

Cy Sb F<sub>2</sub> flies from different sibships were intercrossed leading to four classes of offspring with phenotypes +, Cy, Sb and Cy Sb. In each class brothers and sisters were then mated. This scheme allowed crossing between *Is*<sup>-</sup>/*Is*<sup>-</sup> sibs in the Cy class only if the *Is* gene was located on the third chromosome, or in the Sb class only if the gene was on the 2nd chromosome. However, in the + class all sibs were *Is*<sup>-</sup>/*Is*<sup>-</sup>. As the hatchability of inbred eggs of the respective marker classes indicates (0.36 ± 0.20 for +; 0.54 ± 0.11 for Cy; 0.92 ± 0.07 for Sb sibs), inbreeding depression was associated with the 3rd chromosome.

I believe this observation reflects the action of a mutator<sup>6,7</sup> or controlling element<sup>8,9</sup>. Such elements which can change the expression of structural genes<sup>10</sup>, perhaps by interacting with a regulatory system<sup>11</sup>, are transposable to different loci in the genome<sup>9,10</sup>. Transposition<sup>10</sup> or chromosomal contamination<sup>12-14</sup> might account for normal hatchability of *Is*<sup>-</sup>/*Is*<sup>+</sup> eggs bearing an induced chromosome as is the case when 1 parent possesses an *Is*<sup>-</sup> allele<sup>2</sup>. According to this mutator hypothesis<sup>6</sup>, disruption of genetic suppression of mutator activity through hybridisation between populations or shifts from inbreeding to outbreeding can lead to an increase in mutation frequency. These mutations or chromosomal abnormalities are then revealed by inbreeding.

Since inbreeding depression appears to be directly associated with mutator activity and related phenomena<sup>15,16</sup>, inbred matings may play a major role in the course of evolutionary processes. My hypothesis differs from the classical view of inbreeding depression, which postulates concealed dele-

terious genes<sup>17</sup>. Of course both mechanisms could be operative.

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### The karyotype of *Typhlonectes compressicauda* (Amphibia: Gymnophiona) with comments on chromosome evolution in caecilians<sup>1</sup>

M.H. Wake, J.C. Hafner, M.S. Hafner, L.L. Klosterman and J.L. Patton

*Museum of Vertebrate Zoology and Department of Zoology, University of California, Berkeley (CA 94720, USA), 23 January 1979*

**Summary.** *Typhlonectes compressicauda* has a diploid number of 28. Its karyotype, when compared to that of other caecilians, suggests some discordance in the hypothesized model of chromosome reduction in the evolution of amphibian lineages.

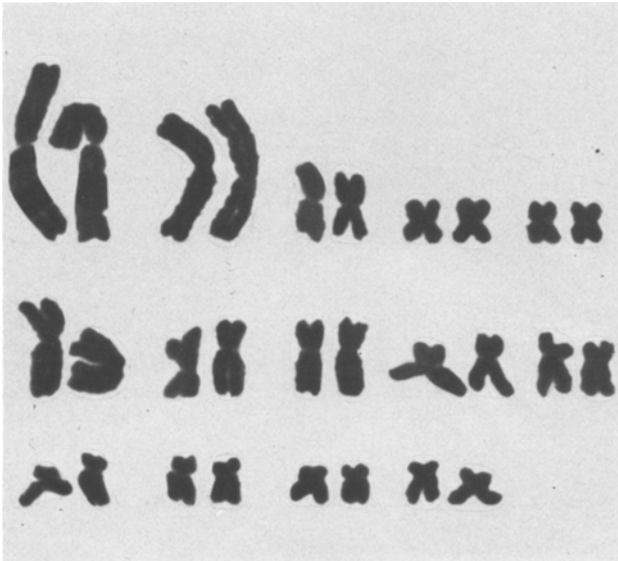
Karyotypic information is now available for 15 species representing 3 of the 5 currently recognized families of caecilians<sup>2-4</sup>. The only member of the aquatic New World family Typhlonectidae karyotyped thus far is *Chthonerpeton indistinctum*<sup>5</sup>. This species, while having a number of derived morphological and physiological features that are associated with its aquatic habitus, also has the lowest diploid number reported for caecilians (2n = 20) and it lacks microchromosomes. Based on this and similar lines of evidence, it has been suggested that karyotypes provide evidence in support of the hypothesis that the general pattern of amphibian chromosome evolution is one of reduction in chromosome number (with loss of microchromosomes)<sup>6,7</sup>. Moreover, this reductional trend in chromosome evolution may be correlated with derived states in other features of amphibian biology<sup>8-11</sup>. In this report we describe the karyotype of another member of the family Typhlonectidae, *Typhlonectes compressicauda*, and reconsider the 'reduction' hypothesis of chromosomal evolution in light of new evidence presented herein.

