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LIZARD KARYOTYPES FROM THE GALAPAGOS ISLANDS: CHROMOSOMES IN PHYLOGENY AND EVOLUTION

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ABSTRACT. The iguanid lizards, *Conolophus subscristatus, Tropidurus albemarlensis, T. delanonis,* and *T. duncanensis* have similar $2n = 36$ karyotypes. *C. subcristatus* has a 12 metacentric macrochromosome and 24 microchromosome karyotype that is here shown to be primitive for the Iguanidae and probably for all lizards, while the three Galapagos *Tropidurus* have identical patterns to *Tropidurus* species from eastern South America and differ from the primitive karyotype of *C. subcristatus* by non-Robertsonian modifications of three pairs of macrochromosomes.

All available karyotypic data for the Iguanidae are summarized and used to discuss how one may determine which karyotypes are "primitive" within radiations and what possible roles Robertsonian karyotypic variation may play in the process of evolution. Analysis of karyotypic and systematic information suggests a causal relationship between karyotypic differentiation and the rapid proliferation of new species, such that the need for geographic isolation seems to be minimized by the chromosomal differentiation.

INTRODUCTION

Among the karyotypically well-studied families of squamate reptiles, the iguanid lizards are known to show great chromosomal diversity, with most of the variation apparently resulting from Robertsonian mutations (centric fusions and/or fissions) (Gorman, 1973; Hall, 1973). To more fully understand the biological significance and evolution of this diversity, workers

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at the Museum of Comparative Zoology have been accumulating karyotypes for as many and diverse iguanid species as possible. As part of this program, during the winter of 1969-70 Paull was able to karyotype four iguanid species from the Galapagos Islands. Two of the four principal phyletic branches of the family, the "iguanines" and the "tropidurines" (Savage, 1958; Etheridge, 1964) are represented in these islands, and both were sampled in the study. All four species showed a 2n = 36, 12 metacentric macrochromosome, 24 microchromosome pattern which is believed by some to be primitive for the Iguanidae or, indeed, for all lizards (Gorman et al., 1967, 1969; Webster et al., 1972; Gorman, 1973).

Addition of karyotypes for these four species to our data base provides the occasion to discuss the evidence of "primitiveness" for karyotypes within a radiation and the role Robertsonian karyotypic variation may play in the process of evolution. However, we must first describe the karyotypes of the Galapagos lizards sampled.

KARYOTYPES OF GALAPAGOS IGUANIDS

(D. PAULL AND W. P. HALL)

Specimens examined: Representatives of two distantly related branches of the Iguanidae have reached the Galapagos, presumably by overwater colonization. The iguanine species in the Galapagos belong to the endemic genera *Amblyrhynchus* (one species, the marine iguana) and *Conolophus* (two species of land iguanas). Of these, *Conolophus subcristatus* was karyotyped. The tropidurine radiation is represented in the archipelago by eight endemic species of *Tropidurus* (lava lizards). Additionally, *Tropidurus* has a South American continental radiation of 12 species (Etheridge *in* Peters and Donoso-Barros, 1970). Island species karyotyped were *Tropidurus albemarlensis, T. delanonis* and *T. duncanensis.* Table 1 lists the species karyotyped and their collection localities.

Methods: All chromosome preparations were made in the Galapagos Islands using laboratory facilities kindly supplied by the Charles Darwin Research Station on Santa Cruz Island. Cells were spread for karyotyping by air drying smears of methanol:acetic acid (3:1) fixed suspensions of testis, bone marrow or spleen tissues prepared directly from colchicine pretreated animals. The techniques used were similar to those of Evans et

Table 1

Galapagos specimens karyotyped

species	locality	individuals karyotyped
Conolophus subcristatus	South Plazas Id., Las Plazas	1
Tropidurus albemarlensis	South Plazas Id., Las Plazas	6
Tropidurus albemarlensis	Bartolome Id., Sullivan Bay	4
Tropidurus albemarlensis	Santa Cruz Id., between Galapagos Hotel and Darwin Station	6
Tropidurus delanonis	Hood Id., behind beach, Gardiner's Bay	5
Tropidurus duncanensis	Duncan Id., small cove on NE end	2

al. (1964), Bianchi and Contreras (1967) and Patton and Hsu (1969).

Results: All species had 36 chromosomes, with 12 biarmed macrochromosomes and 24 microchromosomes (Fig. 1). No cytologically distinct sex chromosomes or intrageneric variation of any kind was seen. However, conspicuous differences in arm ratios and relative sizes of the macrochromosomes were noted between the genera (Fig. 1).

