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Chromosomal evolution within the family Estrildidae (Aves) II. The Lonchurae

L. Christidis
Department of Population Biology, Research School of Biological Sciences, Australian National University, P.O. Box 475, Canberra City, 2601, Australia, and
Division of Wildlife and Rangelands Research, C.S.I.R.O., Australia

Abstract

Thirteen species of estrildid finches belonging to the Lonchurae were examined cytogenetically by G- and C-banding. The major forms of karyotypic change, both within and between species, were pericentric inversions and changes in the amount of heterochromatin. It appears that the direction of chromosome change in this lineage is towards an entirely telocentric karyotype because inversions converting a biarmed chromosome into a telocentric one only occur when all the macrochromosomes of smaller size are also telocentric. A comparison of hybrid fertility data and karyotypic differences indicates that genic factors affecting gonadal development, and not chromosomal rearrangements, are the primary influence in determining hybrid fertility. The chromosomal data was also used to clarify systematic relationships within the Lonchurae and demonstrate that the genus *Lonchura* as presently construed is polyphyletic.

Introduction

This is the second in a series of publications which examine the patterns of chromosome change within the passerine family of grassfinches, Estrildidae. The first dealt with the 'true' grassfinches, Poephilae (Christidis, in press). In the present paper the results for the mannikins, Lonchurae are presented. This is the most widely distributed group of estrildids occurring throughout Africa, southern Asia and Australia. The 13 species examined in the present study include representatives from all three continents and cover the five currently recognized genera (Mayr, 1968). As in the case of the Poephilae, the data collected are used to determine taxonomic relationships within the tribe and also to examine the possible role of karyotypic change in avian evolution.

Material and methods

The cytological and banding techniques employed in this study are those outlined in Christidis (1983, 1986). The 13 species examined were: *Lonchura castaneothorax* (4 males, 2 females); *L. flaviprymna* (1 male, 3 females); *L. maja* (1 male); *L. malacca atricapilla* (1 male, 1 female); *L. punctulata* (4 males, 5 females); *L. striata* (1 male, 2 females); *L. pectoralis* (7 males, 3 females); *L. bicolor* (1 male); *Padda oryzivora* (3 males); *Chloebia gouldiae* (4 males, 2 females); *Erythrura trichron* (2 males, 1 female); *Amadina erythrocephala* (2 males, 1 female); *A. fasciata* (2 males, 1 female).

The species nomenclature follows Mayr (1968).

Results

Standard and C-banded karyotypes

All 13 species have a diploid set of 78 chromosomes. The rationale and format for karyotypic description follows Christidis (1983, in press). The first seven largest pairs of chromosomes, which invariably include the Z-chromosome, are regarded as

macrochromosomes; the remainder are designated microchromosomes.

(1) Lonchura castaneothorax

Chromosome 1 is metacentric and this is followed in order of size by an acrocentric pair and a sub-metacentric pair (Fig. 1). The Z-chromosome is next in size and sub-metacentric while the smaller W-chromosome is acrocentric. Of the remaining chromosomes, pair 4 is acrocentric while all the rest are telocentric.

The C-banded karyotype (Fig. 2) shows the distinct centromeric C-bands which occur on the macrochromosomes other than pair 3, where only faint bands are present. Most microchromosomes possess centromeric C-bands but there are some which are either entirely C-positive or entirely C-negative. In addition to the centromeric C-band, the Z-chromosome also possesses a terminal C-block on the long arm. The W-chromosome appears uniformly stained in contracted cells but displays a series of bands in prometaphase preparations.

(2) Lonchura flaviprymna

The four individuals examined all possessed a karyotype (Fig. 3) identical to that of *L. castaneothorax*. The karyotypic similarity between the two species extends also to the C-banding patterns (Fig. 4) of both the autosomes and the sex-chromosomes.

(3) Lonchura maja

In gross morphology, the autosomal complement

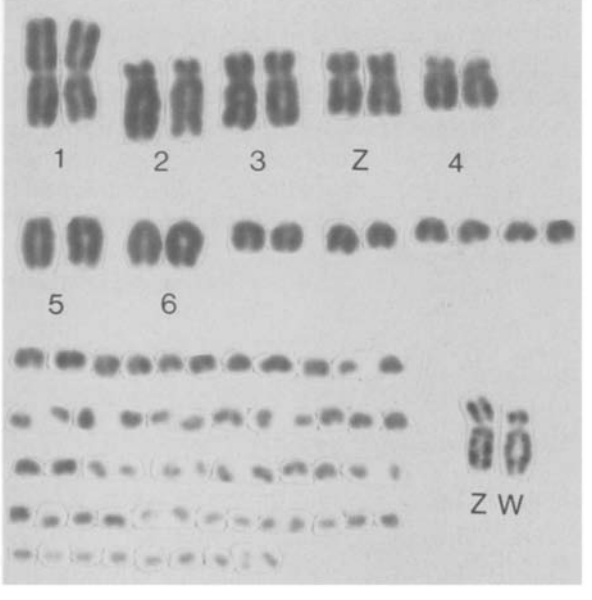

Fig. 1. Giemsa-stained karyotype of a male *Lonchura castaneothorax*. Inset shows sex-chromosomes of a female.

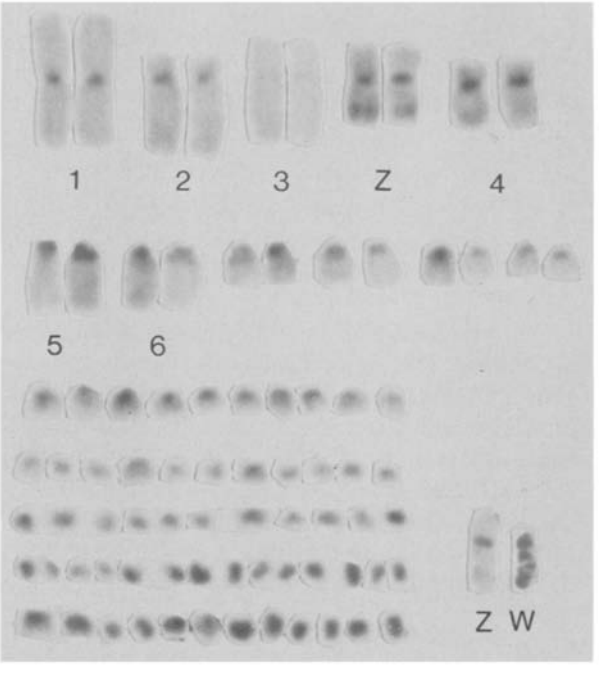

Fig. 2. C-banded karyotype of a male *Lonchura castaneothorax*. Inset shows sex-chromosomes of a female.

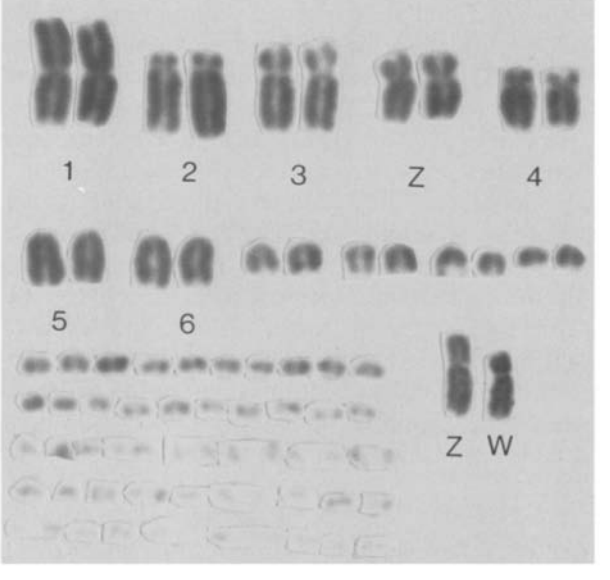

Fig. 3. Giemsa-stained karyotype of a male *Lonchura flaviprymna*. Inset shows sex-chromosomes of a female.