**Material and methods.** 3 individuals (2 females and 1 male) of *Typhlonectes compressicauda* from Cienga Santo Tomás,

Departamento Atlantico, Colombia, were karyotyped. Specimens and karyotypic preparations will be deposited in the Museum of Vertebrate Zoology, University of California, Berkeley. Animals were injected i.p. with a 0.05% colchicine solution 6 h prior to sacrifice. The best preparations were obtained from an animal that had been injected with 0.5 ml of warm yeast suspension both 48 and 24 h prior to colchicine injection<sup>12</sup>. Air-dried slides were prepared using gut epithelium and spleen according to the method of Patton<sup>13</sup> except incubation in hypotonic solution was for 1 h and centrifugation was at 700 rpm. Metaphase spreads in which most or all of the chromosomes were not overlapping were used to determine the diploid number. 17 chromosomal spreads were analyzed.

**Results.** *Typhlonectes compressicauda* has a chromosomal complement consisting of 28 banded elements (figure). The karyotype contains 3 groups of chromosomes: metacentrics (2 large pairs, 3 medium to small pairs); submetacentrics (5 medium-sized pairs); and subtelocentrics (4 small pairs).

**Discussion.** A comparison of the nonpreferentially stained karyotypes of the 2 species of typhlonectid caecilians,



The karyotype of *Typhlonectes compressicauda*.

*Typhlonectes compressicauda* ( $2n=28$ ; figure) and *Chthonerpeton indistinctum* ( $2n=20$ )<sup>5</sup>, reveals few similarities. Although the karyotypes of both species lack microchromosomes, they differ markedly in terms of gross chromosome morphology. For example, the 2 large pairs of metacentric chromosomes found in *T. compressicauda* and several species in the family Caeciliidae (e.g. *Geotrypetes seraphini* and *Caecilia occidentalis*<sup>2</sup>) are noticeably lacking in *C. indistinctum*<sup>5</sup>. Furthermore, the karyotype of *T. compressicauda* consists of totally biarmed elements, whereas that of *C. indistinctum* has 1 acrocentric pair. Although these differences appear to be rather pronounced, a more detailed comparison and final determination of chromosomal homologs within the Typhlonectidae and caecilians in general must await the time when chromosomal banding data are available.

Karyotypic information on the Gymnophiona has accumulated fairly rapidly over the last few years, and although banding data are not as yet available to allow detailed comparisons, the new information allows a re-examination of hypotheses concerning chromosomal trends in the order. Prior to this report, available chromosomal information on caecilians has generally supported the hypothesis that there exists an evolutionary trend towards reduction of diploid number and loss of microchromosomes in the towards reduction of diploid number and loss of microchromo-

somes in the more derived forms. For example, *Ichthyophis* (Ichthyophiidae), considered one of the most primitive caecilians in features of morphology and life history<sup>13-15</sup>, has the highest diploid number reported for caecilians. Conversely, *Chthonerpeton*, a member of the highly derived Typhlonectidae, has the lowest diploid number reported thus far for caecilians. In addition, while the primitive ichthyophiids all have 7 or more pairs of microchromosomes, the more derived caeciliids and typhlonectids have fewer pairs or lack microchromosomes entirely.

A re-evaluation of the caecilian chromosomal data, plus the addition of new information, reveals several facts inconsistent with the chromosomal reduction paradigm. For example, within the Typhlonectidae, *T. compressicauda* has several morphological features that appear more highly derived than those of *C. indistinctum* (e.g. lung structure, reproductive morphology, aspects of kidney morphology, etc.)<sup>16</sup>. However, contrary to predictions based on the chromosome reduction hypothesis, the derived form (*T. compressicauda*) has the higher diploid number of the 2 forms.

The chromosomal reduction hypothesis also predicts that more primitive forms would, in general, have more microchromosomes than related derived forms. However, among the caeciliids, the forms *Caecilia occidentalis* and *Siphonops paulensis*, which are primitive in several morphological and life history features<sup>16</sup>, entirely lack microchromosomes<sup>17</sup>. More derived caeciliids, such as *Geotrypetes seraphini*, *Dermophis mexicanus*, and *Gymnopsis multiplicata*, all have 4 or more pairs of microchromosomes.

Further evidence that appears contrary to the chromosomal reduction hypothesis stems from recent taxonomic revision of the Ichthyophiidae<sup>4,14</sup>, a family considered primitive in many characters. The genus *Uraeotyphlus* ( $2n=36$ ), now considered an ichthyophiid<sup>4</sup>, has a lower diploid number than does the caeciliid *Geotrypetes seraphini* ( $2n=38$ )<sup>2</sup> which is derived in features of morphology and life history<sup>16,19</sup>.

These discrepancies between the hypothesized chromosomal reductionary trend within caecilians and primitive versus derived states based on life history and morphology do not constitute a refutation of the hypothesis. Indeed, within caecilians there appears to be a general pattern of lower diploid numbers in primitive forms with higher diploid numbers in more derived forms; the model need only accommodate a moderate degree of discordance, or alternatively, be modified to account for the discrepancies mentioned above. Generalizations, though, concerning trends in caecilian chromosome evolution may be difficult to formulate at present, inasmuch as proportionately few species of caecilians have been karyotyped, and taxonomic relationships within the order are as yet unsettled<sup>4,13,15,19</sup>.

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