In *Conolophus subcristatus* (Fig. 1, lower), taking the macrochromosomes in order of size, beginning with the largest, pair one is very slightly submetacentric; pair two is distinctly submetacentric, with the long arm slightly less than twice as long as the short; pairs three and four are almost exactly metacentric and, in many spreads, indistinguishable in size; pair five is nearly metacentric; and pair six is submetacentric, with the long arm about 1.5 to 2.0 times the length of the short arm. Pairs one and two are similar in length, three and four are slightly but distinguishably shorter than two, five is distinguishably shorter than four, and six is conspicuously shorter than five. Some of the microchromosomes seem to be metacentric or submetacentric, but our preparations do not resolve their structures well enough to allow them to be unequivocally paired.
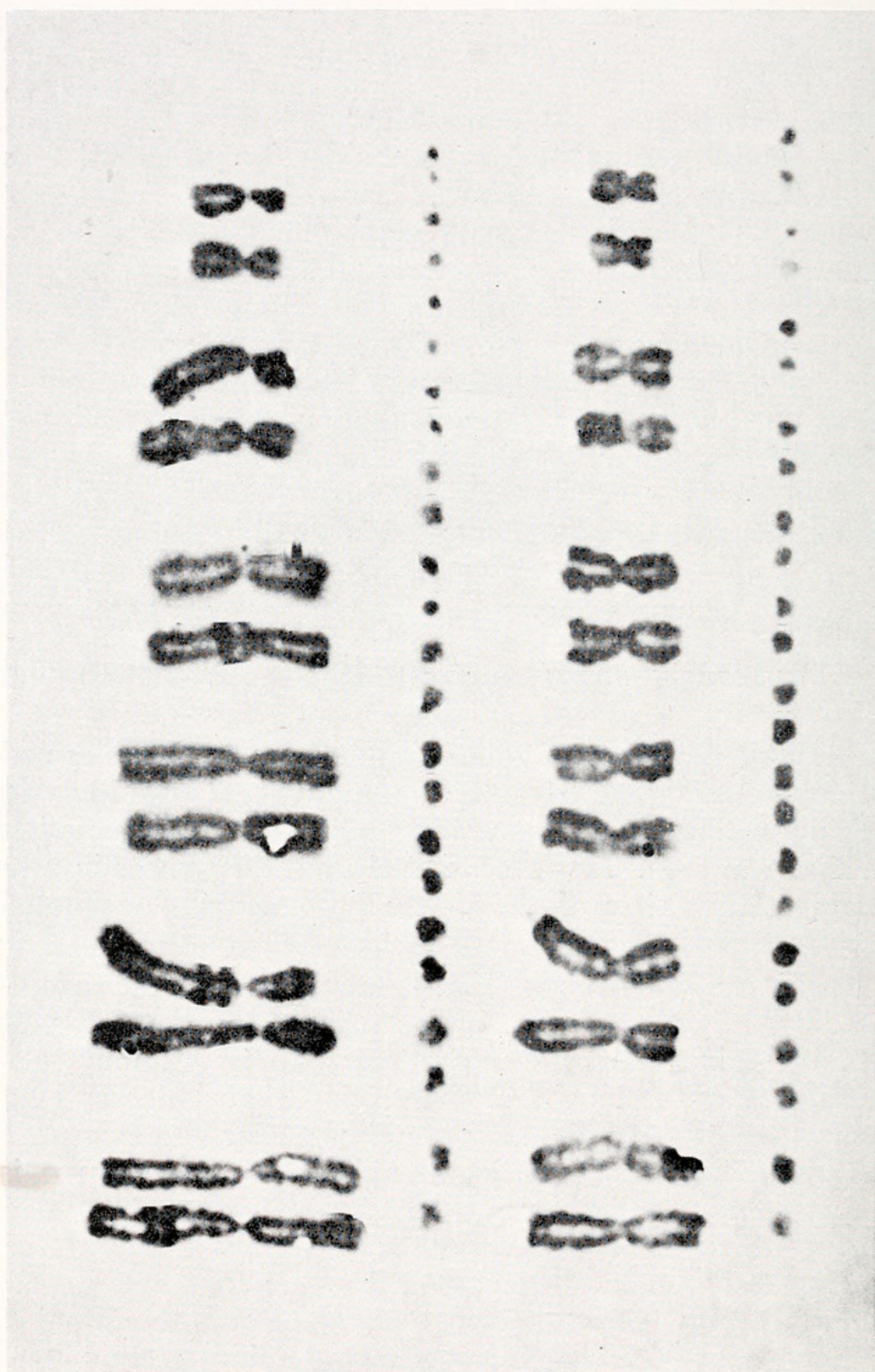
Figure 1. Comparison of male karyotypes from *Tropidurus delanonis* (above) and *Conolophus sub-cristatus* (below). Both figures are printed to the same magnification.
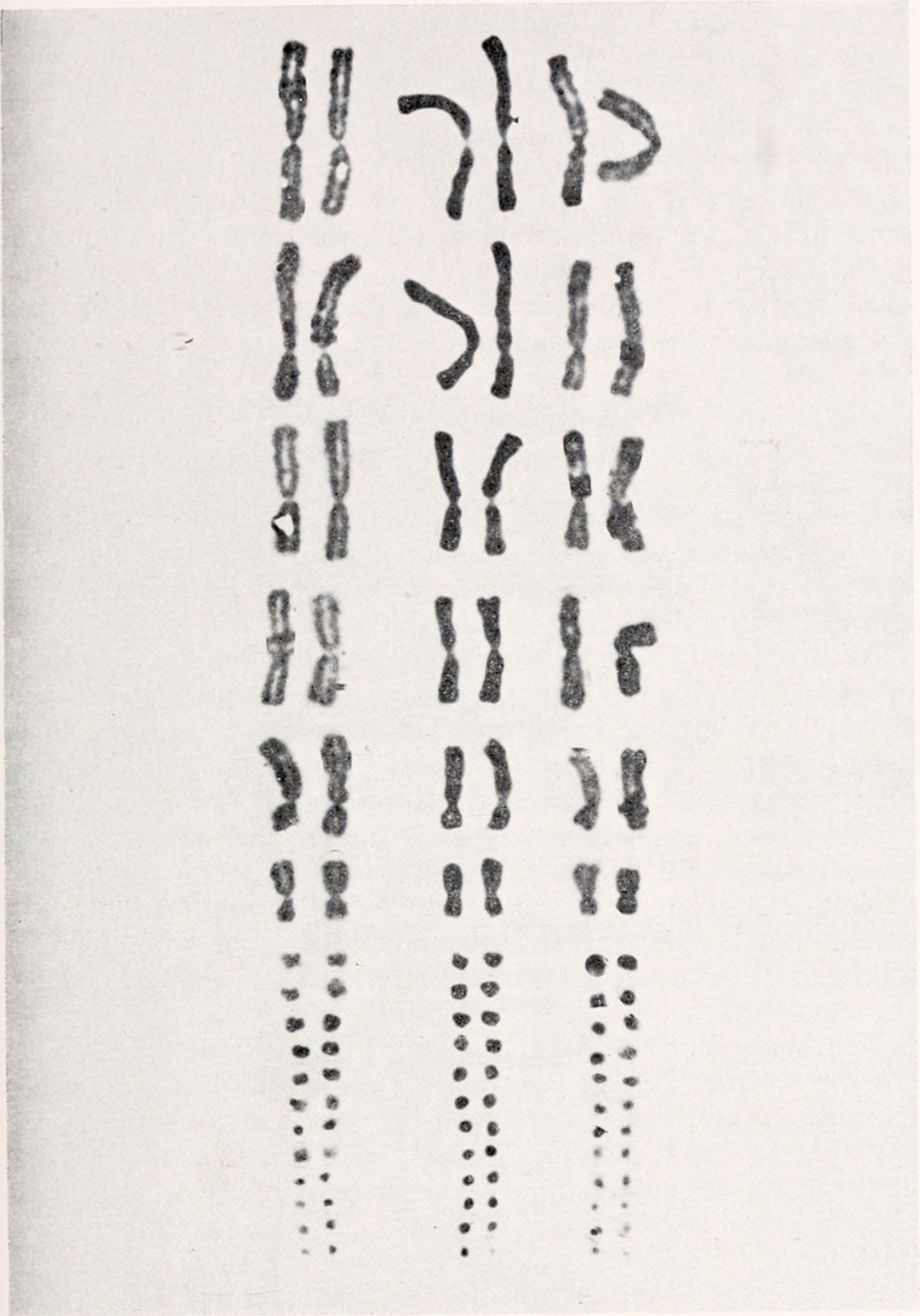
Figure 2. Comparison of male *Tropidurus* karyotypes. The species are *T. delanonis* (left), *T. duncanensis* (middle), and *T. albemarlensis* (right). The karyotypes are printed to the same magnification.

In *Tropidurus* (Fig. 1, upper; Fig. 2) pairs one through five show a fairly even gradation in length, with pair six being conspicuously smaller than five. Comparing the arm ratios to those of *Conolophus*, *Tropidurus* pair two is more submetacentric, with the long arm being slightly more than twice the length of the short; and *Tropidurus* pair five, rather than being metacentric, is almost subacrocentric, with the long arm about 2.5 times the length of the short. Again, some of the microchromosomes appear to be metacentric or submetacentric, but they are not adequately resolved to allow accurate pairing.

PRIMITIVE KARYOTYPES

(E. E. WILLIAMS AND W. P. HALL)

Comparisons with other iguanid genera and other families of lizards suggest that the *Tropidurus* pattern is derived with respect to the *Conolophus* pattern, which may be primitive for several families, including the Iguanidae.

As Gorman (1973) in the latest review of reptilian chromosomes has emphasized, our knowledge of lizard karyotypes and especially of iguanid karyotypes has increased immensely since the early work of Matthey (1931, 1933). In the iguanids even such very speciose genera as *Sceloporus* and *Anolis* have now been sampled very extensively and at least one or two species have been examined in all major subgroups of the family (Table 2). The more species studied, the more widely one chromosomal arrangement is demonstrated: that with a 2n of 36, with 12 metacentric macrochromosomes and 24 microchromosomes.

The kind of 2n = 36 karyotype characteristic of the Galapagos *Tropidurus* (i.e. 2n, arm ratios, etc.) has also been reported for representatives of this genus in eastern South America (Gorman et al., 1967; Peccinini, 1969; and Becak et al., 1972); however, we are not aware of its occurrence in any other genera. On the other hand, the 2n = 36 *Conolophus* karyotype, or at least the details of its macrochromosomal pattern, is found in many different lizard groups. In the Iguanidae (Table 2) precisely this macrochromosomal pattern is found in such diverse groups as the anolines (Gorman, 1973), sceloporines (Cole, 1970; Pennock et al., 1969; Gorman, 1973; Hall, 1973), *Crotaphytus* (Montanucci, 1970), iguanines (Cohen et al., 1967; Gorman et al., 1967; Robinson, 1974), oplurines (Gor-

Table 2

Genera are those in Peters and Donoso-Barros, 1970 unless otherwise noted. Reference for number of species karyotyped and diploid number is Gorman 1973 or this paper unless otherwise noted.

