

New Karyotypic Data on 15 Genera of Lizards in the Family Iguanidae, With a Discussion of Taxonomic and Cytological Implications

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Abstract. Karyotypic data are presented for 14 species of iguanid lizards assigned to 14 genera and for 9 species of iguanids in the genus *Anolis*. A basic chromosomal formula of six pairs of large metacentric chromosomes and 12 pairs of microchromosomes characterizes many of the representatives of the family: *Oplurus sebae* from Madagascar; eight species of *Anolis*; the anoline species *Anisolepis grilli*; the large iguanines *Ctenosaura pectinata*, *Cyclura cornuta*, *Iguana iguana* and *Sauromalus obesus*; the basiliscine *Basiliscus vittatus*; and two tropidurines, *Tropidurus torquatus* and *Leiocephalus schreibersi*. Within the tropidurines there has been chromosome evolution. *Liolaemus lutzae* has only 11 pairs of microchromosomes, the largest of which is considerably larger than the others and probably represents centric fusion from the original 12 pairs. *Plica plica* differs from the other tropidurines and all other iguanids examined in having eight pairs of macrochromosomes – four metacentric pairs and four acrocentric pairs. Evidence is presented to show that this is a condition derived from six pairs of metacentrics. The sceloporine *Uma notata* is characterized by six pairs of metacentric macrochromosomes and 11 pairs of microchromosomes. A reduced number of microchromosomes from the presumably primitive number of 12 also characterizes all other sceloporines listed in the literature. *Cupriganus achalensis*, a recently described genus and species, also has 12 macrochromosomes and 24 microchromosomes. The largest pair of microchromosomes appears heteromorphic in the male. *Anolis auratus* has seven pairs of macrochromosomes and eight pairs of microchromosomes; this is typical of the group within *Anolis* to which it belongs. This species is a beta *Anolis*, a group that was characterized in the literature as having seven pairs of metacentric macrochromosomes. The other major subgroup of *Anolis* has the more typical six pairs of macrochromosomes. One species of iguanid, *Polychrus marmoratus*, has a karyotype so different from the remainder of the family that it is impossible to assess its relationship. There are 20 acrocentric chromosomes and ten microchromosomes in the female. In male meiosis there are 14 bodies, 13 bivalents and a presumed sex trivalent. The diploid number is 29;

there are 19 acrocentric and one metacentric macrochromosomes and nine microchromosomes. This is interpreted as an X_1X_2Y sex-determining mechanism.

Introduction

R. MATTHEY (1949) reviewed the data on karyotypes of lizards. Most species have a sharp break between macro (M) and micro (m) chromosomes. A formula of 12 metacentric M chromosomes and 24 m chromosomes characterizes at least one species in several diverse families: Iguanidae, Agamidae, Chamaeleontidae, Gerrhosauridae and Amphisbaenidae. It appears that this formula has been evolved in parallel several times and that once this condition is attained it is conservative.

The first definitively established iguanid karyotype was that of *Anolis carolinensis* (MATTHEY, 1931). HALL (1965) has summarized all available information on iguanid karyotypes. He listed the formula 12 metacentric M and 24 m for the following genera: *Anolis*, *Crotaphytus*, *Dipsosaurus* and *Phrynosoma*. HALL characterized the genera termed 'sceloporine' (not a formal subfamilial designation; see ETHERIDGE, 1964) as having 12 metacentric M chromosomes and a reduced number of microchromosomes, ranging from 10 to 22. HALL's data include members of the genera *Holbrookia*, *Callisaurus*, *Urosaurus*, *Uta* and *Sceloporus*.

Karyotypic variation in *Anolis* has been discussed by GORMAN (1965) and GORMAN and ATKINS (1966). This was found to conform rather well to the classification of ETHERIDGE (1960), which divides *Anolis* into alpha and beta major groups. The beta anoles appear to be characterized by 14 macrochromosomes and a series of microchromosomes. In most species these macrochromosomes are all metacentric, but in *A. biporcatus* and *A. conspersus* there is male chromosomal heteromorphism and one of the macrochromosomes is acrocentric (GORMAN and ATKINS, 1966).

Most alpha *Anolis* have the more typical pattern of 12 metacentric M chromosomes and a series of microchromosomes. However, at least one species group of alpha anoles, the Lesser Antillean *bimaculatus* group, has an increased number of macrochromosomes, which decrease gradually in length so that the break between macro and micro is not sharply differentiated. This species group also has a complex sort of male chromosomal heteromorphism.