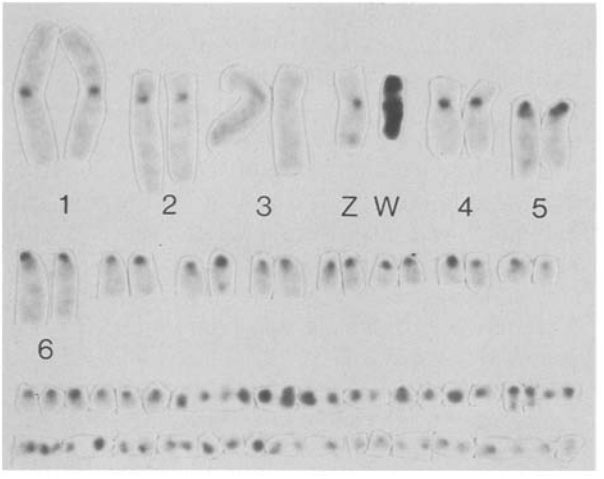

Fig. 4. C-banded karyotype of a female *Lonchura flaviprymna*.

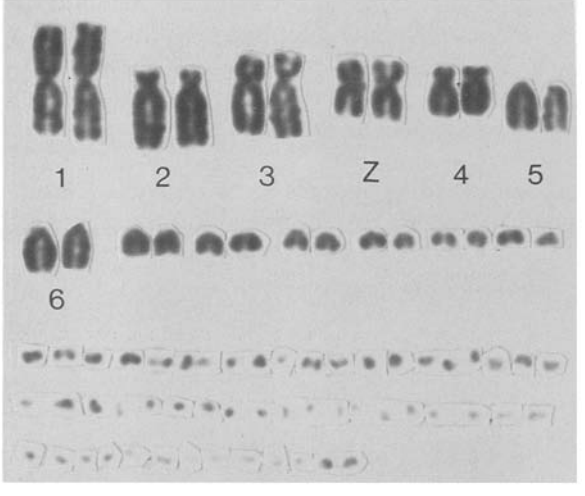

Fig. 5. Giemsa-stained karyotype of a male *Lonchura maja*.

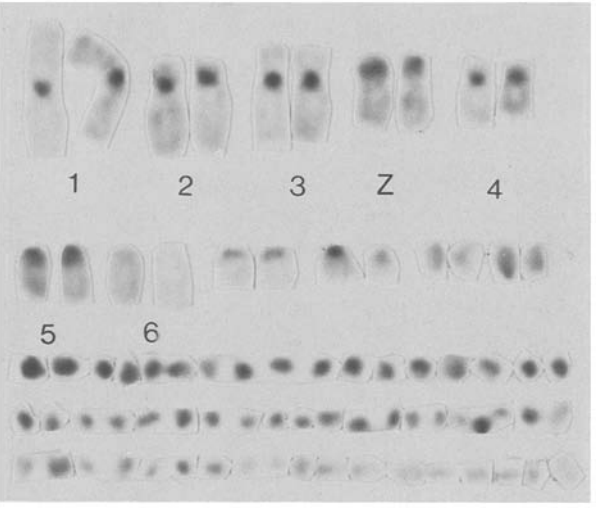

Fig. 6. C-banded karyotype of a male *Lonchura maja*.

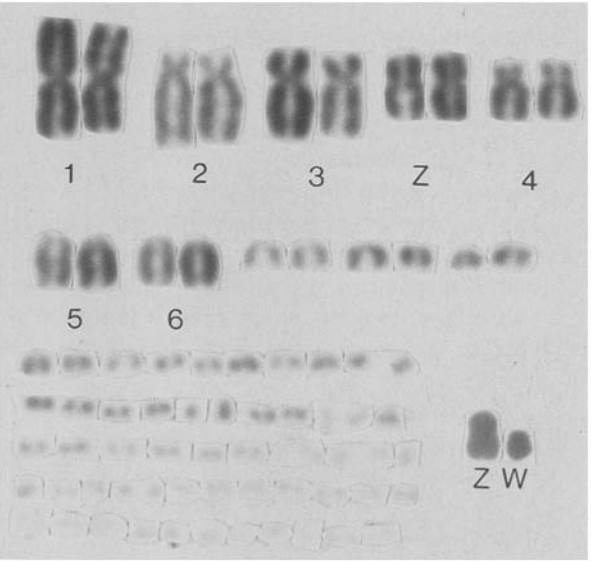

Fig. 7. Giemsa-stained karyotype of a male *Lonchura malacca*. Inset shows sex-chromosomes of a female.

of this species (Fig. 5) is identical to that of the previous two species. The Z-chromosome, however, differs in being metacentric rather than submetacentric. Additionally there are no C-bands on chromosome 6, whereas the centromeric C-bands of autosomes 1 to 5 are much larger. The microchromosomes are a more heterogenous assemblage of C-positive and C-negative elements (Fig. 6).

Unlike its condition in *L. castaneothorax*, the Z-chromosome of *L. maja* does not have centromeric heterochromatin, nor does it display a C-positive region on the telomere of the long arm. Instead there is a substantial C-block on the short arm which accounts for its metacentric nature.

(4) Lonchura malacca

The autosomal complement is similar to that of *L. maja* in both gross morphology (Fig. 7) and C-band distribution (Fig. 8). However, the Z-chromosome of *L. malacca* shares more in com-

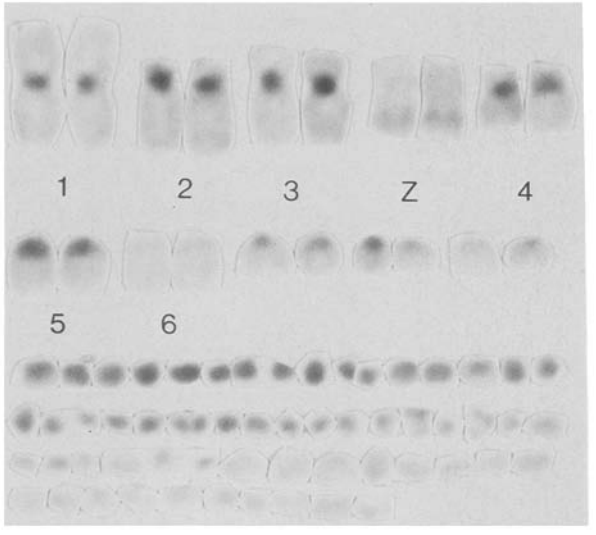

Fig. 8. C-banded karyotype of a male *Lonchura malacca.*

mon with that seen in *L. castaneothorax*, in that it displays a sub-metacentric nature and a terminal C-block on the long arm.

(5) Lonchura punctulata

Since several chromosomal polymorphisms were evident in this species, the karyotype shown in Figure 9 is the commonest type observed both in the present study and in the previously published report of Prasad and Patnaik (1977). It is similar to that of *L. castaneothorax* except that autosomal pair 5 is acrocentric rather than telocentric, in *L. punctulata*. Such a karyotype was observed in six individuals. On the other hand in the three individuals examined by Ray-Chaudhuri (1976) autosomal pair 6 was acrocentric rather than telocentric. An individual heterozygous for the acrocentric 6 was also found in the present study (Fig. 10). This individual was additionally heterozygous for an acrocentric pair 7 and a metacentric pair 8. A further male was heterozygous for an acrocentric pair 7 while a single female was homozygous for the metacentric pair 8 (Fig. 10). Finally, Ansari and Kaul (1978) described two individuals of *L. punctulata* which were claimed to be heterozygous for a reciprocal translocation involving an unidentified macrochromosome and a microchromosome. Since the rest of the karyotype possessed the same number of macrochromosomes as in the standard for this species, and only three unpaired chromosomes were observed, it is more likely that these two individuals were heterozygous for fusions involving two pairs of microchromosomes, possibly pairs 7 and 8.