Genus	Number of species in genus	Number of species karyotyped	Range of known 2n
Amblyrhynchus	1[1]	—	—
Anisolepis	2	1	2n=36
Anolis	ca 200[2]	80 +[3]	2n=25-48
Aperopristis[4]	1	—	—
Aptycholaemus	1	—	—
Basiliscus	4	1	2n=36
Brachylophus	2[5]	—	—
Callisaurus	2[6]	2	2n=34
Chalarodon	1[7]	—	—
Chamaeleolis	2[8]	1	2n=36
Chamaelinorops	1[9]	1	2n=36[3]
Conolophus	2	1	2n=36
Corytophanes	3	—	—
Crotaphytus	5[10]	3	2n=36
Ctenoblepharis	8[11]	—	—
Ctenosaura[12]	7	1	2n=36
Cyclura	8[13]	1	2n=36
Diplolaemus	3	—	—
Dipsosaurus	3[14]	1	2n=36[3]
Enyalioides	7	1	2n=36[3]
Enyalius	8[15]	—	—
Holbrookia	3[16]	2	2n=34[3]
Hoplocercus	1	—	—
Iguana	2	1	2n=34
Laemanctus	2	—	—
Leiocephalus[17]	20	5	2n=32-36[3]
Leiosaurus	4	—	—
Liolaemus	50 +[18]	8	2n=30-40
Morunasaurus	2	—	—
Ophryoessoides	8[19]	—	—
Oplurus	6[7]	1	2n=36
Petrosaurus	2	2	2n=34[3]
Phenacosaurus	3[20]	1	2n=36

Table 2 (Continued)

Genus	Number of species in genus	Number of species karyotyped	Range of known 2n
Phrynosaura	3	—	—
Phrynosoma	14[21]	9	$2n=34$
Phymaturus	2[22]	—	—
Plica	2	1	$2n=40$
Platynotus[23]	1	—	—
Polychrus	6[24]	4	$2n=20\text{--}30$[25]
Pristidactylus[26]	4	1	$2n=36$
Proctotretus	3	—	—
Sator	2[6]	1	$2n=34$[27]
Sauromalus	7[6]	4[28]	$2n=36$
Sceloporus	$64+$[29]	$45+$	$2n=22\text{--}46$[3]
Stenocercus[19]	29	—	—
Strobilurus[30]	1	—	—
Tropidurus	20	4	$2n=36$
Uma	5[31]	3	$2n=34$
Urocentron	4[30]	—	—
Uranoscodon	4	—	—
Urosaurus	10[6]	5	$2n=34$[3]
Urostrophus	3	—	—
Uta	6[32]	6	$2n=34$

Because they do not appear on the Etheridge dendrogram, two recently described genera have been omitted from the table:

Vilcunia Donoso-Barros and Cei, J. Herp. 5: 90. 1971.

Pelusaurus Donoso-Barros, Neotropica 19: 132. 1973.

Both are said to be allied to Liolaemus and Proctotretus. Etheridge (personal communication) infers from their descriptions that they are allied to the Liolaemus-Phrynosaura-Ctenoblepharis complex and not to Proctotretus.

[1]Eibl-Eibesfeldt, I. 1962. Neue Unterarten der Meerechse, Amblyrhynchus cristatus, nebst weiteren Angaben zur Biologie der Art. Senckenbergiana, Biol. 43: 177–199.

[2]This is only a rough approximation. Continental members of the genus are in general poorly understood, and species are still being discovered in Hispaniola and Cuba.

[3]We include unpublished data from material in the Museum of Comparative Zoology.

[4]Etheridge (personal communication) after examination of specimens prefers to recognize the genus as distinct from *Leiosaurus*. Cf Müller, L., 1922: Über *Aperopristis paronae* Peracca und die Genera *Aperopristis* Peracca und *Leiosaurus* Dumeril and Bibron. Senckenbergiana **4**: 153–159.

[5]Avery, D. and W. W. Tanner, 1970. Speciation in the Fijian and Tongan iguana *Brachylophus* (Sauria, Iguanidae) with description of a new species. Great Basin Nat. **30**: 166–172.

[6]Smith, H. and E. H. Taylor, 1950. An annotated checklist and key to the reptiles of Mexico, exclusive of the snakes. Bull. U. S. Nat. Mus. **199**: 1–253. *Cophosaurus* (*Holbrookia*) *texana* is placed with *Callisaurus* here. See Norris, K. S., 1958. The evolution and systematics of the iguanid genus *Uma* and its relation to the evolution of other North American desert reptiles. Bull. Amer. Mus. Nat. Hist. 114: 247–326, and Axtell, quoted by Norris. The only important character separating the two genera is the condition of the ear opening, which is evaluated as less important than characters separating other sceloporine genera. In fact, it would not be unreasonable to lump the three sand-swimming genera, *Callisaurus*, *Holbrookia* and *Uma*. This larger genus would still have only 10 species.

[7]Angel, F. 1942. Les Lezards de Madagascar. Mem. L'Acad. Malgache **34**: 1–193.

[8]Garrido, O. H. and A. Schwartz, 1968. Cuban lizards of the genus *Chamaeleolis*. Quart. J. Fla. Acad. Sci. **30**: 197–220.

[9]Thomas, R. 1966. A reassessment of the herpetofauna of Navassa Island. J. Ohio Herp. Soc. **5**: 73–89.

[10]Montanucci, R. 1969. Remarks on the *Crotaphytus-Gambelia* controversy (Sauria: Iguanidae). Herpetologica **25**: 308–314. Montanucci, R. 1970. Analysis of hybridization between *Crotaphytus wislizenii* and *Crotaphytus silus* (Sauria, Iguanidae) in California. Copeia 1970: 104–123.

[11]Cei, J. 1974. Two new species of *Ctenoblepharis* (Reptilia, Iguanidae) from the arid environments of Central Argentina (Mendoza Province). J. Herp. **8**: 71. In contrast to Cei, we continue to recognize *Phrynosaura* as distinct from *Ctenoblepharis*. On the key character of juxtaposed versus imbricate dorsals, Cei's two new species are *Ctenoblepharis*.

[12]Etheridge follows an unpublished MS by Clayton E. Ray in uniting *Enyaliosaurus* and *Ctenosaura*.

[13]*fide* Albert Schwartz and Michael Carey, who are preparing a revision of the genus.

[14]Smith and Taylor 1950, as in footnote 6 above.

[15]Etheridge, R. 1969. A review of the iguanid genus *Enyalius*. Bull. Brit. Mus. (N.H.), Zool. **18**: 233–260.

[16]Williams, K. L. and H. M. Smith, 1958. Herpetologica **13**: 265–267.

[17]Etheridge, R. 1966 (The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus*. Copeia 1966: 79–91) listed 16 species in his restricted genus *Leiocephalus*. Subsequent to 1966, Schwartz, by reinterpretation of already described forms, has raised the number to 20. O. H. Garrido, 1973 (Nueva especies de *Leio-*

cephalus (Lacertilia, Iguanidae) para Cuba. Poeyana No. 116: 1-19) has added a 21st species.

[18]Richard Sage (personal communication) believes the taxonomy of *Liolaemus* to be still in a very primitive state. He suggests that the genus may contain as many as 100 biological species.

[19]Fritts, T. H. 1974. A multivariate evolutionary analysis of the Andean iguanid lizards of the genus *Stenocercus*. Mem. San Diego Soc. Nat. Hist. 7: 1-89. Fritts reallocates to *Stenocercus* a number of the species formerly placed in *Ophryoessoides*, leaving only six described and two undescribed species in the genus.

[20]Lazell, J. D. 1969. The genus *Phenacosaurus* (Sauria: Iguanidae). Breviora No. 325: 1-24.

[21]Presch, W. 1969. Evolutionary osteology and relationships of the horned lizard genus *Phrynosoma* (family Iguanidae). Copeia 1969: 250-275.

[22]Cei, J. M. and L. P. Castro, 1973. Taxonomic and serological researches on the *Phymaturus patagonicus* complex. J. Herp. 7: 237-247.

[23]Etheridge (in a letter): "I know of no reference that presents evidence for or against recognition of this genus. Most, but not all, recent authors include the species *semitaeniatus* in *Tropidurus*.