Materials and Methods

A microtechnique modified from the method of MOORHEAD *et al.* (1960) for culturing peripheral blood leukocytes was used to obtain metaphase plates. The medium consisted of 20% fetal calf serum and 80% mixture 199. Blood was obtained by cardiac puncture or after decapitation. Leukocytes were cultured for four days or eight days at 30°C. Twenty-four hours prior to harvesting, Colcemid was added to the cultures to accumulate cells in metaphase.

In addition, direct preparations of gonads were made without culture or Colcemid treatment. To obtain meiotic figures, testes were minced in 0.7% sodium citrate at room temperature for 10 to 15 min. The cell suspension was centrifuged, the supernatant removed, and the cells were then immediately mixed in 3:1 methanol-acetic acid fixative. The fixed cells were recentrifuged, the old fixative was then removed, and a small volume (0.5 to 2.0 ml, depending upon the size of the pellet) of fresh fixative added. The cells were resuspended in this fresh fixative, and air-dried slides were made as in the leukocyte culture method.

Our attempts to study meiosis in female lizards have so far been unsuccessful. Human chorionic gonadotropin was injected into female lizards in an attempt to induce superovulation (JAGIELLO, 1965). Although meiotic figures were not seen, the hormone treatment seemed to induce a high mitotic rate in the ovaries of treated animals. Ovaries were prepared in the manner outlined for testes.

Results

We have examined four species grouped by SAVAGE as iguanines (SAVAGE, 1958). *Ctenosaura pectinata*, *Cyclura cornuta*, and *Iguana iguana* were borrowed from various sources; their sex was not determined. A female *Sauromalus obesus* was examined. All these four species have the typical iguanid karyotype of 12 metacentric macrochromosomes and 24 microchromosomes (Fig. 1).

Basiliscus vittatus, a basiliscine closely related to the iguanines (ETHERIDGE, 1964), also appears to have the typical iguanid karyotype. We examined meiotic chromosomes of a male and found that there are six pairs of macrochromosomes and 12 pairs of microchromosomes. In mitosis there are 12 macrochromosomes and 24 microchromosomes (Fig. 2).

One sceloporine, *Uma notata*, was examined. As in the sceloporines cited by HALL (1965), there is a reduced number of microchromosomes. Diakinesis shows six large bivalents and 11 microbivalents. At mitotic metaphase there are 12 metacentric M chromosomes and 22 m chromosomes (Fig. 3).

Four species grouped by ETHERIDGE (1964) as tropidurines were examined. Two of them, *Leiocephalus schreibersi* from Haiti and

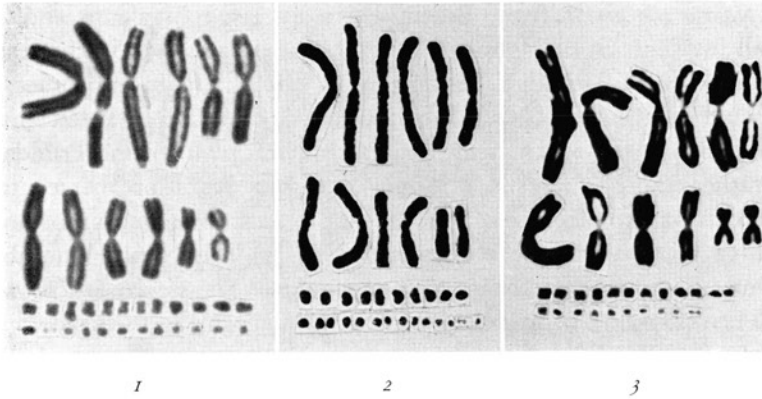


Fig. 1. Karyotype of the iguanine *Ctenosaura pectinata* showing 12 metacentric macrochromosomes and 24 microchromosomes (leukocyte culture). Giemsa stain.

Fig. 2. Karyotype of the basiliscine *Basiliscus vittatus* (male) showing 12 metacentric macrochromosomes and 24 microchromosomes (mitosis from testis). Giemsa stain.

Fig. 3. Karyotype of male *Uma notata* showing 12 metacentric macrochromosomes and 22 microchromosomes (leukocyte culture). Giemsa stain.