The C-banding patterns of the individuals examined also reveal a high degree of intraspecific poly-

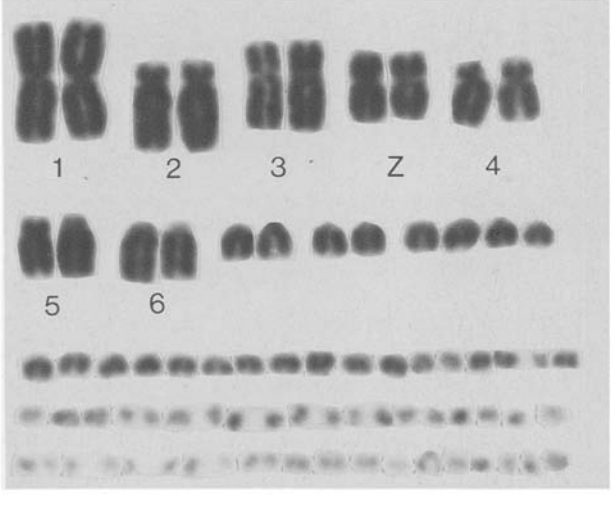

Fig. 9. Giemsa-stained karyotype of a male *Lonchura punctulata.*

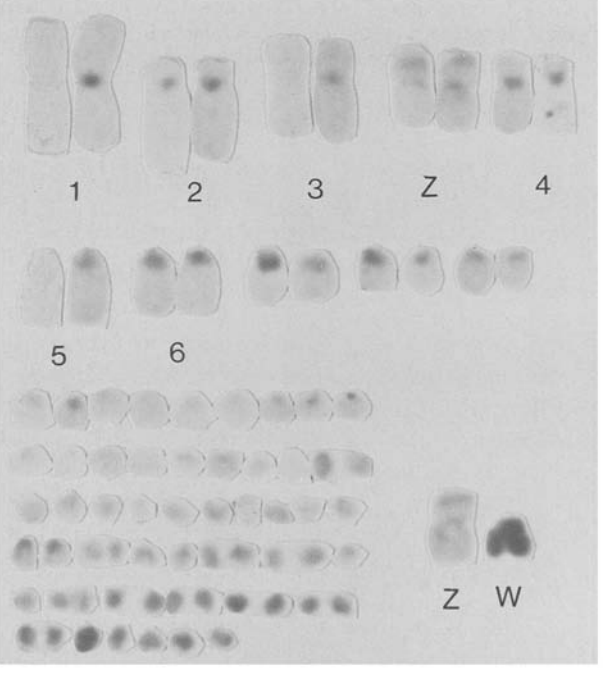

Fig. 10. C-banded karyotype of a male *Lonchura punctulata.* Inset shows sex-chromosomes of a female.

morphism. This is clearly illustrated in the C-banded male karyotype (Fig. 11) where polymorphisms are present in three of the six largest pairs of autosomes (1, 3, 5) each of which is heterozygous for the presence and absence of a centric C-band. The microchromosomes, conversely, display a C-banding pattern similar to that of the previously described species. A similar pattern was observed in two other individuals. The remainder also displayed polymorphisms for the presence or absence of centromeric C-bands on these same autosomes. A summary of these results is presented in Table 1.

Considering the degree of polymorphism involving the autosomes, it is surprising that the sex-chromosomes are invariant. The Z-chromosome possesses a centromeric C-band and a terminal band on the short arm, while the acrocentric W-chromosome is entirely heterochromatic (Fig. 11).

(6) Lonchura striata

The three individuals examined possess an autosomal complement (Fig. 12) identical to the standard form described for *L. punctulata*. This is consistent with previously published reports on the cytogenetics of *L. striata* (Takagi, 1972; Ray-Chaudhuri, 1976). The W-chromosome, however, is a sub-metacentric microchromosome. *L. striata* has faint centromeric C-bands on the largest seven pairs of autosomes and a large terminal band on the short arm of the Z-chromosome (Fig. 13). The majority of microchromosomes are C-negative and only the W-chromosome is entirely heterochromatic.

Table 1. Frequency of variants for centromeric heterochromatin in *Lonchura punctulata*. (+: Centromeric heterochromatin; −: Absence of centromeric heterochromatin).

Individual	Chromosome						
	1	2	3	4	5	6	Z
1	+ −	+ +	+ −	+ +	+ −	+ +	+ +
2	+ −	+ +	+ −	+ +	+ −	+ +	+ +
3	+ −	+ +	+ −	+ +	+ −	+ +	+ +
4	− −	+ +	− −	+ +	− −	+ +	+ +
5	− −	+ +	− −	+ +	− −	+ +	+ +
6	− −	+ +	− −	+ +	− −	+ +	+ +
7	− −	+ +	− −	+ +	+ +	+ +	+ +
8	− −	+ +	+ +	+ +	+ −	+ +	+ +
9	− −	+ −	− −	+ +	+ +	+ +	+ +

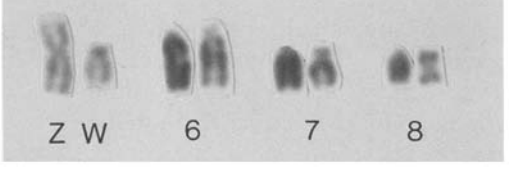

Fig. 11. Sex-chromosomes of a female and alternate morphs for chromosomes 6, 7 and 8 in *Lonchura punctulata*.

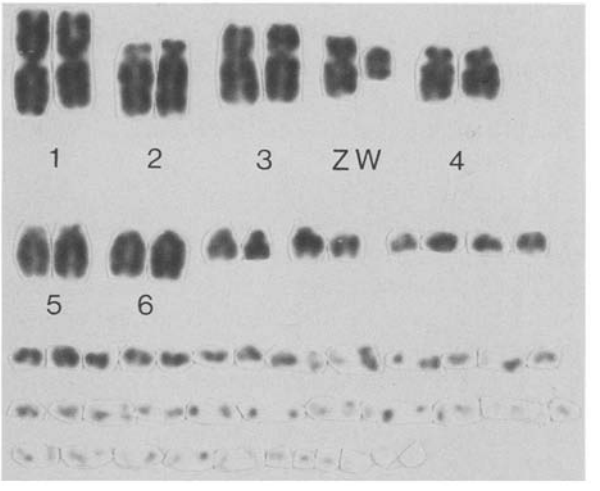

Fig. 12. Giemsa-stained karyotype of a female *Lonchura striata*.

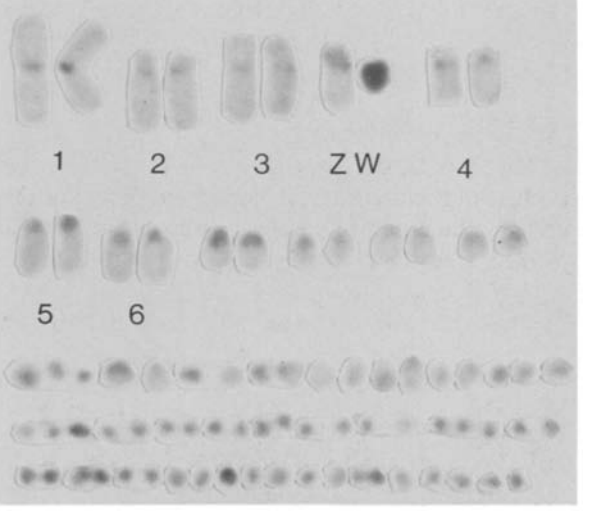

Fig. 13. C-banded karyotype of a female *Lonchura striata*.