[24]Gorman, G. C., R. B. Huey and E. E. Williams, 1969. Cytotaxonomic studies on some unusual iguanid lizards assigned to the genera *Chamaeleolis*, *Polychrus*, *Polychroides* and *Phenacosaurus*, with behavioral notes. Breviora No. 316: 1-17. *Polychroides* synonymized with *Polychrus*.

[25]Peccinini, D. 1969. Variaçao nos cromossomos do lagarto *Polychrus marmoratus* (Sauria, Iguanidae) de diferentes localidodes (*Nota preliminar*). Rev. Brasil. Biol. 30: 1-4. (The *Polychrus* from São Paulo with $2n=20$ is actually *P. acutirostris* [P. Vanzolini, pers. comm.]. See also Peccinini, D., Beçak, O. Frota-Pessoa and Iris Ferrari, 1971. Sex determination of the "pseudo-XO/XX" type in the Brazilian lizard *Polychrus* sp. (Sauria, Iguanidae). Caryologia 24: 129-139, and Beçak, M. L., W. Beçak and L. Denaro, 1972. Chromosome polymorphism, geographical variation and karyotypes in Sauria. Caryologia 25: 313-326.

[26]"Barrio (1969) has demonstrated *Cupriguanus araucanus* Gallardo 1964 is conspecific with *Leiosaurus fasciatus* Dorbigny in Dumeril and Bibron 1837. Barrio used the combination *Cupriguanus fasciatus*. However, *Leiosaurus fasciatus* was in 1843 designated the type of *Pristidactylus* by Fitzinger. If *fasciatus* is congeneric with *achalensis*, the type of *Cupriguanus*, the latter becomes a junior synonym of *Pristidactylus* which then would be regarded as having four species, *fasciatus* Dorbigny 1837, *scapulatus* Burmeister 1861, *achalensis* Gallardo 1964 and *casuhatiensis* Gallardo 1968." Etheridge (personal communication).

[27]Lowe, C. H. and M. D. Robinson, 1971. The chromosome pattern in *Sator grandaevus* (Reptilia: Iguanidae), Baja California, Mexico. J. Arizona Acad. Sci. 6: 282.

[28]Robinson, M. D. 1974. Chromosomes of the insular species of the

chuckwalla lizards (genus *Sauromalus*) in the Gulf of California, Mexico. Herpetologica **30**: 162-167.

²⁹Sixty-four *Sceloporus* species are currently recognized. When taxonomic revisions suggested by Hall, 1973 are incorporated, this number will be raised to about 72, with considerable uncertainty remaining concerning the number of biological species to be recognized within the *torquatus* and *formosus* species groups.

³⁰Etheridge, R. 1968. A review of the iguanid lizard genera *Uracentron* and *Strobilurus*. Bull. Brit. Mus. (N.H.), Zool. **17**: 48-64.

³¹Williams, K. L., P. S. Chrapliwy and H. M. Smith, 1959. A new fringe-footed lizard from Mexico. Trans. Kans. Acad. Sci. **62**: 166-162; Mayhew, W. W. 1964. Taxonomic status of California populations of the lizard genus *Uma*. Herpetologica **20**: 170-183.

³²Ballinger, R. E. and D. W. Tinkle, 1972. Systematics and evolution of the genus *Uta* (Sauria: Iguanidae). Misc. Publ. Mus. Zool. Univ. Michigan No. 141: 1-83.

man et al., 1967) and the tropidurines (Gorman et al., 1967). In other families (Table 3) this pattern has been demonstrated in the Agamidae (Arronet, 1965; Gorman and Schochat, 1972; Hall, 1970; Sokolovsky, 1972), in the Teiidae (Gorman, 1970), in the Gerrhosauridae (Matthey, 1933; Hall, unpub.) and in the Amphisbaenidae (Huang et al., 1967).

This most widely distributed *Conolophus*-like karyotype is a source of controversy. On the one hand, it has been called "primitive" (Gorman and others). On the other hand, it has been interpreted, as by Cole (1970, 1971b), as derived in at least some iguanids, or, as by M. J. D. White, as a possible example of an exceptionally stable configuration that has been repeatedly evolved within a group. (White at one time called this "the principle of homologous change," but he now prefers to call it "karyotypic orthoselection" [see White, 1973 for discussion].)

Those who deny the primitiveness of the 2n = 36 pattern hold very firmly to the concept that primitive karyotypes in lizards consist entirely of acrocentrics with karyotypic evolution then occurring by centric fusions of them.

This view, that acrocentrics are *prima facie* primitive, has rested on the belief that fusion is cytologically much easier than fission and hence much more common (Matthey, 1949; White, 1954, 1959; Reiger et al., 1968). In particular, the generation of a new centromere, which supposedly occurs in fission, has seemed to lack any mechanism that would readily permit the

event, while fusion has been interpreted as the result of the (conceptually) less difficult process of reciprocal translocation followed by loss of a centromere carrying small segments of one or both chromosomes.

However, there are now many cases for which fission is an obligatory explanation of the origin of the karyotypes of highly derived groups and species — too many cases to allow any doubt of the reality of fission as one possible path of karyotypic evolution — whatever its mechanism. Even White (1973) now admits its existence under the name "centric dissociation" in certain cases. Morescalchi (1973) finds fission the hypothesis of choice for the origin of the karyotypes of certain species of *Hyla* and *Eleutherodactylus*. In reptiles, Webster et al. (1972)

Table 3

Karyotypes in Non-Iguanid Lizard Families

12V + 24m or direct derivatives occur in some member	Only karyotypes *not* readily related to 12V + 24m known
Agamidae	Gekkonidae
Chamaeleontidae	Pygopodidae
Xantusiidae (6V + 12I + 24m)	Lacertidae
	Anniellidae
Gerrhosauridae	
Teiidae (see Gorman, 1970)	
Anguidae	
Helodermatidae (10V + 4I + 24m)	
Varanidae	
Scincidae (see Greer et al., in prep.)	

Based on karyotypic data in Gorman (1973), unless otherwise noted.

presented evidence for the highly derived phyletic position of *Anolis monticola*, the one species within that very large genus that has a 2n as high as 48. It is similarly inescapable that fissioning has occurred several times in *Sceloporus* (Hall and Selander, 1973; Hall, 1973). A recent discussion in the journal *Evolution* has summarized some of the mammalian evidence for fission (Lawlor, 1974; Baker et al., 1975). It is no longer reasonable to peremptorily reject fission as a plausible mode of Robertsonian karyotypic evolution.

The argument for the primitiveness of the 12 macro- and 24 microchromosome pattern for iguanids and for lizards, however, does not depend on the supposed plausibility or implausibility of fission. The argument becomes easier to accept if fission is admitted in certain cases, but primitiveness for a karyotype, as for any other character state, can be determined on its own merits, independent of any theoretical mechanism for the evolution of that character state.

A large literature now exists dealing with objective recognition of primitiveness. Kluge and Farris (1969) may stand as an example. They would use the following criteria (1969:5), listed in order of reliability:

    (1) The primitive state for any particular group is likely to be present in many representatives of closely related groups.

    (2) A primitive state is more likely to be widespread within a group than is any one more advanced state.

    (3) The primitive state is likely to be associated with states of other characters known from other evidence to be primitive.

They add that "closely related groups can be selected through estimates of overall similarity that make no assumptions about primitive conditions."

"Widespread" they define not by counting taxa but as occurring in several taxa that otherwise would have little in common. They would also use "available fossil material."

At least in intention these criteria have merit, but, in general, such criteria are especially difficult to use in our present stage of knowledge of karyotypes. Fossils are clearly unavailable. It is still rare for karyotypes to be known for even a substantial number of any group and, on the contrary, those at hand may be a very biased sample. The problem of real similarity may

be serious; diploid number by itself is meaningless; there must be near identity in chromosome morphology paralleling taxonomic relationships inferred on other grounds.

