

membrane and one may classify them into 2 types: electron-dense particles and electron-transparent ones, both types with a diameter of 700–1900 Å (Figures 1–3). The first type seems to predominate. Occasionally neurofilaments occur in the nerves (Figure 1) and the neurosecretory axons make intimate contact with the gland cells at the synaptic regions (Figure 3). The presynaptic part is distinguished by the presence of an accumulation of small vesicles and a few similar vesicles may be found near the synapse in the postsynaptic cytoplasm. Perhaps this facilitates the control of the activity of the glands by means of neurohormonal and neural transmitter substances.

The facts that the prothoracic glands of *Cerura vinula* L. are innervated by nerves that contain neurosecretory granules and show synaptic contacts with the gland cells, makes a direct hormone delivery to the gland cells highly probable.

Zusammenfassung. Die Prothoraxdrüsen von *Cerura vinula* L. werden von Nerven innerviert, deren Axone neurosekretorische Grana enthalten und ausserdem in synaptischer Verbindung mit den Drüsenzellen stehen. Diese beiden Tatsachen sprechen für eine direkte Aktivierung der Prothoraxdrüsen durch Neurohormone.

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Three Probable Cases of Parthenogenesis in Lizards (Agamidae, Chamaeleontidae, Gekkonidae)

Neither parthenogenesis nor triploidy has previously been reported in the infraorder Iguania, comprising the families Iguanidae, Agamidae, and Chamaeleontidae. During a study of agamid karyotypes certain butterfly lizards, *Leiolepis belliana* Gray, possibly from northern Malaysia, were found to be apparently triploid parthenogenones while others from Thailand were diploid and bisexual. Literature surveys revealed two other previously unsuspected cases of lizard parthenogenesis; one in the Chamaeleontidae and the other, which probably involves triploidy as well, in the Gekkonidae.

The *Leiolepis* examined were imported from animal dealers in Bangkok (Thailand) and Singapore by RICHARD R. ROSS. The Singapore dealer told Dr. Ross that his *Leiolepis* came from near the Malaysia-Thailand border. These will subsequently be called the 'Singapore' *Leiolepis*. The 'Bangkok' specimens probably came from Tak province in northern Thailand, according to the dealer who supplied them.

Karyotypes were made from testis, spleen, or bone marrow by air- or flame-drying hypotonically pretreated, 3:1 methanol-acetic acid fixed cell suspensions¹⁻³. The lizards were injected with Velban or colchicine to arrest mitoses 2–8 h before preparation. Slides were stained with 1% or 2% aceto-orcin. The 'Singapore' *Leiolepis* were in poor condition when karyotyped and provided about 20 mitotic figures each, while many figures were examined from each 'Bangkok' specimen.

The 5 'Bangkok' *Leiolepis* karyotyped (2 ♂♂, 3 ♀♀) all had the probably primitive 36 chromosome pattern typical of many lizards (Figures 1, a and 2), including at least some members of each of the 3 iguanian families (Iguanidae⁴⁻⁸, Agamidae^{4,8}, Chamaeleontidae^{4,9,10}). Each of the 13 'Singapore' females examined had karyotypes of about 54 chromosomes (Figure 1, b) readily interpreted as triploid. 18 macrochromosomes were present in all cells examined from each 'Singapore' specimen, and at least some cells in most had the expected 36 microchromosomes, although these were difficult to count because of their large number and small size. Usually 1 chromosome of the largest trio (I in Figure 1, b) in most of the triploid figures is differentiated by very conspicuous secondary constriction, which may be the nucleolus organizer (*n* in Figure 1). This differentiation is probably a developmental phenomenon, reported for some mam-

mals¹¹, but it might result from a clonal chromosomal polymorphism. There were no indications of sex chromosomal heteromorphism in any of the karyotypes.

Constant triploidy almost always requires parthenogenetic reproduction¹² and is usually taken as presumptive evidence for it. In support of this conclusion, all 33 'Singapore' *Leiolepis* obtained were female. The probability of randomly collecting 33 females and no males from a bisexual population is about 1 in 10¹⁰, assuming an equal ratio and random distribution of the sexes.

Although no theory requires parthenogenesis to have a hybrid origin^{12,13}, most lineages of parthenogenetic vertebrates are thought to have originated as interspecific hybrids, with triploid clones deriving from backcrosses between diploid parthenogenones and males of related bisexual species (see MASLIN¹⁴ and SCHULTZ¹⁵ for references). One possible exception to the hybrid origin scheme is the parthenogenesis of certain Amazonian populations of *Cnemidophorus lemniscatus*, where there

¹ E. P. EVANS, G. BRECKON and C. E. FORD, *Cytogenetics* 3, 289 (1964).

