question arises: where did the microchromosomes go? Everything points to the fact that microchromosomes bear important functions in birds, otherwise they would not have been conserved for over a hundred million years. But then, why did they disappear in considerable numbers, independently in several cases, the number of which is increasing with the number of avian species studied karyologically?

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