When a group has been as well sampled as the Iguanidae now are, however, the Kluge and Farris criteria begin to be applicable and the comparative method can lead to sound results when appropriately applied. Cole misrepresents, indeed caricatures, the comparative approach when, in opposing the concept of the 12 + 24 karyotype as ancestral in iguanids, he says (1970:31):

> "These conclusions are based on the assumption that the general karyotypic condition found in the majority of species that were available for sampling, at whatever level of the taxonomic hierarchy one happened to be working with, was, therefore, the most primitive,"
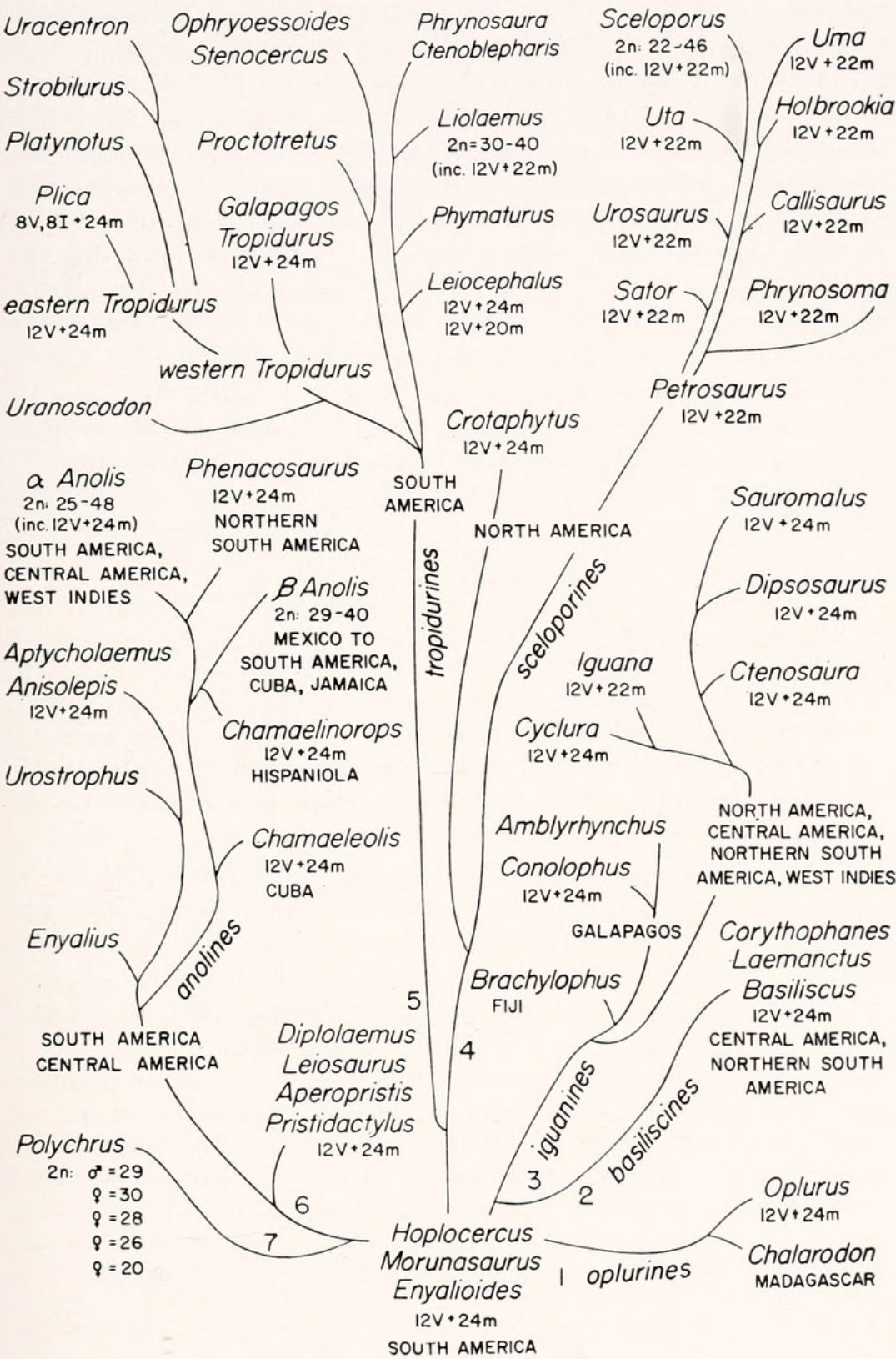
and, again (1970:31):

> "If I were to simply employ the principal [sic] on which these authors' arguments are based, I would reach a rather different conclusion for the *spinosus* group, for in this group the karyotype of the *lundelli* subgroup (12 biarmed macrochromosomes plus 10 smaller chromosomes, most of which are clearly biarmed; a 12 + 10 karyotype) would then be considered ancestral because it occurs in five of the nine species in the species group and none of the three remaining general karyotypes of the group is represented in more than two species."

Our own reasoning has a quite different base than that portrayed by Cole. We start from a base that is broad and quite independent of the ideas of Cole or ourselves.

Figure 3 provides a dendrogram of the phylogenetic relationships of the genera of the Iguanidae which represents the present

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Figure 3. Phylogeny and karyotype distribution in the family Iguanidae. The base dendrogram summarizes phylogenetic conclusions of Richard Etheridge from his osteological studies and is reproduced here with his permission from a privately circulated figure. The available karyotypic information for the family (references cited in Table 3) is superimposed on this dendrogram and indicates (1) the basic diploid karyotype for each genus chromosomed or (2) in karyotypically variable genera, the most primitive karyotype in the genus plus the range of 2n known for it. "V" chromosomes are metacentric macrochromosomes, "I" are acrocentric macrochromosomes, and "m" are microchromosomes. Thus, an 8V,8I+24m karyotype has a 2n of 40 with eight metacentric macrochromosomes, eight acrocentric macrochromosomes, and 24 microchromosomes.

Uracentron

Ophryoessoides
Stenocercus

Phrynosaura
Ctenoblepharis

Sceloporus
2n: 22-46
(inc. 12V+22m)

Uma
12V+22m

Strobilurus

Uta
12V+22m

Holbrookia
12V+22m

Platynotus

Proctotretus

Liolaemus
2n=30-40
(inc. 12V+22m)

Plica
8V,8I+24m

Galapagos
Tropidurus
12V+24m

Phymaturus

Urosaurus
12V+22m

Callisaurus
12V+22m

eastern *Tropidurus*
12V+24m

Leiocephalus
12V+24m
12V+20m

Sator
12V+22m

Phrynosoma
12V+22m

western *Tropidurus*

Uranoscodon

Crotaphytus
12V+24m

Petrosaurus
12V+22m

α *Anolis*
2n: 25-48
(inc.12V+24m)
SOUTH AMERICA,
CENTRAL AMERICA,
WEST INDIES

Phenacosaurus
12V+24m
NORTHERN
SOUTH AMERICA

SOUTH
AMERICA

NORTH AMERICA

Sauromalus
12V+24m

Dipsosaurus
12V+24m

tropidurines

sceloporines

β *Anolis*
2n: 29-40
MEXICO TO
SOUTH AMERICA,
CUBA, JAMAICA

Iguana
12V+22m

Ctenosaura
12V+24m

Aptycholaemus
Anisolepis
12V+24m

Chamaelinorops
12V+24m
HISPANIOLA

Cyclura
12V+24m

Urostrophus

Chamaeleolis
12V+24m
CUBA

Amblyrhynchus

Conolophus
12V+24m

NORTH AMERICA,
CENTRAL AMERICA,
NORTHERN SOUTH
AMERICA, WEST INDIES

GALAPAGOS

Corythophanes
Laemanctus

Enyalius

anolines

Brachylophus
FIJI

5

Basiliscus
12V+24m
CENTRAL AMERICA,
NORTHERN SOUTH
AMERICA

SOUTH AMERICA
CENTRAL AMERICA

Diplolaemus
Leiosaurus
Aperopristis
Pristidactylus
12V+24m

4

iguanines

basiliscines

Polychrus
2n: ♂=29
♀=30
♀=28
♀=26
♀=20

6

7

3

2

Oplurus
12V+24m

Hoplocercus
Morunasaurus
Enyalioides
12V+24m
SOUTH AMERICA

1 *oplurines*

Chalarodon
MADAGASCAR

views of Richard Etheridge and Richard Estes, extending those of Savage (1958), Etheridge (1964) and Presch (1969). This has been based wholly on osteology and thus it gives us a picture of relationships constructed without knowledge of or reference to karyotypes. We have then superimposed on this dendrogram the range of karyotypes for each iguanid genus for which these are known. We use both the published reports summarized by Gorman, 1973 (most references cited by Gorman are not repeated) and our still unpublished data. We use the latter despite the lack of formal (and especially pictorial) documentation because it fills out much of the picture of karyotypic variation in the Iguanidae without significantly altering it.