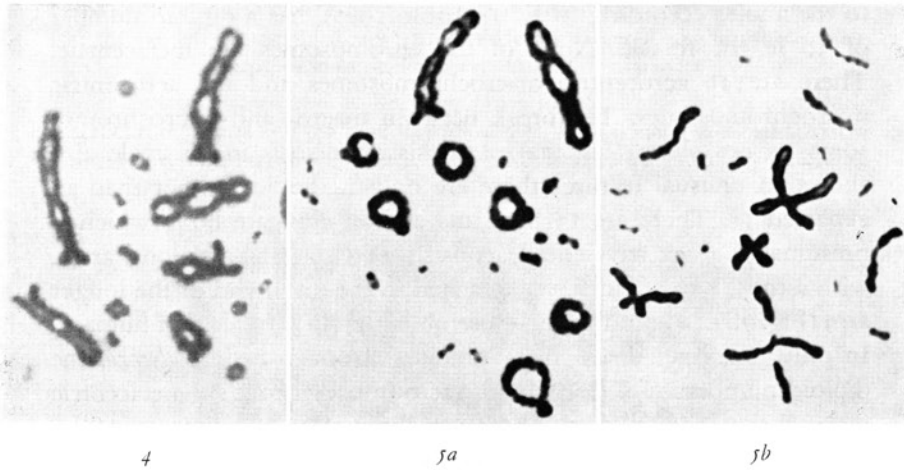


Fig. 4. Diakinesis in the tropidurine *Tropidurus torquatus*. There are six large and 12 small bivalents. Giemsa stain.

Fig. 5. *Plica plica*. *a*. Diakinesis. Eight large bivalents and 12 small bivalents are shown. *b*. Metaphase II. Four metacentric and four acrocentric macrochromosomes are clearly shown. Giemsa stain.

Tropidurus torquatus from Brazil, have six large bivalents and 12 small bivalents in diakinesis (Fig. 4). Mitoses were seen in the testis of *Tropidurus*. Although resolution of the microchromosomes is difficult, it appears that there are 24 of these, as well as 12 metacentric macrochromosomes. A third species, *Plica plica* from Trinidad, is rather more interesting. There are four pairs of metacentric macrochromosomes, four pairs of acrocentric macrochromosomes and 12 pairs of microchromosomes (Fig. 5). The diploid number is thus 40, the highest known in the iguanidae. The *nombre fundamental* (MATTHEY, 1949), or number of chromosomal arms in the karyotype, is identical in *Plica* and the two tropidurines mentioned above. That is, the 12 metacentric microchromosomes correspond to 24 macrochromosomal arms, as do 8 metacentric (= 16 arms) and 8 acrocentric (= 8 arms) macrochromosomes. *Liolaemus lutzæ* from Brazil is the fourth tropidurine species that we examined. In diakinesis there are six macrobivalents and only 11 microbivalents, the largest of which is considerably larger than all the rest. At mitotic metaphase there are 12 metacentric macrochromosomes, two large 'microchromosomes' and 20 small microchromosomes (Fig. 6).

One species of iguanid differs significantly in karyotype from all others known to the authors. *Polychrus marmoratus*, closely related to the anoles according to ETHERIDGE (1960), has a diploid number of 30 in the female. None of the chromosomes are metacentric. There are 20 acrocentric macrochromosomes and ten acrocentric microchromosomes. The break between macro- and microchromosomes is not sharp (Fig. 7a). Analysis of meiosis in the male also shows an unusual feature; there are only 14 bodies, rather than an expected 15. There are 13 bivalents and an elongate body which is presumably a sex trivalent. It consists of two subequal long arms, with a third arm of small size attached to the distal end of the longer arm (Fig. 7b); in appearance, it resembles the X-Y bivalent of humans. In only one metaphase plate obtained from a male *Polychrus* the diploid number is 29. There are 19 acrocentric and one submetacentric macrochromosomes. Thus there are three unpaired chromosomes: an acrocentric (X_1), a microchromosome (X_2) and the submetacentric (Y) chromosome. Although only one metaphase plate was seen, the sex-chromosome findings correspond to the trivalent in meiosis (Fig. 7c). This same sex-determining mechanism has independently evolved at least twice in the genus *Anolis* (GORMAN and ATKINS, 1966).