(7) Padda oryzivora

The gross karyotypic organisation (Fig. 14) is identical to that of *L. punctulata* and *L. striata* and is also consistent with the findings of Takagi (1972). The C-banding pattern of *P. oryzivora* is particularly interesting. Distinct heterochromatic bands are confined to the centromeres of the seven largest pairs of autosomes and to the terminal segment of the short arm of the Z-chromosome (Fig. 15). On the basis of their C-banding pattern, the remaining autosomes can be divided into two groups: approximately half of them are devoid of any C-band heterochromatin while the remainder are entirely heterochromatic.

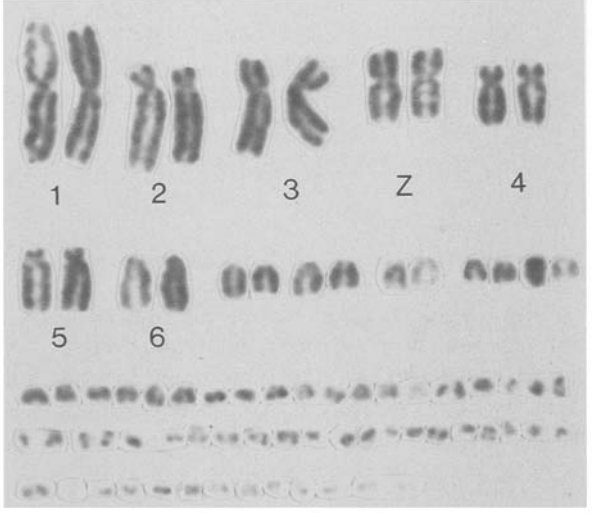

Fig. 14. Giemsa-stained karyotype of a male *Padda oryzivora.*

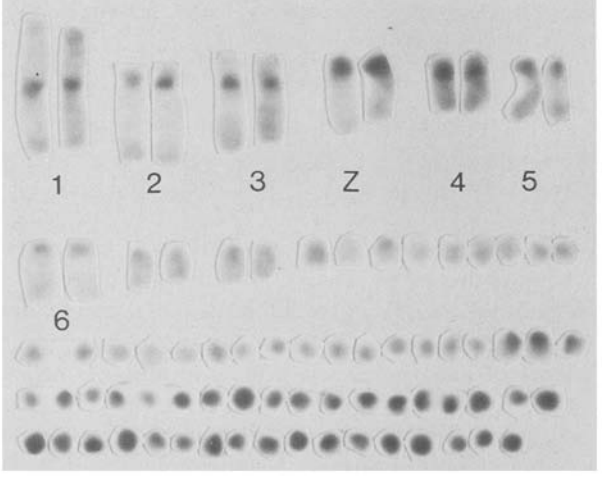

Fig. 15. C-banded karyotype of a male *Padda oryzivora.*

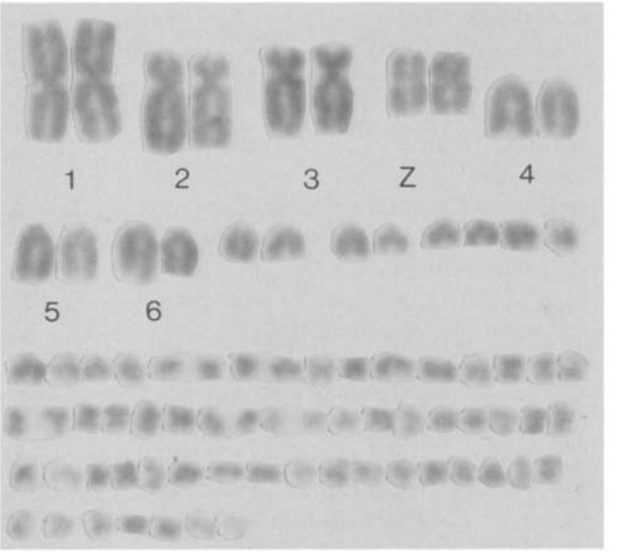

Fig. 16. Giemsa-stained karyotype of a male *Lonchura pectoralis.*

(8) Lonchura pectoralis

The karyotype of this species (Fig. 16) is quite distinct from other lonchurid species. Chromosome 1 is metacentric while chromosomes 2 and 3 are acrocentric and indistinguishable on the basis of gross morphology. The remaining autosomes are telocentric, although three individuals out of ten carried an acrocentric 6 in a heterozygous condition (Fig. 17). One male was heterozygous for a metacentric and a sub-metacentric Z-chromosome while the remaining ten individuals were fixed for the metacentric morph (Fig. 17). The W-chromosome is a telocentric microchromosome (Fig. 17).

This species has an exceptionally large amount of heterochromatin compared with the other species of *Lonchura*. Distinct blocks of centromeric heterochromatin are evident on the autosomal macrochromosomes and on the largest 11 pairs of microchromosomes (Fig. 18); and the remaining microchromosomes are almost entirely heterochromatic. The individual depicted in Figure 18 is heterozygous both for the Z-chromosome and for pair 6. The acrocentric form of chromosome 6 lacked a centromeric C-band in all three individuals carrying it. The difference between the two Z-chromosomes is due to the lack of a terminal C-block in the sub-metacentric form. This C-block is

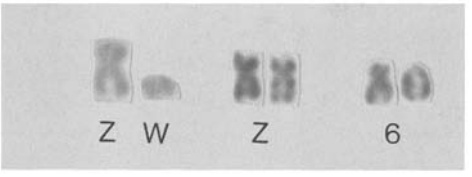

Fig. 17. Sex-chromosomes of a female and alternate morphs of the Z-chromosome and chromosome 6 in *Lonchura pectoralis.*

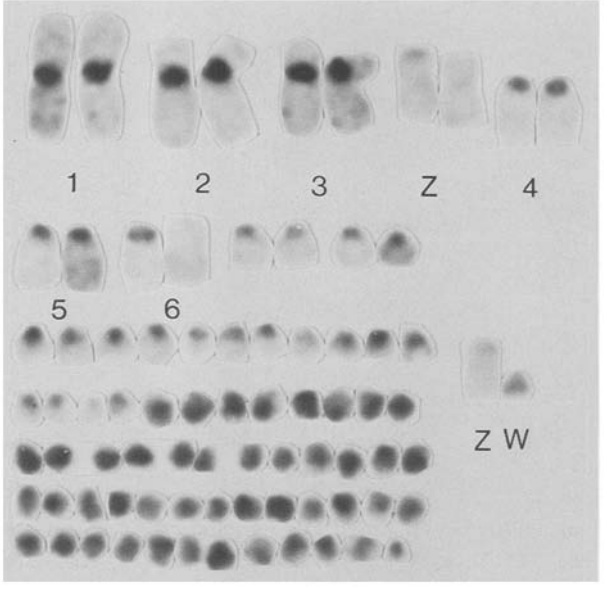

Fig. 18. C-banded karyotype of a male *Lonchura pectoralis.* Inset shows sex-chromosomes of a female.

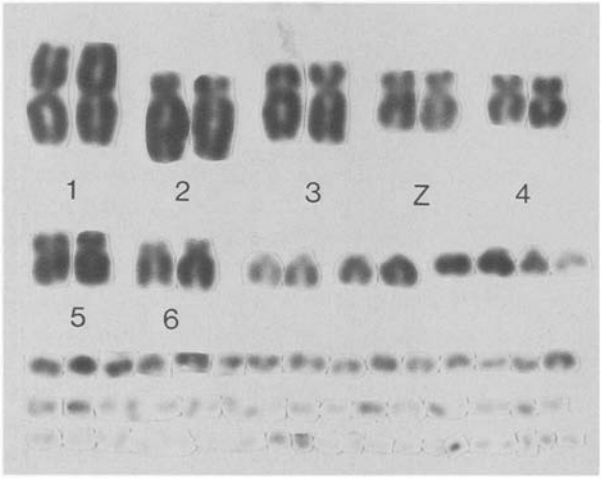

Fig. 19. Giemsa-stained karyotype of a male *Lonchura bicolor.*

present on all the metacentric Z-chromosomes. The W-chromosome of *L. pectoralis* is entirely heterochromatic (Fig. 18).