The Etheridge scheme recognizes a basal stock (called "morunasaurines" by Estes and Price, 1973) from which seven major lineages arise (Polychrus, the *Anolis-Enyalius-Diplolaemus* lineage, the "tropidurines," the "sceloporines" plus *Crotaphytus*, the "iguanines," the "basiliscines," and the "oplurines").

Karyotypes are known for one genus of morunasaurines (one species of *Enyalioides* — our unpublished data); in this and in six of the seven derived lineages (*all* except *Polychrus*) the "primitive" 12 + 24 karyotype is known to occur or is the only karyotype known. Furthermore, in every one of the derived lineages (except *Polychrus*) those genera closest to the base on Etheridge's diagram — i.e. those believed for osteological reasons to be the more primitive members of each lineage (and, in fact, each sublineage) — have either the 12 + 24 karyotype or a 12 + 22 karyotype that differs from the primitive condition by the absence (by loss or fusion) of a pair of microchromosomes. In the iguanine line, for example, all genera in the sublineage containing *Iguana, Ctenosaura, Dipsosaurus* and *Sauromalus* have a 12 + 24 or (*Iguana*) 12 + 22 karyotype.

The sceloporine line is especially instructive in this and other respects. *Crotaphytus*, an early offshoot of this line, has 12 + 24 (Cohen et al., 1967; Montanucci, 1970). *Every* primitive sceloporine and some *Sceloporus* have 12 + 22 (several authors, summarized in Hall, 1973). Within *Sceloporus* (a morphologically more derived genus) numbers range from 12 + 10 to 24 + 22; if the 12 + 22 pattern is accepted as primitive for the genus, it is clear that both fusions and fissions must have been involved in the evolution of its karyotypic diversity.

The tropidurine line is not well sampled, but as we have shown above, *Tropidurus* from eastern South America and the

Galapagoan *Tropidurus* (derived from western South American stock) have the basic 12 + 24 pattern, although their karyotypes are slightly derived in non-Robertsonian ways. The only West Indian *Leiocephalus* published (Gorman et al., 1967) also has the basic pattern. Besides confirming the 12 + 24 pattern in Hispaniolan species, Hall (unpub.) has found representatives of the Cuban branch of the genus to have 12 + 20 patterns. In the speciose genus *Liolaemus*, the single species so far reported (Gorman et al., 1967) has 12 + 22, although slides made by Richard Sage and examined by Hall indicate the presence of considerable karyotypic variation in this genus $(2n \sim 30–40)$[1].

In the line leading to *Anolis*, the primitive genera *Chamaeleolis*, *Phenacosaurus* and *Chamaelinorops* (Hall and Williams, in preparation) have 12 + 24 karyotypes, as do many of the alpha section of the genus *Anolis* itself. The 12 + 24 pattern is also found in the related lineage including the genera *Pristidactylus* and *Anisolepis*.

Given this evidence, it is difficult to contest the hypothesis that the 12 + 24 pattern is primitive in the Iguanidae. It is possible to go to greater detail: arguments similar to those above support the idea that even the detailed chromosome size and arm ratios found in *Conolophus* must be primitive for iguanids.

Additionally, when we notice (1) that quite similar 12 + 24 karyotypes are found in other lizard families (Table 3), both in families that everyone agrees are closely related to the Iguanidae, i.e. the Agamidae and the Chamaeleontidae, and in families that are just as universally regarded as not closely related (Gerrhosauridae, Anguidae, Amphisbaenidae); (2) that still other families (Scincidae, Helodermatidae, Varanidae) have karyotypes easily derivable from 12V + 24m (Gorman, 1973), it then becomes clear that, using the most neutral descriptive terms, the 12 + 24 karyotype is an extraordinarily stable and conservative pattern. To us it is evident that the most careful and skeptical use of the Kluge and Farris criteria of primitive-

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[1] Although variation in chromosome number was clearly demonstrated in this material, the preparations were not of good quality and the data were complicated by the inclusion of unnamed taxa (clearly *Liolaemus*, however). Further work will be required before publication is warranted. However, we think that the existence of substantial karyotypic variation in this genus should be noted.

ness points unequivocally to the ancestral position of the 12 + 24 karyotype not only for iguanids, but for all lizards.

On the other hand, there is no doubt that some lizard families and at least one group within the Iguanidae have karyotypes that are very difficult to reconcile with derivation from a 12 + 24 pattern (Gorman, 1973). The Gekkonidae will serve as an example of the first case; *Polychrus* is, of course, the second. We are impressed that these deviant families and groups are in general isolated cases, neither closely related to one another, nor arguable as ancestral to forms with the 12 + 24 karyotype. In all of these cases, morphological and other evidence suggests long separation from plausible basal stocks, and hence leads all the more strongly to the conclusion that the *Conolophus*-like 12 + 24 pattern is the one primitive for lizards.

EVOLUTIONARY ROLE OF ROBERTSONIAN CHANGE

(W. P. HALL AND E. E. WILLIAMS)

Let us point out immediately that there is no antithesis between primitiveness and stability — the two explanations that have been proposed for the iteration of one chromosome pattern throughout a large number of species. On the contrary, the genera which show only the widespread chromosome patterns which we believe to be primitive seem *not* to be the ones that have radiated widely. This is a point which we want to stress, especially for the Iguanidae. Karyotypically conservative groups, so far as we can see, have produced only few species. Of the more than 50 genera of iguanids, only three — *Anolis, Sceloporus* and *Liolaemus* — are very large, each including more than 50 species (several times 50 in *Anolis*), or have produced high levels of sympatry (5+ syntopic species in several areas of the ranges of *Anolis* or *Sceloporus*). Of the others, only *Stenocerus* (as revised by Fritts, 1974), *Tropidurus* (if the Galapagos species are included), and *Leiocephalus* (a purely insular radiation in the West Indies) have as many as 20 species, and no others have as many as 15. Excepting *Polychrus*, whose several karyotypes bear little obvious relationship to one another and none to any other iguanid, the other small, conservatively speciating genera show on current evidence little or no intrageneric variation in karyotypes, and indeed very little variation among genera. Of the 14 non-sceloporine small iguanid genera (in-

cluding *Crotaphytus*) sampled, 11 have the 12 + 24 pattern. All of the primitive sceloporines (eight genera) and *Iguana* among the iguanines have 12 + 22. Only *Plica*, aside from *Polychrus*, stands out in showing a notably different karyotype (16 + 24), and its modifications seem relatively simple (presumably fissions of four of the primitive metacentric macrochromosomes). Of the genera of middle size (20–29 species), the four sampled species of *Tropidurus* have again the 12 + 24 pattern but differ somewhat in arm ratios from the usual condition, and while some *Leiocephalus* have the 12 + 24 pattern, others have 12 + 20 (reduction in two pairs of microchromosomes — Hall, unpublished). *Stenocercus* has not yet been sampled.

Contrasting strongly with this picture of conservative speciation and karyotypic evolution in the small iguanid genera is a picture showing extensive, usually Robertsonian karyotypic variation in each of the three prolifically speciose genera. In *Anolis* 2n's range from 25 to 48 (Gorman, 1973; Hall, unpub.), in *Sceloporus* they range from 22 to 46 (Gorman, 1973; Hall, 1973), and in a few *Liolaemus* they range from 30 to 40 (Sage and Hall, unpublished).