Anisolepis grilli, an anoline species from Brazil, is characterized by

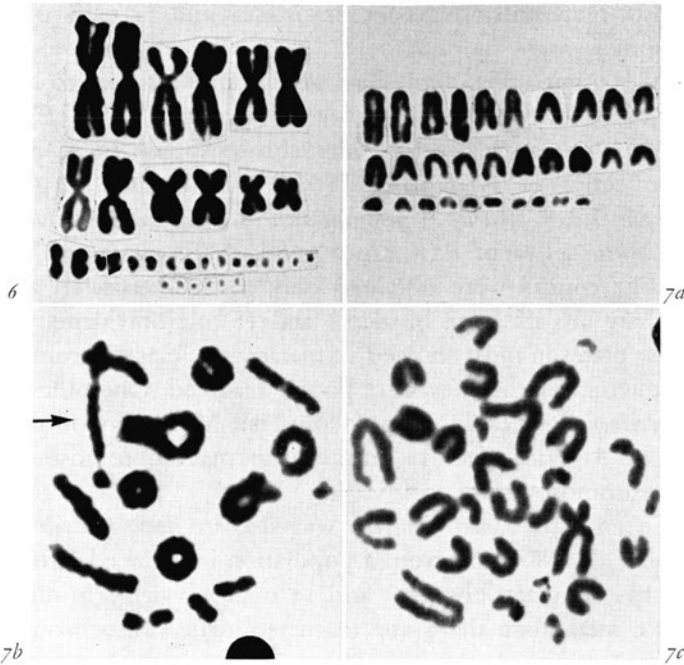


Fig. 6. Karyotype of *Liolaemus lutzae* (male) showing 12 metacentric macrochromosomes and 22 microchromosomes. The largest pair of microchromosomes (on the far left of the third row) is considerably larger than the other microchromosomes (leukocyte culture). Giemsa stain.

Fig. 7. *Polychrus marmoratus*. a. Karyotype of a female. There are 20 acrocentric macrochromosomes and ten microchromosomes. b. Diakinesis in a male. Arrow points to presumed trivalent. Giemsa stain. c. Mitosis in a male (leukocyte culture).

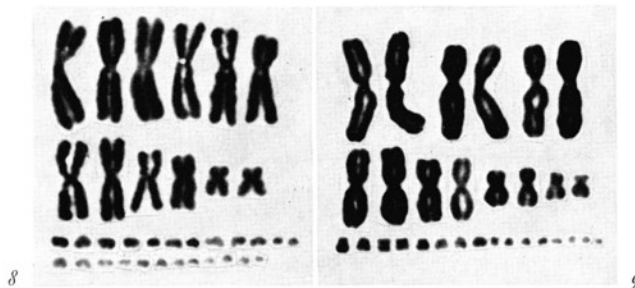


Fig. 8. Karyotype of male *Anolis equestris*. There are 12 metacentric macrochromosomes and 24 microchromosomes. Giemsa stain.

Fig. 9. Karyotype of male *Anolis auratus*. There are seven pairs of metacentric macrochromosomes and eight pairs of microchromosomes. Giemsa stain.

six pairs of metacentric macrochromosomes and 12 pairs of microchromosomes.

Several Haitian alpha *Anolis* that were examined seem to have the typical iguanid and alpha anole karyotype (GORMAN, 1965) of 12 metacentric M chromosomes and 24 microchromosomes. In *A. coelestinus* (*coelestinus* series of ETHERIDGE, 1960) we obtained meiotic and mitotic cells. In *A. olssoni*, *A. semilineatus*, *A. hendersoni*, *A. chlorocyanus* (all *carolinensis* series of ETHERIDGE) and *A. ricordi* (*ricordi-roosevelti* series) clear counts were obtained only in diakinesis. In all these species there are six large bivalents and 12 microbivalents. Mitotic metaphase plates in most showed 12 metacentric macrochromosomes, but the microchromosomes were poorly resolved. One other species in the *carolinensis* series, *A. allisoni* from Half Moon Cay off the coast of Central America, has 12 metacentric macrochromosomes and 24 microchromosomes.

The Cuban giant *Anolis equestris* was also studied. A male sent to us by Mr. C. R. WARREN from a population introduced into Miami, Florida, has six macrobivalents and 12 microbivalents in diakinesis. In mitotic metaphase there are 12 metacentric macrochromosomes and 24 microchromosomes (Fig. 8).