² J. L. PATTON, *J. Mammal.* 48, 27 (1967).

³ L. A. PENNOCK, D. W. TRINKLE and M. W. SHAW, *Chromosoma* 24, 467 (1968).

⁴ R. MATTHEY, *Les Chromosomes des Vertebres* (F. Rouge, Lausanne 1949).

⁵ G. C. GORMAN, L. ATKINS and T. HOLZINGER, *Cytogenetics* 6, 286 (1967).

⁶ G. C. GORMAN, Thesis, Harvard University (1968).

⁷ W. P. HALL, paper read at the 1966 annual meetings of the Am. Soc. Ichthyologists and Herpetologists, Lawrence, Kansas.

⁸ W. P. HALL, unpublished.

⁹ R. MATTHEY, *Rev. Suisse Zool.* 64, 709 (1957).

¹⁰ R. MATTHEY and J. VAN BRINK, *Bull. Soc. Vaud. Sci. Nat.* 67, 333 (1960).

¹¹ T. C. HSU, B. R. BRINKLEY and F. E. ARRIGHI, *Chromosoma* 23, 137 (1967).

¹² E. SOUMALAINEN, *Adv. Genet.* 3, 193 (1950).

¹³ R. A. BEATTY, *Parthenogenesis and Polyploidy in Mammalian Development* (Cambridge University Press, London 1957).

¹⁴ T. P. MASLIN, *Syst. Zool.* 17, 219 (1968).

¹⁵ R. J. SCHULTZ, *Am. Naturalist* 103, 605 (1969).

appears to be only one potential source species^{16,17}. GÜNTHER PETERS of the Humboldt Museum, Berlin, who has seen my specimens, is reviewing *Leiolepis* and any speculations on the origin of parthenogenesis in this group must be deferred until his review is complete.

During a literature search, 2 other probable cases of lizard parthenogenesis, 1 apparently involving triploidy, were brought to light. These merit verification and further study. The gecko, *Gehyra variegata ogasawarisimae* Okada (1930)¹⁸, from Chichijima, one of the Bonin Islands, Japan [US Admin., Treaty of San Francisco], has 63 chromosomes (MAKINO and MOMMA¹⁹), the highest $2n$ of any gecko except the clearly triploid *Hemidactylus garnotii*²⁰. MAKINO and MOMMA made karyotypes from

embryonic ovaries only because they found no males and then cited the odd number of chromosomes as evidence for female sex chromosomal heteromorphism, still unconfirmed in lizards^{4,21}. However, particularly in view of the seeming lack of males, these *Gehyra* might be parthenogenetic triploid derivatives of a 42 chromosome diploid ancestral stock. The geckos, *Tarentola mauritanica*²², *Bunops tuberculatus*, and *Cyrtodactylus kotschy*²³ all have $2n$'s of 42, which may thus be common in the Gekkonidae.

The third possible case of parthenogenesis was brought to my attention by A. ROSS KIESTER. SCHMIDT²⁴ found only females in a collection of 63 '*Rhampholeon boulengeri*' (Chameleontidae) [= *Brookesia spectrum* *affinis*, sensu LOVERIDGE, 1951²⁵] from the Ituri Forest (Congo). 61 were from Medje and 2 were from Poko. I examined *Brookesia spectrum* in the Museum of Comparative Zoology collection: 4 additional *B. s. affinis* from Mayala, Ituri Forest, were female. However, males were found in small collections of *B. s. spectrum* from Ja River and Kribi, both in Cameroun, and of *B. s. boulengeri* from Upper Mulinga, Idjwi Id., Congo. I diagnosed the sexes by exposing gonads in the MCZ specimens, but errors in sex determination by SCHMIDT²⁴ would seem to be precluded by the males' greatly enlarged hemipenal swellings and much longer tails. MATTHEY⁹ karyotyped 2 species of *Brookesia*, including *spectrum*: *B. stumpffi* (Madagascar) has the common and probably primitive lizard karyotype of 36 chromosomes. *B. [Rhampholeon, sensu Matthey] spectrum*, from an unspecified locality has a

