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# Fission in the Evolution of a Lizard Karyotype

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**Abstract**. *The lizard* Anolis monticola *has a diploid chromosome number of 48 (24 macrochromosomes and 24 microchromosomes). More primitive members of the genus, as determined by bone morphology, have 12 macrochromosomes and. 2,4 microchromosomes. Since the higher chromosome number is the derived condition, this is a case of karyotypic change by centric fission.*

Chromosome fusion and fission (Robertsonian change) are two alternative explanations for the relation of karyotypes that differ in diploid number but agree in the number of chromosome arms [fundamental number (1)]. Controversy over the mechanism for fission and its frequency have caused many cytogeneticists to favor fusion, often to the complete neglect of fission. Recent studies have removed the grounds for disputing the simplest possible mechanism for fission, simple splitting of the centromere. Light and electron microscopy have shown that the centromere of a bi-armed chromosome contains twice the material in the centromere of a telocentric chromosome (2). Stable telocentric chromosomes, including some that are almost certainly fission products (3), have been demonstrated (2, 4). The frequency and importance of fission in karyotype evolution, however, remain undetermined (5). Cases are needed in which the direction of Robertsonian change can be demonstrated by unequivocal phylogenetic evidence. We present such a case here. Phyletic relationships among West Indian species of *Anolis*, a large Neotropical genus of iguanid lizards, are now well worked out (6). There is karyotypic information for approximately 85 percent of the more than 80 species in the West Indies (7). In this context it is possible to demonstrate unequivocally that the karyotype of *Anolis monticola*, a lizard restricted to the Massif de la Hotte in southwestern Haiti, originated through multiple centric fissions.

Using a slight modification of a standard method (8), we made chromosome preparations from testis tissue of 46 individuals from eight localities (9). Forty-one individuals had a diploid complement of 12 pairs of macro-chromosomes and 12 pairs of micro-chromosomes (Figure 1A). The morphology of the macrochromosomes was clearest in second-division meiotic metaphase (Fig. 1B). Four individuals had a diploid number of 46, with one pair of metacentric chromosomes (Fig. 1D), and one individual had a diploid number of 47. Chiasmata are almost invariably terminal in male A. monticola (Fig. 1E), so that the bivalents arelinear or ring-shaped; in the 2n = 47 individual the trivalent is linear (Fig. 1F). There is both inter- and intra-population variation in the morphology of the macrochromosomes (compare Fig. 1, B and D). In all individuals some but not all of the macrochromosomes are telocentric.

On the basis of the morphology of the caudal vertebrae the genus *Anolis* can be divided into an alpha and a beta section (6). Figure 2 presents the karyotypic and morphological information for the alpha section, to which *A. monticola* belongs. The shape of the interclavicle divides the alpha section into two groups, one with an arrow-shaped interclavicle comparable to that of other iguanids and the other with a derived T-shaped interclavicle. Primitive species groups within the group with an arrow-shaped interclavicle have a splenial (a bone in the lower jaw which is lost in advanced forms) and a high number of inscriptional ribs (reduced in derived forms) (6). In the Greater Antilles the osteologically most primitive species in this group (for example, the giant species *Anolis ricordii* of Hispaniola and *Anolis cuvieri* of Puerto Rico) have a karyotype of 12 meta-centric macrochromosomes and 24 microchromosomes (Fig. 1C) (7, 10). The most primitive species of the Lesser Antillean *Anolis roquet* group likewise have this karyotype (11).

*Anolis monticola* is one of the advanced alpha species with a T-shaped interclavicle. The only member of this group which retains the primitive splenial is *Anolis equestris* of Cuba, which again has the 2n = 36 karyotype (10). The only member of the group which has a high number of inscriptional ribs is *Anolis occultus* of Puerto Rico, which also has 2n = 36 (7). All members of the *monticola* species group are osteologically advanced in having the T-shaped interclavicle and a reduced number of inscriptional ribs and in lacking a splenial.

Most *Anolis* species are characterized by a well-developed dewlap, an extensible throat fan supported by hyoid cartilages. The dewlap is secondarily reduced or lost in several unrelated species groups (12). Among the species of the *monticola* group *Anolis chrislophei* has a large dewlap and uniform squamation and lacks a bold body pattern, all characters suggesting that it is the most primitive species of the group (*13*); *A. christophei* again has the 2n = 36 karyotype. *Anolis monticola* has a reduced dewlap, non-uniform squamation, and a bold ocellate body pattern. It is clearly a highly derived form.