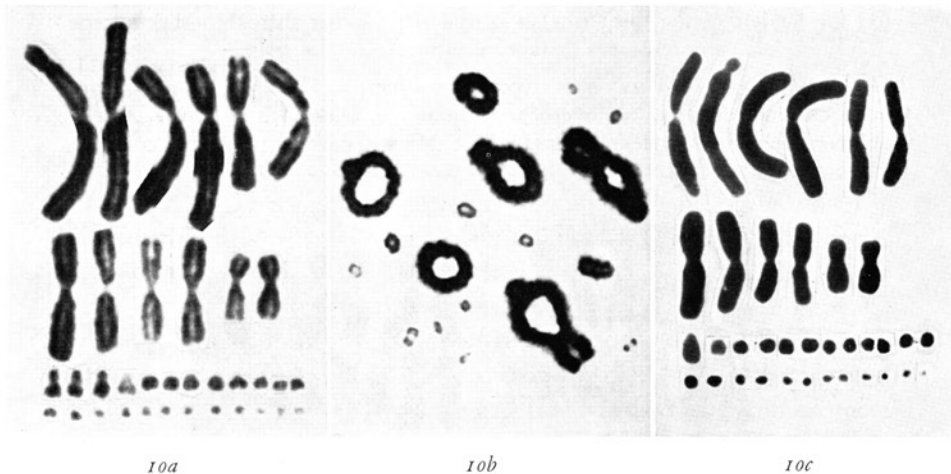


Fig. 10. *a.* Karyotype of female *Oplurus sabbae* (leukocyte culture) showing 12 metacentric macrochromosomes and 24 microchromosomes. Giemsa stain. *b.* Diakinesis in *Cupriganus achalensis*. There are six large and 12 small bivalents. *c.* Karyotype of *C. achalensis* (mitosis from testis) showing 12 macrochromosomes and 24 microchromosomes. The largest pair of microchromosomes appears heteromorphic.

Chromosome Complements of Iguanid Lizards

Species	Sex	No. of macro- chromosomes ¹ (M)	No. of micro- chromosomes (m)	2n	Male meiosis		
					M	m	n
<i>Ctenosaura pectinata</i>	undetermined	12	24	36	—	—	—
<i>Cyclura cornuta</i>	undetermined	12	24	36	—	—	—
<i>Iguana iguana</i>	undetermined	12	24	36	—	—	—
<i>Sauromalus obesus</i>	female	12	24	36	—	—	—
<i>Basiliscus vittatus</i>	male	12	24	36	6	12	18
<i>Uma notata</i>	male	12	22	34	6	11	17
<i>Tropidurus torquatus</i>	male	12	24	36	6	12	18
<i>Leiocephalus schreibersi</i>	male	12	—	—	6	12	18
<i>Liolaemus lutzae</i>	male	12	22	34	6	11 ²	17
<i>Plica plica</i>	male	16 ³	—	—	8	12	20
<i>Polychrus marmoratus</i>	female	20 ⁴	10	30	—	—	—
<i>Polychrus marmoratus</i>	male	20 ⁴	9	29	10	4	14 ⁵
<i>Anisolepis grilli</i>	male	12	24	36	6	12	18
<i>Anolis auratus</i>	male	14	16	30	7	8	15
<i>Anolis chlorocyanus</i>	male	12	24	36	6	12	18
<i>Anolis coelestinus</i>	male	12	24	36	6	12	18
<i>Anolis olssoni</i>	male	12	—	—	6	12	18
<i>Anolis semilineatus</i>	male	—	—	—	6	12	18
<i>Anolis hendersoni</i>	male	—	—	—	6	12	18
<i>Anolis ricordi</i>	male	—	—	—	6	12	18
<i>Anolis allisoni</i>	male	12	24	36	—	—	—
<i>Anolis equestris</i>	male	12	24	36	6	12	18
<i>Oplurus sebae</i>	female	12	24	36	—	—	—
<i>Cupriganus acbalensis</i>	male	12	24 ⁶	36	6	12	18

¹ All macrochromosomes are metacentric unless otherwise noted.² One large microbivalent.³ Eight acrocentric and eight metacentric.⁴ All acrocentric in female, one submetacentric in male.⁵ Sex trivalent included.⁶ Heteromorphic pair of microchromosomes.