(9) Lonchura bicolor

The first three pairs of macrochromosomes are morphologically similar to their counterparts in the *L. castaneothorax* karyotype while autosomes 4, 5 and 6 are all biarmed and individually distinguishable on the basis of size and centromere position (Fig. 19). Although no female was examined, the Z-chromosome can be assumed to be fourth in size in common with the rest of the genus.

The C-banding pattern for *L. bicolor* is unusual in that the heterochromatin is restricted to 12 pairs of chromosomes (Fig. 20). Distinct centromeric C-bands occur on the largest ten pairs of autosomes while the Z-chromosomes have only faint centromeric C-bands. In addition there is a single pair of heterochromatic microchromosomes.

(10) Chloebia gouldiae

This species has a karyotype organisation (Fig. 21) similar to that of *L. castaneothorax.* Two notable differences are the metacentric pair 3 and the almost telocentric pair 4 whose counterparts in *L. castaneothorax* are sub-metacentric and acrocentric respectively. C-band heterochromatin is largely confined to the centromeres of the largest thirteen pairs of autosomes (Fig. 22).

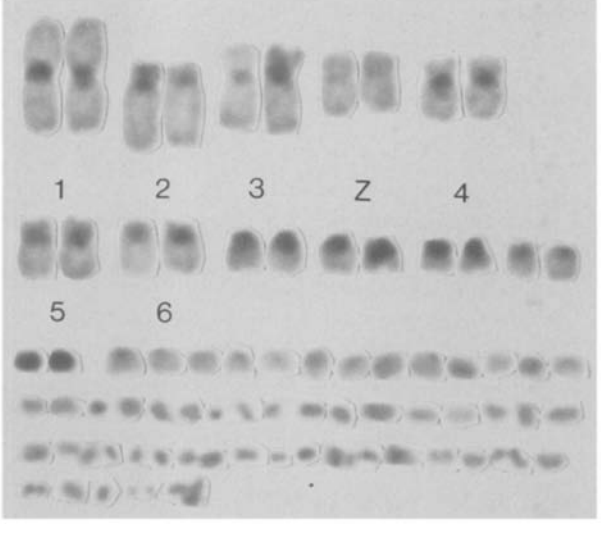

Fig. 20. C-banded karyotype of a male *Lonchura bicolor.*

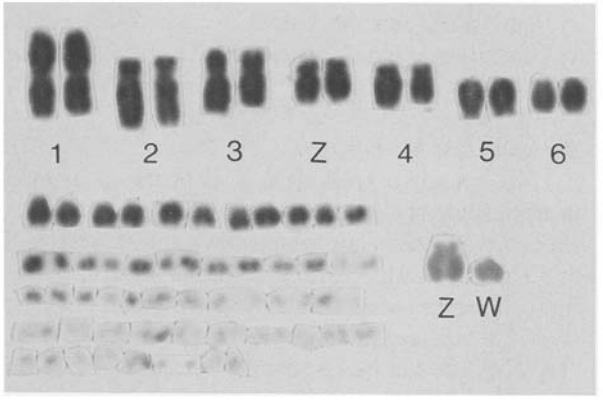

Fig. 21. Giemsa-stained karyotype of a male *Chloebia gouldiae*. Inset shows sex-chromosomes of a female.

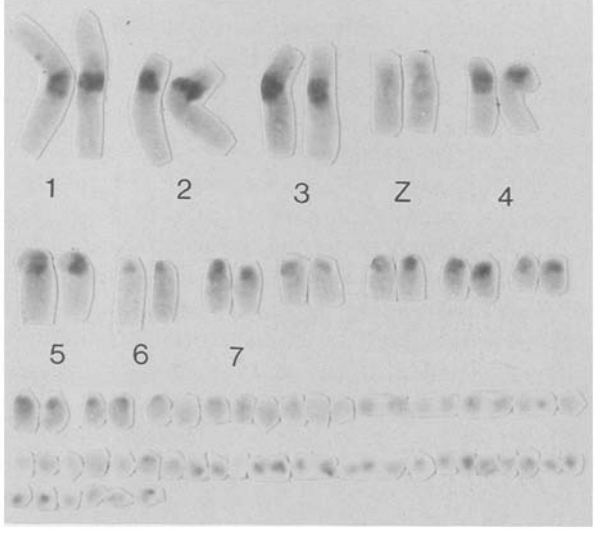

Fig. 22. C-banded karyotype of a male *Chloebia gouldiae*.

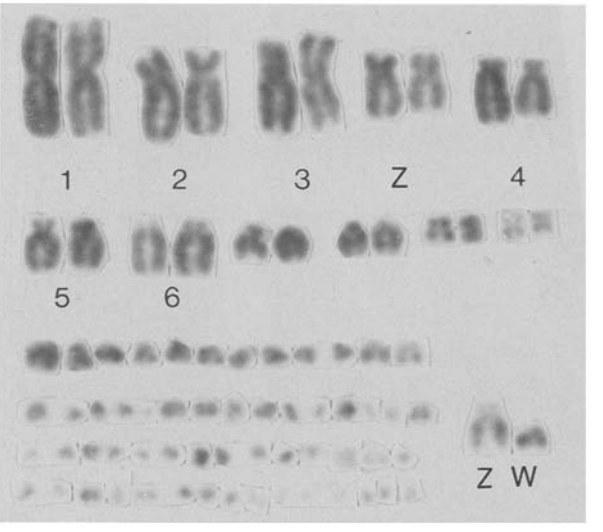

Fig. 23. Giemsa-stained karyotype of a male *Erythrura trichroa*. Inset shows sex-chromosomes of a female.

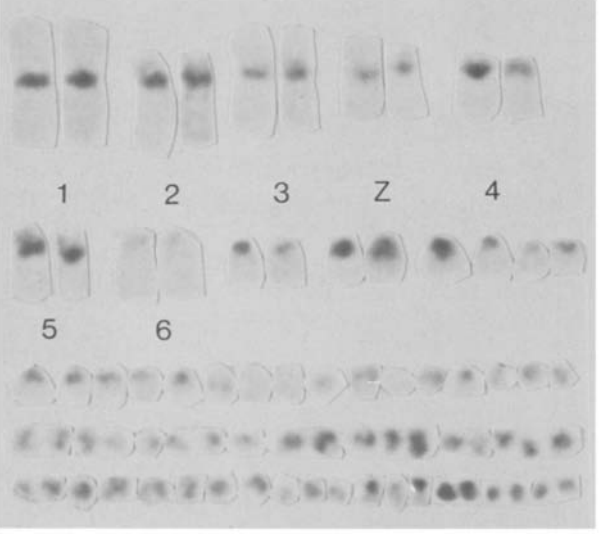

Fig. 24. C-banded karyotype of a male *Erythrura trichroa*.

(11) Erythrura trichroa

Except for two pairs of metacentrics, all the recognizable microchromosomes are telocentric (Fig. 23). The first four pairs of autosomes and the sex-chromosomes have a similar gross morphology to their counterparts in *C. gouldiae*. Chromosomes 5 and 6 are acrocentric in *E. trichroa*.

There are large C-bands at the centromeres of the four largest pairs of autosomes and the Z-chromosome (Fig. 24). Autosome 5 has a heterochromatic short arm while autosome 6 has only a faint centromeric C-band. The larger microchromosomes have C-positive centromeres while the majority of smaller microchromosomes are predominantly heterochromatic.