The apparent association of conservative speciation with conservative karyotypic evolution, and prolific speciation with remarkable karyotypic diversity suggests the possibility of an evolutionarily important causal relationship between karyotypic differentiation and speciation. Though there are undoubtedly other possibilities and explanations that might be raised, it is this possibility of causal relationship that we here want to evaluate. We offer the following arguments to demonstrate that the relationship between speciation and karyotypic diversity is genuine.

(1) *Intrageneric variation in karyotypes.* Since few small genera from six of the seven major iguanid lineages are represented by karyotypes from more than one species, we must agree that we cannot safely compare the amounts of *intrageneric* variation between small and large genera in these lineages. This defect, however, most certainly does not apply to the sceloporine lineage: all nine sceloporine genera and the related *Crotaphytus* are cytologically well known. Half or more of the species from each of these 10 genera have been karyotyped: 3/5 from *Crotaphytus*, 2/2 from *Petrosaurus*, 9/14 from *Phrynosoma*, 2/2 from *Callisaurus*, 3/3 from *Uma*, 2/3 from *Holbrookia*, 1/2 from *Sator*, 6/6 from *Uta*, 5/10 from *Urosaurus*, and 45+/

Table 4

Distribution of karyotypic variation in Iguanidae: interspecies comparisons (large genera except *Sceloporus* omitted).

2n	*Sceloporus*[1]	Other scelo- porines[2]	Other *small* iguanid genera		All small iguanid genera
48	0	0	0		0
46	2	0	0		0
44	2	0	0		0
42	1	0	0		0
40	3	0	1	*Plica plica*	1
38	0	0	0		0
36	1	0	13		13
34	18	33	1		34
32	15	0	0		0
30	2	0	1	*Polychrus marmoratus*	1
28	0	0	1	*Polychrus peruvianus*	1
26	1	0	1	*Polychrus femoralis*	1
24	3	0	0		0
22	13	0	0		0
20	0	0	1	*Polychrus acutirostris*	1
species karyotyped	45+	33	19		52
species known	64+	49	122		171
% karyotyped species with 2n=36 or 34	42%	100%	74%		90%

[1]includes polymorphisms within currently recognized "species."
[2]here including *Crotaphytus*.

64 + from *Sceloporus* (data summarized from Table 2). None
of these genera (except *Sceloporus*) shows any intrageneric vari-
ation, and the only intergeneric difference is between the 12 +
24 *Crotaphytus* and the 12 + 22 sceloporines. Within *Scelo-
porus* only 13 species (15 after taxonomic revisions by Hall)
are known to have the primitive sceloporine condition (2n =
34), while the remaining 32 (40 or 41 after revisions) karyo-
typed species have derived patterns — and most of these belong
to the phylogenetically more advanced large-scaled branch as
defined by Smith (1939). In the sceloporine lineage (Table 4),
the correlation between chromosomal diversity and prolific spe-
ciation is clear cut and does indeed appear to be fundamental.
And even with our poor sampling of the small non-sceloporine
genera, the association between chromosomal conservation and
few species per genus is, at the least, suggestive.

(2) *Intergeneric diversity in karyotypes.* Although compara-
tively few species of the small, non-sceloporine genera have been
karyotyped, still there is less intergeneric diversity observed than
we would expect if variation were randomly distributed in the
family. Phylogenetic relationships inferred from morphology
(Fig. 3) show that many of these genera must have been evolv-
ing as independent lineages for comparatively long times, possi-
bly since the Cretaceous (Estes and Price, 1973). Given so
long a period of evolution, they show remarkably little evidence
of the acquisition or accumulation of chromosomal differentia-
tion. As we have said, there are very few known differences
among genera, and, in fact, few departures from the 12 + 24
pattern. In the 25 small genera sampled (Table 5), the few
observed cases of *inter*generic variation are slight indeed com-
pared to the known *intra*generic variation of the phylogenetically
more recent large genera. Unless the sampling of the small
genera has been biased in some unknown way, this should be
quite significant.

The deviations from the 12 + 24 pattern among the small
genera are again: *Plica* (16 + 24 in no more than four muta-
tional events, and possibly in only one, *fide* Todd, 1970),
Iguana (12 + 22 in one event), all of the "primitive" scelo-
porines (12 + 22 in one event in the common ancestry for all
species), and *Polychrus* (2n's = 20–30 resulting from an un-
determined number of events producing karyotypes derived in
relation both to one another and the 12 + 24 pattern). Con-
trasted to the limited intergeneric variation in the family as a

whole is the remarkable interspecific diversity involving many
mutational events found *within* each of the three especially
speciose genera (cf. Fig. 3). Again, this relationship is clearest
in the well-investigated sceloporine lineage (Hall, 1973, in
prep.).

Table 5

Distribution of intergeneric comparisons in the Iguanidae

lineage	small genera			large genera		
	no. genera	no. karyotyped[1]	Any k'types other than $12 + 24$ or $12 + 22$[2]	no. genera	no. karyotyped	Any k'types other than $12 + 24$ or $12 + 22$
basal stock	3	1	0	0	–	–
oplurines	2	1	0	0	–	–
basiliscines	3	1	0	0	–	–
iguanines	8	6	0	0	–	–
sceloporines & *Crotaphytus*	9	9	0	1	1	1
tropidurines[3]	11	1	1	4	3	2
anolines	3	2	0	1	1	1
anoline relatives	8	3	0	0	–	–
Polychrus	1	1	1	0	–	–
Totals	49	25	2	6	5	4

[1]The number of genera in the lineage for which karyotypic data exist.
[2]The number of genera in the lineage containing one or more species with
  a karyotype deviating from the $12 + 24$ or $12 + 22$ pattern.
[3]*Stenocercus, Tropidurus, Leiocephalus,* and *Liolaemus,* each with 20 or
  more species, are treated as large genera.

(3) *Relative recency of species and of karyotypic diversity.*
If rates of fixation of Robertsonian mutations were independent
of the process of speciation, one expectation might be that many
of the older genera would accumulate karyotypic variants while
phylogenetically recent groups might show little variation, even
though they include many species.

Hall (1973) would adduce *Sceloporus* as a counter-example,
since he believes it to be a phylogenetically quite recent genus.
We summarize Hall's views and arguments here.

(A) While the Iguanidae may have originated in the Cre-
taceous (Estes and Price, 1973), the differentiation of the
present sceloporine genera probably did not antedate the de-
velopment of the xeric habitats in North America during the
Miocene (Axelrod, 1950, 1958). This conclusion is supported
by the facts: (1) that *Crotaphytus* and all sceloporine genera
are largely or entirely restricted to the North American deserts
(except *Sceloporus* itself, which has extensively radiated in
mesic habitats as well as in deserts); (2) that all sceloporine
genera except for the osteologically primitive *Crotaphytus* and
Petrosaurus (Etheridge, 1964; Presch, 1969) and *Sator* (which
simply has not been tested) will "shimmy bury" (Axtell, 1956)
in loose soil or sand for escape or sleeping cover (Stebbins,
1943, 1948; Axtell, 1956; Norris, 1958), a behavior not seen
in any of the other North American or West Indian iguanids
(we know nothing about South American iguanids in this re-
spect); and (3) that all sceloporines but no other North Ameri-
can iguanid genera (including *Crotaphytus*) show a "sink-trap"
type of nasal passage and almost always an associated valvular
nostril[1] (Stebbins, 1943, 1948; Savage, 1958; Hall, unpub.),
which clearly seems to have been evolved in relationship to the
use of shimmy burial for cover in xeric environments where
loose soil is likely to be more readily available for cover than
that provided by plants or permanent burrows in firm soil.

(B) Within the sceloporines, *Sceloporus* seems to be one of
the most recently differentiated genera. Osteological data clearly
show four groups within the sceloporines (Savage, 1958; Ethe-
ridge, 1964; Presch, 1969): the primitive *Petrosaurus;* the
specialized *Phrynosoma;* the group of "sand-swimming" (Norris,
1958) genera, *Callisaurus, Holbrookia* and *Uma;* and the group

[1]*Petrosaurus,* which lives in xeric habitats but which does not shimmy
bury under experimental conditions, has the nasal sink trap but lacks the
nasal valve (Hall, personal observation).

of four genera, *Sceloporus, Urosaurus, Sator* and *Uta*. According to Etheridge (1964), these last four genera cannot be distinguished osteologically. However, comparisons suggest that *Sceloporus*, with its mucronate imbricate scales developed to a degree not found in any of the other North American iguanids (where granular scales seem to be the primitive condition) and with its loss of the gular fold found in all other sceloporines, is the phylogenetically most recent of these four genera.