Anolis auratus, a beta anole from Panama, like the beta species previously reported (GORMAN, 1965), has 14 macrochromosomes, all metacentric. There are 16 microchromosomes. The diploid number is thus 30 (Fig. 9).

Two species of iguanids were studied whose relationships within the family are not particularly clear. *Oplurus sebae* from Madagascar has the common formula of 12 large metacentric macrochromosomes and 24 microchromosomes (Fig. 10a). A female of this species was made available to us through the courtesy of Mr. CHARLES SHAW and the San Diego Zoo.

A male of the recently described genus and species *Cupriganus achalensis* (GALLARDO, 1964) also has 12 metacentric M chromosomes and 24 microchromosomes. At diakinesis there are six large bivalents and 12 microbivalents (Fig. 10b, c). One of these microbivalents appears considerably larger than the other micros. This largest pair of microchromosomes seems to account for a heteromorphic pair of chromosomes at mitotic metaphase.

Results are summarized in the table.

Discussion

Knowledge of the karyotype of iguanids can yield some information on classification and evolutionary relationships within the family. Reciprocally, detailed knowledge of evolution in the group, as elucidated by morphological studies, gives us strong inference about the history of chromosome evolution.

In general, we are struck by the seeming conservativeness of karyotype. Before the present investigation was undertaken, karyotypes of only North American and a few Antillean forms had been described. We now see that 12 metacentric macrochromosomes and 24 microchromosomes characterize diverse genera within the family throughout its range. There is little difference in karyotype of species from Madagascar, Brazil, the Antilles and North America.

WHITE (1954, p. 195) remarks that karyotypic identity in many distantly related lizard groups "would not be encountered with such regularity if the structural changes which have become established in phylogeny were of all possible types. It seems, rather, that in many groups chromosome after chromosome has undergone the same types of structural change, so that they have all retained a similar

morphology." WHITE calls this the *principle of homologous change* (p. 196). He postulates that the distribution of macro- and microchromosomes represents a mechanically satisfactory structural arrangement. There can be little doubt that the identical karyotype of 12 M and 24 m is a manifestation of canalized parallel evolution in various lizard families. Whether modern sub-groups of the Iguanidae have independently evolved this formula, or whether it is a primitive conservative character at the family level, remains unsolved. However, our evidence does not controvert the latter interpretation.

MATTHEY'S (1949) concept of the *nombre fondamental (n.f.)* proves quite valuable for the Reptilia. However, it should be restricted to the number of major chromosome arms. In MATTHEY'S (1949) review a metacentric macrochromosome has two arms, an acrocentric, one arm. A microchromosome is also counted as one arm. We have little basis for evaluating the microchromosomes in relation to the macrochromosomes. Furthermore, although resolution is difficult, some of the microchromosomes in some of the species are clearly metacentric (see Figs. 1 and 10 of *Ctenosaura* and *Oplurus*). If we consider only the number of macrochromosomal arms, then all known iguanids, with the exception of *Polychrus marmoratus* and some *Anolis*, have 24.

Figure 11 is adapted from ETHERIDGE (1964) with chromosome numbers added. This phylogeny shows only the part of the family

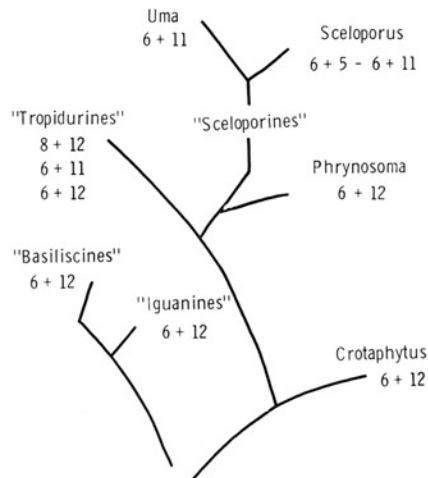


Fig. 11. A possible phylogeny of some iguanid groups, following ETHERIDGE (1964). Numbers indicate the haploid number of macro- and microchromosomes.

which he considered in that work. Our data appear to uphold this phylogeny. Chromosome loss would be of a specialized, advanced character, and this correlates with the phylogenetic position of the sceloporines. Whether microchromosomes are actually lost or are incorporated into one of the larger elements is not clear. Our data on *Uma* do not suggest incorporation. However, resolution of a minute increase, if fused into the macrochromosomal complement, would be extremely difficult.