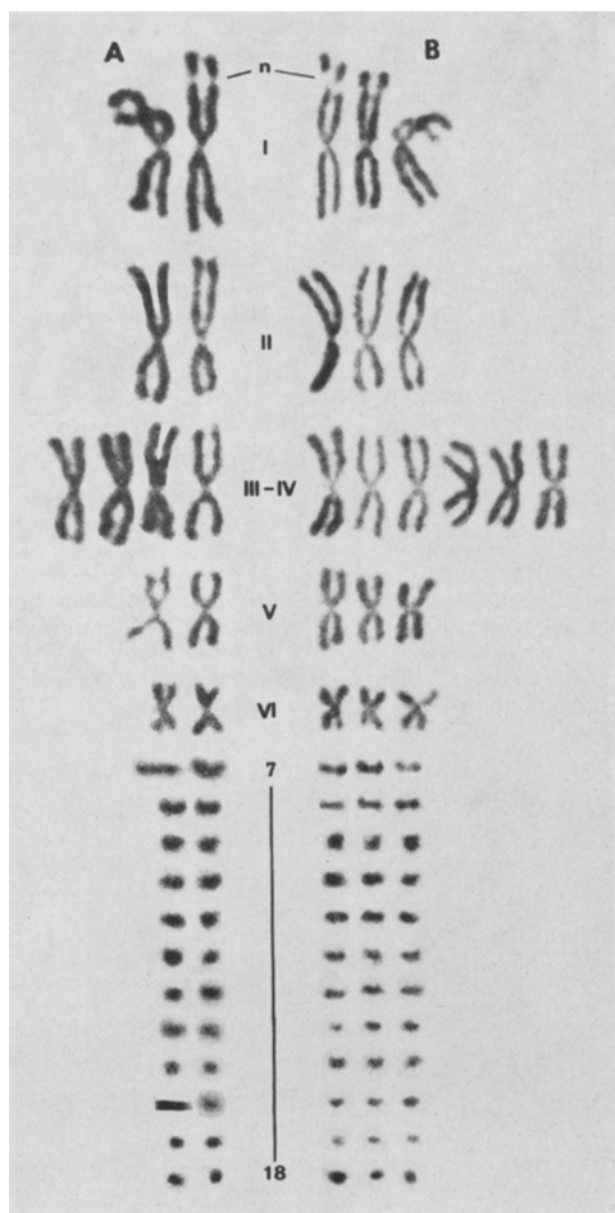


Fig. 1, a (left). Somatic karyotype of ♀ *Leiolepis belliana* from Bangkok, $2n = 36$.

Fig. 1, b (right). Somatic karyotype of ♀ from Singapore, $3n \sim 54$. The probable homologs are arrayed opposite one another for purposes of comparison. 'n' indicates the conspicuous secondary constriction, usually well developed in only a single chromosome of each cell.

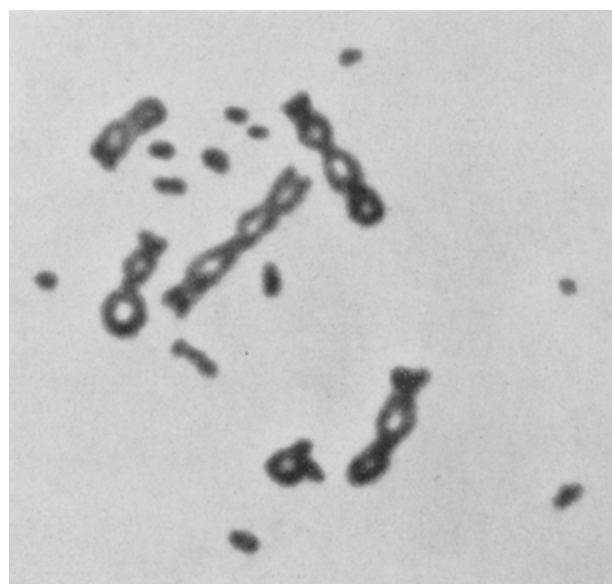


Fig. 2. Diakinesis in a male *Leiolepis belliana* from 'Bangkok'.

¹⁶ D. M. V. M. PECCININI, Thesis, Univ. São Paulo (1969).

¹⁷ P. E. VANZOLINI, Abstract for Latin American Congress of Zoology (Caracas, 1968).

¹⁸ Y. OKADA, Bull. biogeogr. Soc. Japan 7, 187 (1930).

¹⁹ S. MAKINO and E. MOMMA, Cytologia 15, 96 (1949).

²⁰ A. G. KLUGE and M. J. ECKARDT, Copeia 1969, 651 (1969).

²¹ R. MATTHEY and J. M. VAN BRINK, Evolution 11, 163 (1957).

²² R. MATTHEY, Rev. Suisse Zool. 38, 118 (1931).

²³ Y. L. WERNER, Bull. Res. Council Israel 5 B, 319 (1956).

²⁴ K. P. SCHMIDT, Bull. Am. Mus. Nat. Hist. 39, 385 (1919).

²⁵ A. LOVERIDGE, Bull. Mus. comp. Zool. Harvard 706, 177 (1951).