(12) Amadina erythrocephala

Chromosome 1 is metacentric, as are four pairs of microchromosomes while the remaining chromosomes, including the sex pair, are telocentric (Fig. 25). This species possesses the largest amount and the widest distribution of heterochromatin

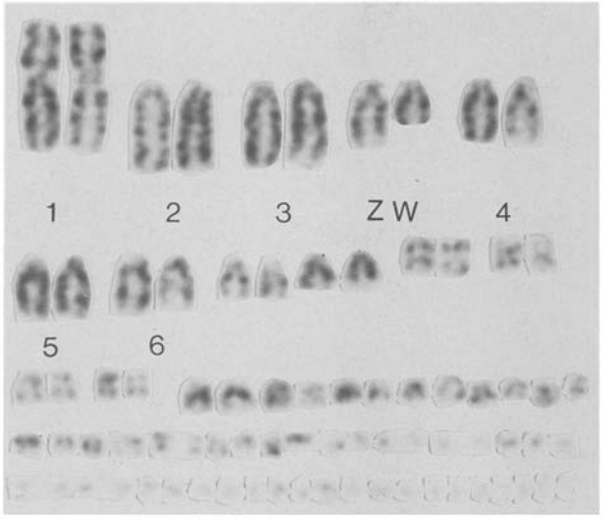

Fig. 25. Giemsa-stained karyotype of a female *Amadina erythrocephala.*

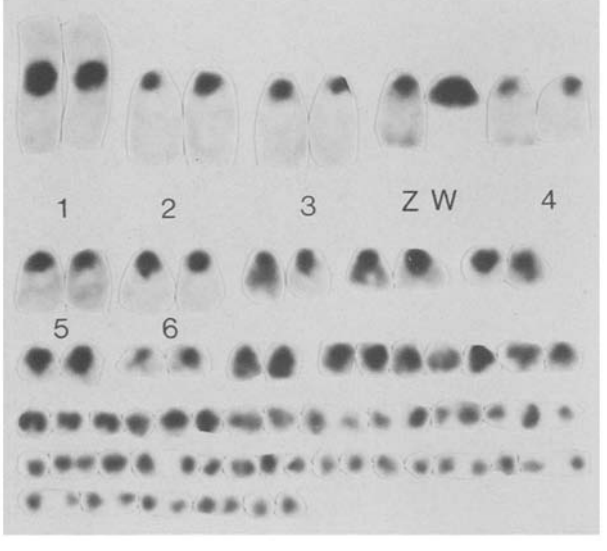

Fig. 26. C-banded karyotype of a female *Amadina erythrocephala.*

reported for any avian species (Fig. 26). Extremely large centromeric C-bands are present on chromosome 1 and there are distinct centromeric C-bands on all the remaining macrochromosomes. The first two pairs of microchromosomes display centromeric C-bands while the remainder, including the W-chromosome, are almost entirely heterochromatic.

(13) Amadina fasciata

The two *Amadina* species display a great deal of karyotypic similarity in gross morphology; the only difference being the telocentric nature of chromosome 1 in *A. fasciata* (Fig. 27). However, although the gross-stained karyotypes of the two *Amadina* species are morphologically similar, the C-banding patterns are not. *A. fasciata* does possess large centromeric C-bands on the macrochromosomes but apart from one pair of heterochromatic microchromosomes, the remainder are C-negative (Fig. 28). This remarkable difference in the amount

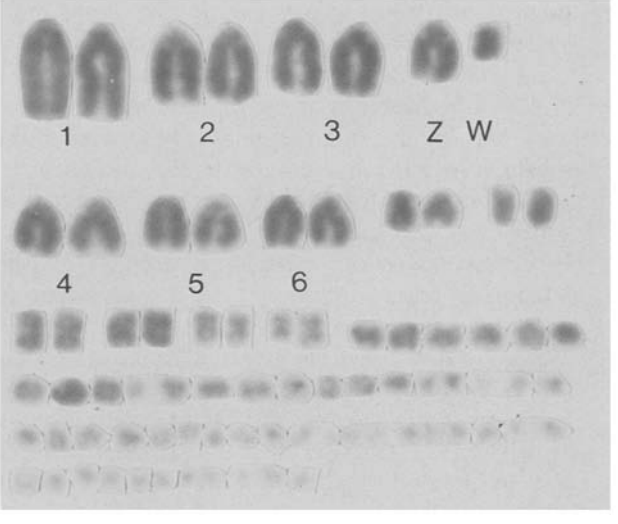

Fig. 27. Giemsa-stained karyotype of a female *Amadina fasciata.*

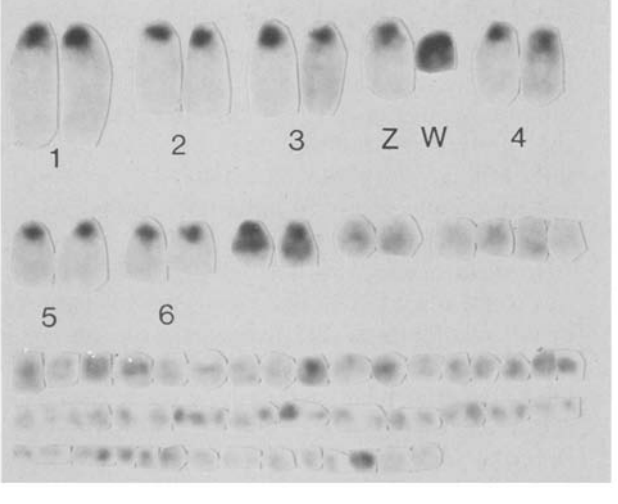

Fig. 28. C-banded karyotype of a female *Amadina fasciata.*

of heterochromatin between these two congeneric species parallels that observed in some marsupial genera (Hayman & Martin, 1974) and the orthopteran *Atractomorpha similis* (John & King, 1983).

Comparative G-band patterns

G-banding data were obtained for seven of the thirteen species studied and the patterns of G-banding in the macrochromosomes are compared in Figure 29. These when supplemented with the gross karyotypic data, provide an adequate appraisal of the structural rearrangements which distinguish different species within the Lonchurae. This is summarised in Table 2 where each species is compared to *Lonchura castaneothorax*.

With the exception of the genus *Amadina*, chromosomes 1 and 2 retain an unchanged morphology throughout the Lonchurae (Fig. 29a and 29b). In *A. erythrocephala* chromosome 1 is telocentric while in *A. fasciata* both 1 and 2 are telocentric. Pericentric inversions most likely account for the telocentric nature of both these chromosomes in *Amadina*, since the standard lonchurid diploid number is retained in the genus. Chromosome 3 exists in four distinct morphologies. The commonest form is sub-metacentric and the alternate morphs are related to it through three independent pericentric inversions (Fig. 29c). This chromosome is acrocentric in *L. pectoralis*, metacentric in *C. gouldiae* and *E. trichroa*, telocentric in *Amadina* and sub-metacentric in the remaining 8 species.

There are three recognizable forms for chromosome 4 (Fig. 29d) and their specific occurrence is summarised in Table 2. G-banding data is incomplete for this chromosome but a comparison of diploid number and C-banding patterns suggests that pericentric inversions can again account for the different morphologies observed.

Excluding intraspecific variation, the majority of species possess a telocentric pair 5 (Fig. 29e). In *E. trichroa*, a heterochromatic arm addition converts this to an acrocentric. The sub-metacentric morph of *L. bicolor* and the acrocentric morph of *P. oryzivora* are probably derived by inversions from the telocentric form. Similarly, most species possess a telocentric pair 6 (Fig. 29f). *L. bicolor* and *E. trichroa* both have an acrocentric pair 6 but the differing centromere positions indicate two separate origins.