The diploid number of 48 observed in *A. monticola* could be derived from the primitive 2n = 36 karyotype by centric fission of the metacentric macrochromosomes. The telocentric morphology of many of the macrochromosomes in the *A. monticola* karyotype is compatible with a fission hypothesis. That the alternative explanation--the *monticola* karyotype is a retained primitive condition--is implausible can be seen in Fig. 2. If the high diploid number is ancestral, at each point marked by an X there must have been an independent evolution of a diploid number of 36. Even if this event occurred the requisite 12 times, it is extremely unlikely that the resulting karyotypes would be as uniform in chromosome morphology as they are known to be. If the diploid number of 36 is accepted as ancestral (10, 14, 15), then fission need be invoked at only two points in the phylogeny, marked by a +. Non-telocentric chromosomes in the karyotype of *A. monticola* are easily interpreted as fission products modified by pericentric inversion. The polymorphism for diploid number in *A. monticola* can be interpreted as secondary centric fusion or incomplete stabilization of a fully fissioned karyotype.

Single or multiple fissions have been advanced as the probable evolutionary pathway to a number of lizard karyotypes. Included are members of the families Teiidae (15), Anguidae (16), and Iguanidae: *Plica plica* (10), *Anolis oculatus* (7), and *Sceloporus grammicus* (17). The occurrence of multiple fissions in the evolution of the karyotype of *A. monticola* strengthens these interpretations.

## References and Notes


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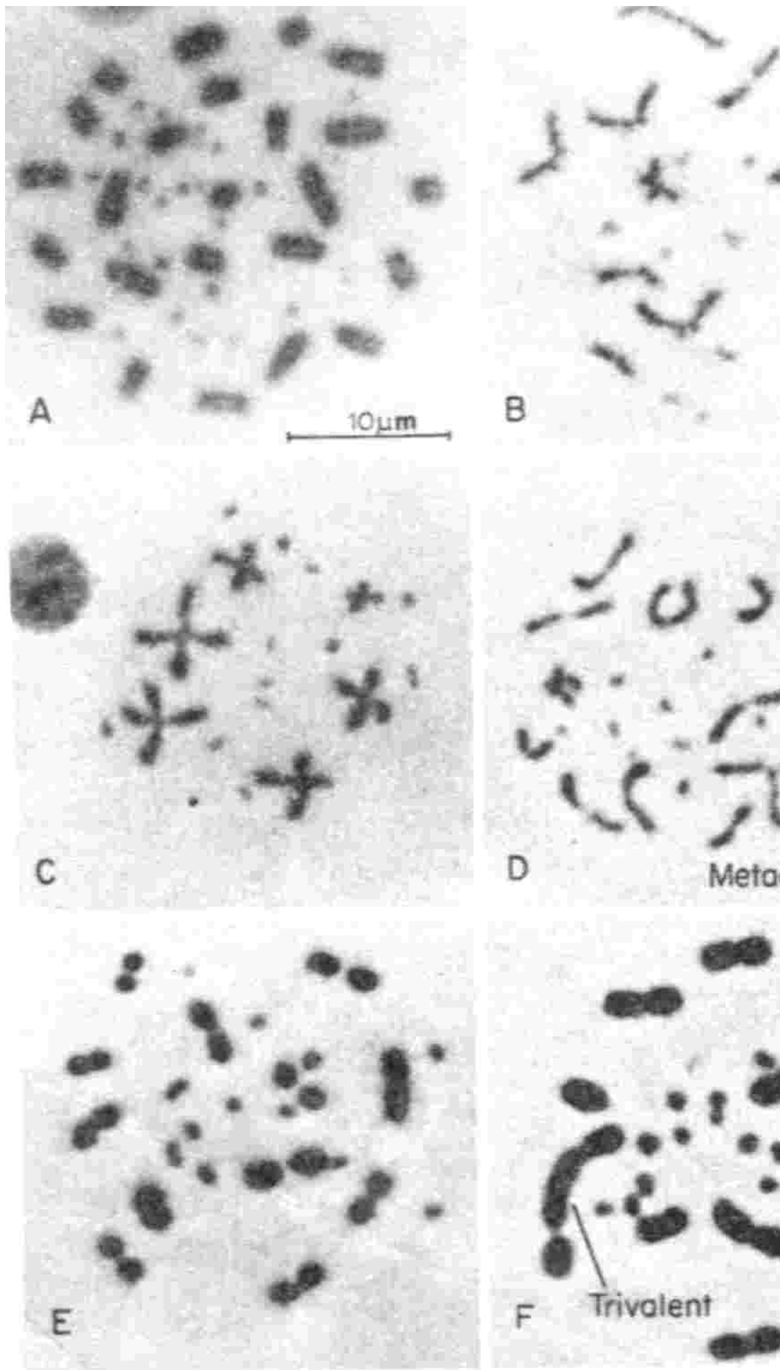