The tropidurines that we studied are extremely interesting. Two species (*Tropidurus torquatus* and *Liocephalus schreibersi*) have the typical formula of six pairs of macrochromosomes and 12 pairs of microchromosomes. *Liolaemus lutzæ* has only 11 pairs of small elements; but, in this case the largest pair of microbivalents is considerably larger than the others and appears to be derived by centric fusion. Complete loss of a chromosome pair seems to be a relatively rare event in evolution, at least in insect groups studied in detail (WHITE, 1954, p. 184).

Plica plica is most intriguing. It will be recalled that this species has eight metacentric and eight acrocentric macrochromosomes, in contrast to the more widespread formula of 12 metacentric macrochromosomes. According to ETHERIDGE (personal communication), who is studying the osteological relationships of iguanids, "*Plica plica* has lost certain elements present in other tropidurines and therefore could not be ancestral to the others." There is, therefore, no evidence that *Plica plica* is a primitive aberrant relict among the iguanids. To account most simply for its karyotype, we must postulate an increase in chromosome number as a result of centric fission – for the number of macrochromosomal arms is identical in *Plica plica* and the other tropidurines. This hypothesis is one of several mechanisms discussed by WHITE (1963), who states, however, that this mechanism is less common than centric fusion.

Detailed discussion of evolution in the genus *Anolis* will be presented in future papers by the authors. The alpha, beta dichotomy – neglecting further specializations within these groups – does merit comment. In the majority of alpha *Anolis*, there are 12 metacentric macrochromosomes and a series of microchromosomes. Comparison of Figures 8 and 9 which show an alpha anole and a beta anole, shows that in the beta anole the seventh pair of metacentric macrochromosomes is relatively small, thus reducing the break between macro- and microchromosomes. Also, in the beta anole the number

of microchromosomes is reduced from 24 to 16. This is exactly the sort of variation shown to occur in the chromosomes of the Chamaeleontidae by MATTHEY (1957) and by MATTHEY and VAN BRINK (1960). They recognize in the chameleons one major group with 12 metacentric macrochromosomes and a series of microchromosomes (ranging from 12 to 24); a second group has a less sharply defined break between M and m, the number of metacentric and submetacentric M chromosomes being 14, 16 and 18, the number of microchromosomes being 14 or 18. Groups three and four of MATTHEY and VAN BRINK (1960) lack a sharp separation between macro- and microchromosomes. In group four there is a strong tendency towards acrocentric macrochromosomes.

It is quite possible that the beta karyotype has evolved by means of complex centric fusions, reducing the number of microchromosome pairs by four in forming an additional macrochromosomal pair.

Polychrus marmoratus is anomalous. ETHERIDGE (1960, p. 113) states that "among iguanid lizards *Polychrus* shows the closest affinities with the anole group – the very close correspondence in multiple characters is an indication of true relationship." Despite the karyotypic variation within *Anolis*, we know of no species which does not have at least six pairs of metacentric macrochromosomes. Yet *Polychrus marmoratus* has no metacentric chromosomes. There is, in fact, no obvious relationship between the karyotype of *Polychrus marmoratus* and the remainder of the iguanids. It may represent a very specialized line which evolved acrocentric chromosomes from metacentrics by pericentric inversion and subsequently lost elements to reduce the diploid number to 30 from the primitive 36. Perhaps *Aptycholaemus*, another iguanid genus that ETHERIDGE believes close to the anole group, will, when studied, give us some hints about the evolutionary sequence involved. There are also other species of *Polychrus* to be examined. However, *Anisolepis*, also supposedly related to both *Anolis* and *Polychrus*, has a karyotype similar to that of the typical alpha anoles and thus sheds no light on the relationship between *Polychrus* and *Anolis*.

The distribution of iguanids today is New World, with presumed relicts in Madagascar and outliers in Fiji and the Galapagos. There is nothing peculiar about the chromosomes of the Madagascar iguanid *Oplurus sebae* that can give us any hint of the relationship of the Madagascar genera to other iguanids.

Our results on the recently described *Cupriganus achalensis* are

suggestive of an X-Y sex chromosome heteromorphism in the largest pair of microchromosomes. This remains to be confirmed.

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