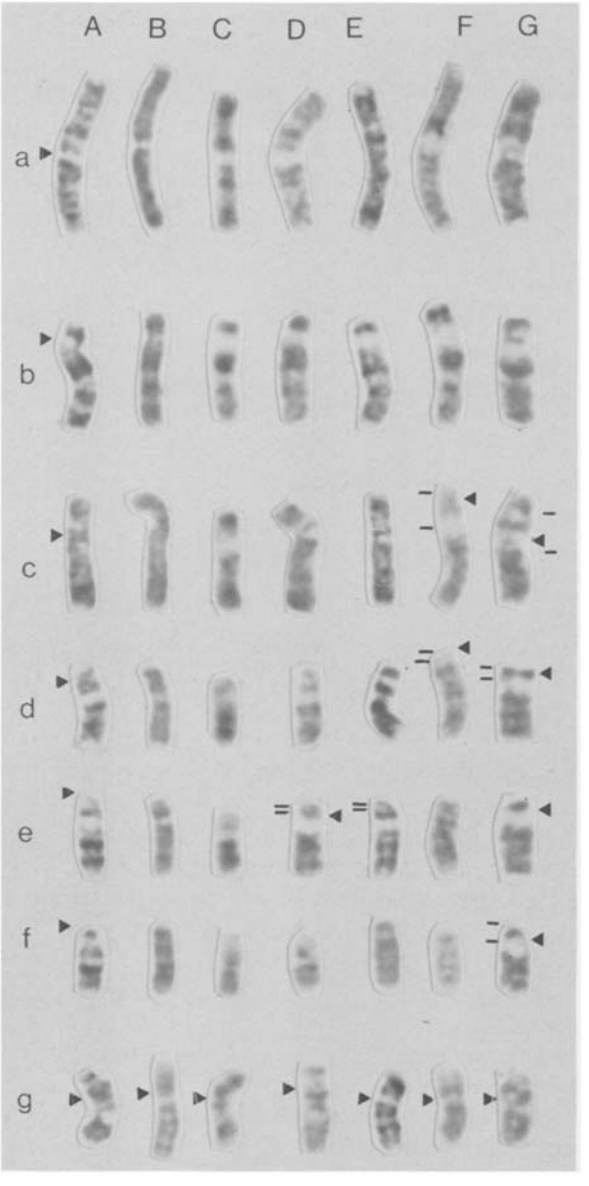

Fig. 29. G-banded comparisons of the macrochromosomes within the Lonchurae. Key: (a: chromosome 1; b: chromosome 2; c: chromosome 3; d: chromosome 4; e: chromosome 5; f: chromosome 6; g: Z-chromosome; A: *Lonchura castaneothorax*; B: *L. flaviprymna*; C: *L. malacca*; D: *Padda oryzivora*; E: *L. punctulata*; F: *L. pectoralis*; G: *Erythrura trichroa*.

Considering the extent of variation amongst the autosomes, it is surprising to find that the sex-chromosomes are relatively invariant within the Lonchurae. Apart from the telocentric Z-chromosome in *Amadina*, no other structural rear-

Table 2. Summary of structural chromosomal differences between species of Lonchurae (species abbreviations incorporate the first letter of the generic name and the first two letters of the specific name). The karyotype of LCA is used as a standard with which to compare those of the other species. The designations 'inv1', 'inv2', etc. refer to different pericentric inversions specific to each chromosome. The lack of a designation indicates that the chromosome morphology is that of LCA.

Chromosome	Species								
	LCA	POR	LPU	LST	LPE	LBI	CGO	ETR	AER	AFA
1	metacentric									inv1
2	acrocentric								inv1	inv1
3	sub-metacentric				inv1		inv2	inv2	inv3	inv3
Z	sub-metacentric								inv1	inv1
4	acrocentric				inv1		inv3	inv3	inv2	inv2
5	telocentric	inv1	inv1	inv1		inv2				
6	telocentric					inv1		inv2		
7	telocentric									
8	telocentric									inv1
9	telocentric							inv1		inv2
10	telocentric									inv1
11	telocentric									inv1

rangements were encountered for this chromosome (Fig. 29g). There is limited inter-specific variation for the presence or absence of centromeric and telomeric C-blocks, and only in *L. pectoralis* is there evidence of an intraspecific C-band polymorphism.

The W-chromosome is similarly highly conserved, there being only three recognizable morphs within the group. Both *L. castaneothorax* and *L. flaviprymna* have a large sub-metacentric W-chromosome which displays differential C- and G-banding. In all the other species the W-chromosome is a small heterochromatic element which is metacentric in *L. striata* and telocentric in the remainder.

The G-banded microchromosomes could not be reliably classified but, apart from intraspecific polymorphism, all the recognizable microchromosomes are telocentric in *Lonchura, Padda* and *Chloebia*. The two species of *Amadina* possess four pairs of metacentric microchromosomes while *E. trichroa* has two such pairs. Interspecific comparisons of diploid number and C-banding patterns suggest that inversions may again account for their origin.

Discussion

Patterns of chromosome change within the Lonchurae

The results of this study indicate that pericentric inversions have played a major role in chromosome repatterning within the Lonchurae. This is particularly apparent at the intra-specific level where inversion polymorphisms have been observed in *L. pectoralis* (this study) and *L. striata* (Ray-Chaudhuri, 1976). The condition in *L. punctulata* is of particular interest. Here inversion polymorphisms were recorded for chromosomes 5, 6, 7 and 8. In addition, there is considerable variation in the presence or absence of centromeric heterochromatin in individual macrochromosome homologues. There are two possibilities that could explain the existence of such a high degree of chromosomal polymorphism in this species. First, it is feasible that the different races of *L. punctulata* (see Goodwin, 1982) are chromosomally distinct and that the individuals examined are in reality inter-subspecific hybrids. Because all the birds studied in both the present study and the other published reports were obtained from avicultural sources, this cannot be discounted. Secondly, *L. punctulata* may be polymorphic throughout its range with no chromosomally distinct isolates. These chromosomal polymorphisms could then be maintained through

a selective advantage conferred on the heterozygotes. Shields (1973) and Thorneycroft (1966, 1975) invoke such an argument to explain inversion polymorphisms in the passerine genera, *Junco* and *Zonotrichia*. There is, however, no empirical evidence to suggest that heterozygotes are fitter than either of the homozygotes in either *Zonotrichia albicollis* or *Junco hyemalis*, despite some evidence for habitat partitioning between the chromosomal forms of *Junco* (Rising & Shields, 1980). Further sampling of native populations is obviously required before the basis of the chromosomal polymorphisms in *L. punctulata* can be determined. Nevertheless, the persistence of so many inversion polymorphisms in this species does suggest that the fertility of chromosomal heterozygotes is not impaired.

Apart from pericentric inversions, chromosomal evolution within the Lonchurae also involves changes in the amount and distribution of C-band heterochromatin, particularly amongst the microchromosomes. The majority of species of Lonchurae display both C-positive and C-negative microchromosomes, although *L. bicolor, L. striata* and *C. gouldiae* have few C-positive microchromosomes. Conversely, in *E. trichroa* there are large amounts of heterochromatin in both macrochromosomes and microchromosomes. The greatest amount of C-band variation is in the genus *Amadina* where all the microchromosomes of *A. erythrocephala* are C-band positive, while *A. fasciata* has few such microchromosomes. Since the number and relative size of the microchromosomes are constant in this genus, these C-band differences may represent a case of euchromatin transformation (King, 1980) in which a euchromatic segment is secondarily heterochromatised in order to protect essential gene combinations from recombination. Why such a phenomenon should involve all the microchromosomes in the one species but not the other is unclear.

If one considers the direction of chromosomal evolution within the Lonchurae as a whole, an interesting pattern emerges. There is a gradual change from a situation where all the macrochromosomes are biarmed, as in *L. bicolor*, to a karyotype consisting solely of telocentric macrochromosomes as in *A. fasciata*. Almost all the intermediate stages between these two extremes were observed in the present study. Furthermore, in each of these karyotypes, the largest macrochromosomes are always biarmed. Since there are grounds for the assumption that the ancestral karyotype had biarmed macrochromosomes (Christidis, in press), the attainment of a karyotype in which all macrochromosomes are telocentric may well have followed an orderly progression in the Lonchurae. Thus, pericentric inversions have occurred in all the macrochromosomes but those which convert a biarmed chromosome into a telocentric are not fixed until similar inversions have also converted all the smaller chromosomes into telocentrics. There are no such constraints on those inversions which do not alter the biarmed nature of a chromosome.