(C) Within *Sceloporus*, again based on characteristics of the squamation, it seems clear that Smith's (1939) small-sized, small-scaled species are more closely related to the other sceloporines than is the large-sized, large-scaled branch. To summarize the cytosystematics of these two divisions, the phylogenetically more primitive small-scaled branch contains 20 species by present taxonomy: 12 of these are karyotypically conservative,[1] five have not been karyotyped, and the three that are karyotypically derived are also highly derived ecologically (*merriami*, $2n = 46$, is a specialized cliff-face dweller and *scalaris* and *aeneus*, $2n = 24$, are specialized montane bunch grass dwellers). Within the morphologically more advanced large-scale branch, according to present taxonomy, *only* the single species, *S. orcutti*, has the primitive $12 + 22$ pattern, while all other karyotyped species are derived. At present (very conservative taxonomy) this branch contains a minimum of 43 species, of which all but 13 (all 13 are in chromosomally highly derived species groups) have been karyotyped.

This phylogenetically most recent radiation of the sceloporines (the large-scaled *Sceloporus*) has covered the entire ecological and geographical range of lizards in North America (Smith, 1939) and shows simultaneously a truly remarkable karyotypic diversity (2n's from 22 to 46). It is also notable that the most ecologically differentiated small-scaled species in the genus (the *scalaris* group species [$2n = 24$] and the *merriami* [$2n = 46$]) are also among the karyotypically most highly derived forms.

The one egregious example of chromosomal diversity in a small genus, *Polychrus*, seems in the very fact of its uniqueness equally a counter-example to the generality of the proposition that deviant karyotypes tend to accumulate in all genera with time.

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[1]Karyotypically at least to a first approximation: Cole (1971) notes that *maculosus* has a $2n = 31$, $X_1X_2Y \male$ (based on three specimens, only one a male) and that in *pyrocephalus* chromosome 1 shows a pericentric inversion.

Polychrus is seen on Etheridge's diagram as an isolated basal twig, truly very old and very distinct, entirely suitable as a group in which deviant karyotypes might accumulate. But each of the other six major groups is as old in Etheridgean terms. If karyotypic diversity is a product only of time, even a random and superficial sampling of the other small genera should, so it seems to us, have resulted in more cases of highly derived karyotypes than are in fact in front of us.

Our own surmise regarding *Polychrus* is that the six forms currently recognized, all highly arboreal, may represent only the few survivors of an old and formerly more prolific lineage of tree dwellers that, perhaps, has been largely replaced by the radiation of *Anolis* in the arboreal habitat.

CHROMOSOMAL EVOLUTION IN THE IGUANIDAE: TWO MAJOR PATTERNS

We do not deny that the history of karyotypic change is not now and never will be known from direct evidence, that the real and unique historical process must be inferred from its products, nor that the survey of iguanid karyotypes, though it is already impressive, is incomplete. We insist, however, that the present sample is large enough to justify conjecture and to point to the kinds of evidence that will verify or negate postulated sequences.

Our picture of chromosomal evolution in lizards, and perhaps also in many other groups, is that there are both periods of chromosome conservatism with usually slow geographic modes of speciation (Mayr, 1963) and episodes of karyotypic instability associated with rapid proliferations of new species (Hall, 1973). We believe that both *Anolis* and *Sceloporus* exhibit these phenomena (cf. especially Webster et al., 1972; Williams and Webster, 1973; and Hall and Selander, 1973), and presumably *Liolaemus* also does. Todd (1970) suggests a similar relationship between karyotypic diversification and prolific speciation in the Canidae.

To us the comparative data strongly suggest that karyotypic diversification and speciation are in many cases functionally related, such that the temporal and/or geographic requirement for the separation of populations is somehow minimized (not eliminated but very greatly reduced) when chromosomal differences become fixed between them. White's model of "stasi-

patric" speciation (White et al., 1967; White, 1968; Key, 1968) offers one mechanism, and others are possible (Hall, 1973; in prep.). Here we wish to emphasize only that Robertsonian mutations frequently are found fixed between species of rapidly proliferating groups but only rarely are found as intrapopulation polymorphisms. (Wallace, 1959, provided an early note of this phenomenon in *Drosophila*.) Given this distribution of Robertsonian mutations, we think it especially significant that, among the varieties of chromosomal rearrangements, the Robertsonian ones probably have the least impact on the meiotic assortment or recombination of *balanced* genomes; but, on the other hand, at least in mammals where breeding and cytological studies have been made, these mutations are increasingly implicated as a significant source of chromosomal malassortment in meiosis serving to reduce the effective fertility of chromosomally heterozygous individuals (Polani et al., 1965; Gustavsson, 1971a, b; Cattanach and Mosely, 1973). Once a chromosomal difference is established, reduced heterozygote fertility could then serve in appropriate circumstances as an *intrinsic* partial barrier to gene flow between karyotypically differentiated homozygous populations, thereby reducing the requirement for extrinsic barriers to gene flow before speciation could ensue (Hall, 1973; in prep.).

Then, assuming some model of chromosomal speciation based on cytogenetically reduced fertility in heterozygotes, the probability or frequency of such speciation in given lineages should be highly dependent on parameters of their genetic systems such as: mutation rates, malassortment rates, population structures, mating systems, ets. Chromosomal speciation might then be precluded in some lineages because of unfavorable genetic systems that would allow speciation only by conservative geographic modes; on the other hand, genetic systems of other lineages may especially favor chromosomal speciation, and thus allow great proliferations of species, even in the absence of strong extrinsic barriers to gene flow. Such a chromosomal speciation theory can easily account for the associations of karyotypic diversity and prolific speciation found in *Sceloporus, Anolis,* and apparently in *Liolaemus.*

The test of the chromosomal speciation model of karyotypic evolution as it pertains to the iguanids will be found in the still unsampled or inadequately sampled iguanid radiations, particularly those of South America. *Stenocercus,* now with 29

recognized species and with notable sympatry, is certainly crucial. The karyotypic variation in *Liolaemus* and *Leiocephalus* must be confirmed, and the karyotypic patterns in these two genera adequately documented. We suggest that the species of mainland *Tropidurus*, which seem to have rather complicated distributions (Peters and Donoso-Barros, 1970), may also repay careful attention. Only such a wider survey of the karyotypes of the Iguanidae can provide either a verification of the evolutionary patterns we have suggested here, or, by demonstrating new patterns, require alternative models.

RESUMEN

Los iguanidos: *Conolophus subcristatus, Tropidurus albemarlensis, T. delanonis,* y *T. duncanensis* tienen cariotipos similares de 36 cromosomas. *C. subcristatus,* con 12 macrocromosomas metacéntricos y 24 microcromosomas, tiene un cariotipo que se demuenstra ser "primitivo" dentro la familia Iguanidae, y que probablemente es también primitivo entre todos de los lagartijos. Los cariotipos 2n = 36 de los tres *Tropidurus* son iguales y también al *Tropidurus* del este de Suramérica, pero ellos son diferentes del cariotipo primitivo porque hay modificaciones "no-Robertsonianas" de tres pares de los macrocromosomas. La filogénia y todos de los datos cromosómicos de la Iguanidae están resumidos para una discusión sobre la determinación de que cariotipos son "primitivos" dentro radiaciones de especies, y también sobre los funciones que sirven las mutaciones de Robertson en el proceso de evolución. Análisis de la información sobre los cariotipos y sistemática demuenstra una conexión causal y cerca entre la diferenciación cariotipica y la proliferación rápida de especies nuevas, donde el requisito para aislamiento geográfico se minimiza a causa de la diferenciación cromosómica.

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