Figure 1. (A) *Anolis monticola*, mitotic metaphase, 2nn = 48; (B) *A. monticola*, second-division meiotic metaphase, 2n = 48; (C) *A. christophei*, second-division meiotic metaphase, 2n = 36; (D) *A. monticola*, second-division meiotic metaphase a showing large metacentric chromosome, 2n = 46; (E) *A. monticola*, diakinesis, 2n = 48; (F) *A. monticola*, diakinesis showing a chromosome trivalent. In == 47. All chromosome spreads are from males and are reproduced to the same scale.

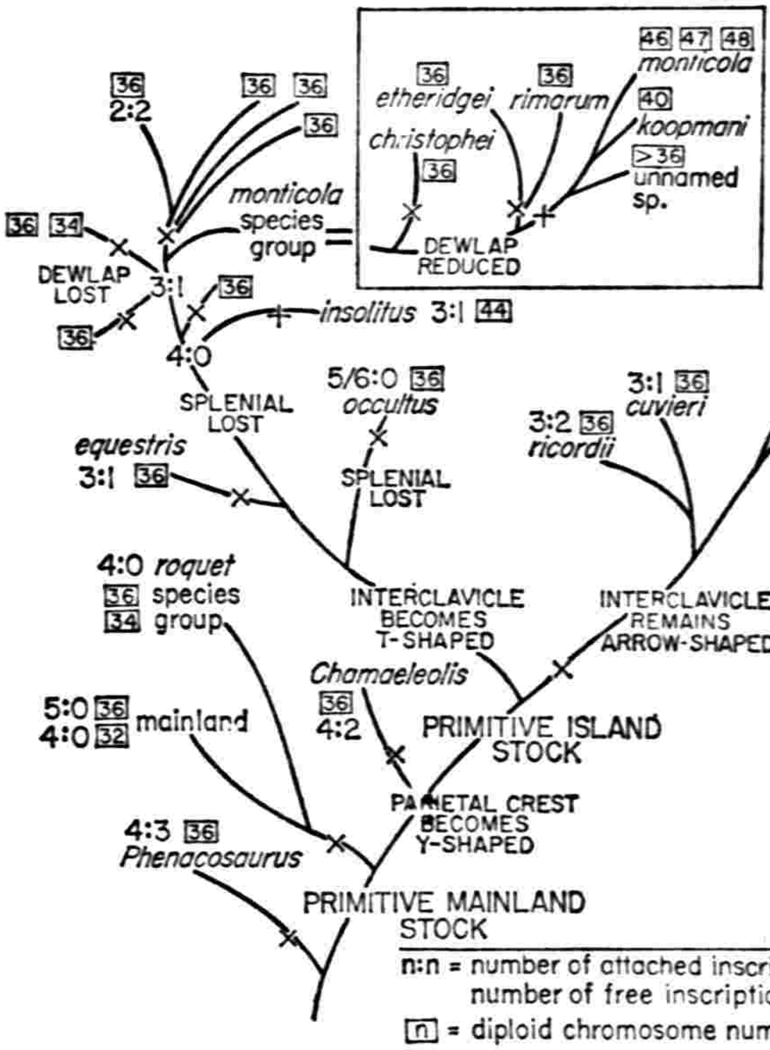


Figure 2. Phyletic diagram of the West Indian alpha *Anolis* [modified from (6)]. The highly derived position of *A. monticola* is shown. An X marks each independent incident of homologous fusion that must have occurred if the karyotype of *A. monticola* is ancestral, that is, not the result of fission. A + marks each incident of fission according to the premises of this report. *Phenacosaurus* and *Chamaeleolis* are, respectively, primitive mainland and island anoline genera.