There are several examples in animals where a particular type of chromosomal change has occurred repeatedly within a lineage to produce a uniform karyotype. In iguanid lizards for example, a series of fusions has led to the production of an entirely metacentric karyotype (King, 1981). White (1973, 1975) has termed this phenomenon karyotypic orthoselection and suggests two main explanations to account for it.

The first assumes that similar rearrangements have similar phenotypic effects and hence are adaptive in the same environment. The classic example of this situation, found in the mollusc *Thais lapillus* (Staiger, 1954) where chromosomal dissociations predominate in populations adapted to either sheltered (2n = 36) or exposed (2n = 26) localities, has now been seriously questioned because the associations between karyotype and environment are not as rigid as once believed (Bantock & Page, 1976). No obvious adaptational trends within the Lonchurae can be correlated with the observed chromosomal changes and thus there is no basis for accepting an external-adaptational hypothesis of the kind formulated by White (1975).

The second explanation involves the presumed need for the numbers, sizes and shapes of the chromosomes to be compatible with the dimensions of the spindle and the surrounding cytoplasm of the cell in order to allow for regular separation at division (White, 1973, p. 407). Such cytomechanical constraints do not appear to apply in avian karyotypes which regularly consists of both large and minute chromosomes. At present, no functional significance can be attributed to the patterns of chromosome change observed in the Lonchurae.

Relationships between hybrid fertility and karyotype

Although interspecific hybrids between lonchurine species are common in captivity, there are few crosses in which unambiguous data are available on the fertility of the hybrids. It is of interest to relate the only cases of this kind with the chromosomal data reported in the present study.

Crosses between *L. castaneothorax* and *L. flaviprymna* are known to produce fully fertile hybrids as also do crosses between *L. cantans* and *L. malabarica* (Gray, 1958). There are no fixed chromosomal differences between either pair of species and they are considered to be conspecific by some authors (Delacour, 1943; Wolters, 1957).

More interesting are those crosses producing sterile or partially sterile hybrids. Crosses of *L. cantans* and *L. malabarica* with either *L. striata* or *L. malacca* produce infertile hybrids even though only minor chromosome differences distinguish the species. In these cases therefore, there are grounds for concluding that genic differences affecting either gonadal or gametic development may be the cause of hybrid sterility. Conversely, crosses involving *L. castaneothorax* with either *L. maja* or *L. malacca* produce fertile males but sterile females. The hybrid females are sterile as a result of incomplete gonadal development (see references in Gray, 1958) yet, with the exception of the W-chromosome, the parental species share an identical karyotype. *L. castaneothorax* has a large W-chromosome which displays differential G- and C-banding, while *L. malacca* has a much smaller W-chromosome which is uniformly banded. Thus the possibility exists that neither of the W-chromosomes are compatible with a hybrid genetic background in these particular species. Such a possibility is consistent with the view that the W-chromosome controls the development of the ovaries in female birds (Mittwoch, 1971). Moreover, the available data, as reviewed for both the Lonchurae (present study) and Poephilae (Christidis, in press) suggest that genic factors affecting gonadal development and not chromosomal rearrangements are primarily responsible for determining hybrid fertility.

Chromosomal phylogeny of the Lonchurae

The chromosomal data can be used to construct a phylogeny for the Lonchurae. The approach used has been described in detail elsewhere (Christidis, in press) and is based on the method of Hennig (1966). As discussed in Christidis (loc. cit.), chromosome morphologies shared with *Poephila guttata* are assumed to reflect the primitive condition for the Estrildidae and so cannot be used in determining phylogenetic relationship. While the chromosomal data do not allow the determination of distinct lineages within the Lonchurae, they do permit the recognition of five distinct chromosomal groups (Fig. 30).

The genus *Amadina* forms a highly derived group with up to nine pericentric inversions separating *A. fasciata* from the presumed primitive karyotype. The second group, comprising *E. trichroa* and *C. gouldiae*, is defined by derived inversions on chromosomes 3 and 4. *E. trichroa* also possesses uniquely derived inversions on chromosomes 6, 9 and 12. The chromosomal data confirm the presumed close affinities between *Chloebia* and *Erythrura* (Ziswiler *et al.*, 1972), and support their treatment as part of the Lonchurae (Mayr, 1968).

The next three groups largely concern species currently included in the genus *Lonchura*. Derived inversions on chromosomes 3 and 4 distinguish *L. pectoralis* from the rest of its congeners. This species has sometimes been included in its own monotypic genus *Heteromunia* (Immelmann, 1965), although the currently accepted classification gives

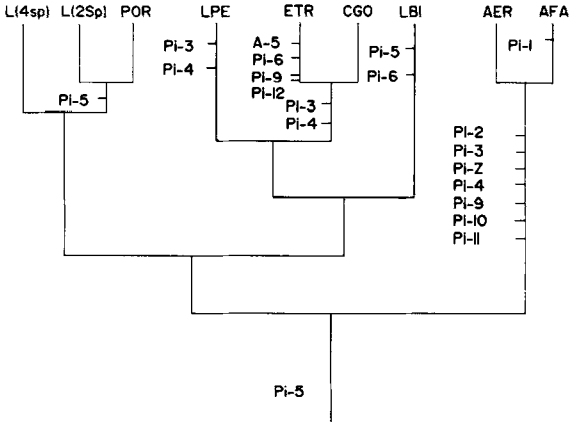

Fig. 30. Chromosomal relationships within the Lonchurae. Key: L: *Lonchura*; POR: *Padda oryzivora*; LPE: *Lonchura pectoralis*; ETR: *Erythrura trichroa*; CGO: *Chloebia gouldiae*; LBI: *Lonchura bicolor*; AER: *Amadina erythrocephala*; AFA: *Amadina fasciata*. Pi: pericentric inversions; A: heterochromatic addition; Number following either Pi- or A- refers to the specific chromosome.

Heteromunia subgeneric status (Mayr, 1968). The chromosomal data are consistent with generic separation of *L. pectoralis*. Both *Amadina* and *L. pectoralis* possess a telocentric pair 4 but electrophoretic data (Christidis, unpublished results) indicates that this is a convergence.

The next distinct group comprises *L. bicolor* which displays derived inversions on chromosomes 5 and 6. This lineage appears monotypic due to the lack of availability of closely related species and further work is required before its exact affinities can be determined.

In the final group are included *P. oryzivora*, and the remaining species of *Lonchura*. Of these, *L. castaneothorax, L. flaviprymna, L. maja* and *L. malacca* have identical autosomal karyotypes, while *L. punctulata, L. striata* and *P. oryzivora* share an acrocentric pair 6. That *Padda* shares an identical karyotype with other members of the *Lonchura* suggests that it is not a distinct genus. The morphological differences used to justify its separation have also been questioned frequently (Wolters, 1957; Guttinger, 1976; Goodwin, 1982) and an amalgamation of the two genera would be consistent with the chromosomal data.

Finally, the karyotypes of *L. cantans* and *L. malabarica*, which have been previously reported (Hirschi *et al.*, 1972; Kaul & Ansari, 1974; Ray-Chaudhuri, 1976; Prasad & Patnaik, 1977) can also be incorporated into this scheme. The karyotypes of both are identical to that of *L. castaneothorax* despite the report of Ray-Chaudhuri (1976), who found autosomes 5 and 6 to be biarmed, whereas they are clearly telocentric in all the other studies. This may represent a polymorphism or else reflect population differentiation. Even so, these two species belong to the *L. castaneothorax* chromosomal group, an alignment consistent with behavioural studies (Kunkel, 1959; Baptista, 1973), and contrary to their current segregation into a separate subgenus (Mayr *et al.*, 1968).

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