$2n$ of 20, the lowest number reported for any lizard. Since the *spectrum* locality is unspecified, the karyotypic data may provide little information on the possible parthenogenesis of the Ituri Forest population. However, since the genus *Chamaeleo* shows several species with $2n$'s of 22 from which the *B. spectrum* karyotype might be more directly derived than it can be from the $2n = 36$ karyotype of *B. stumpffi*^{9,10}, karyotypic analysis of the remaining *Brookesia* species might indicate separate origins of the mainland and Madagascar dwarf chameleons, and might thereby support the older classification of *Rhampholeon* for the mainland forms and *Brookesia* for the Madagascar species²⁶.

Zusammenfassung. Nachweis von Triploidie und Parthenogenese bei Reptilien (Agamidae, Chamaleontidae und Gekkonidae).

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²⁶ I thank E. E. WILLIAMS for his many suggestions, A. R. KESTER, W. B. NEAVES and G. C. GORMAN for their comments and R. R. ROSS for obtaining *Leiolepis*. This study was aided by N.S.F. Grant No. GB 6944 to E. E. WILLIAMS.

The Influence of Temperature upon the Change from the Male to the Female Phase in *Ophryotrocha puerilis puerilis*, a Polychaete Worm

The influence of different temperature conditions upon the relative durations of the sexual phases has been investigated on the progeny of individuals of *Ophryotrocha puerilis puerilis* which were collected at the Leghorn Aquarium. 1107 individuals, born from 6 different pairs, were divided into 3 groups of 369 individuals, in which the progenies of the 6 pairs were represented by equal samples. One group was kept at the temperature of 10°C, the other two groups at 18°C and at 21°C.

It has been demonstrated that the change from the male to the female phase takes place at a mean length of 16.04 ± 0.4 chaetigerous segments, at the length of 17.09 ± 0.3 segments and at the length of 18.16 ± 0.2 segments at temperatures of 21°C, 18°C and 10°C respectively (Figure 1). In other words the increase in temperature anticipates sex change as compared with the increase in number of chaetigerous segments.

Each individual was isolated, and subjected to the temperature of the group to which it was assigned, when

it reached the length of 10 chaetigerous segments. The individuals which were kept at the temperatures of 18°C and of 21°C changed from the male to the female phase within 11 ± 2 and 12 ± 1 days respectively after the beginning of the treatment. Differences are not significant. On the other hand, individuals from the same strains, which were kept at the temperature of 10°C, changed sex in 40 ± 2 days (Figure 2). It is demonstrated therefore that higher temperatures anticipate sex change also when age is taken into consideration. Although different strains underwent sex change at significantly different lengths and ages, they nevertheless reacted to temperature conditions in the same way.

The above results present analogies with data on sex reversal in the Atlantic and Mediterranean populations of *Ophryotrocha puerilis*. Individuals from Mediterranean strains, which are adapted to the warmer sea, change sex at mean lengths which are lower than those of individuals from Atlantic strains, which were kept at the same temperature conditions¹. In such instances, differences are of genetic origin inasmuch as Atlantic and Mediterranean populations show a high degree of genetic isolation².

¹ G. BACCI, Pubbl. Staz. Zool. Napoli 26, 110 (1955).

² G. BACCI and M. LA GRECA, Nature 171, 1115 (1953).

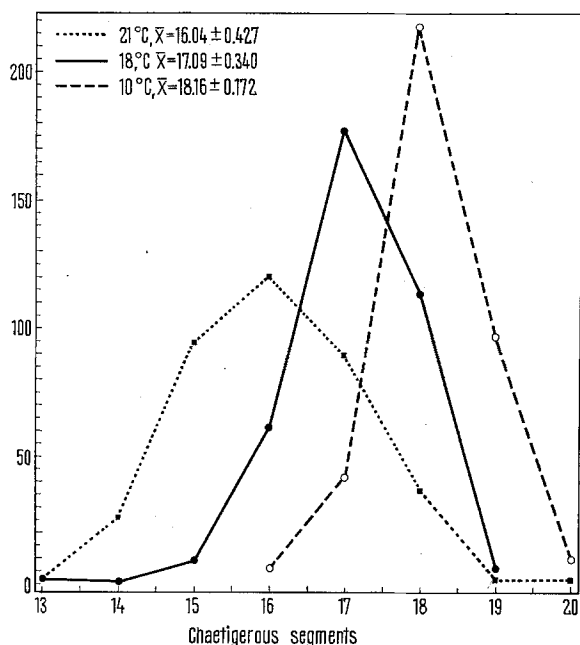


Fig. 1. The abscissae indicate the number of chaetigerous segments shown by individuals which are kept at different temperature conditions when they change from the male to the female sex phase.

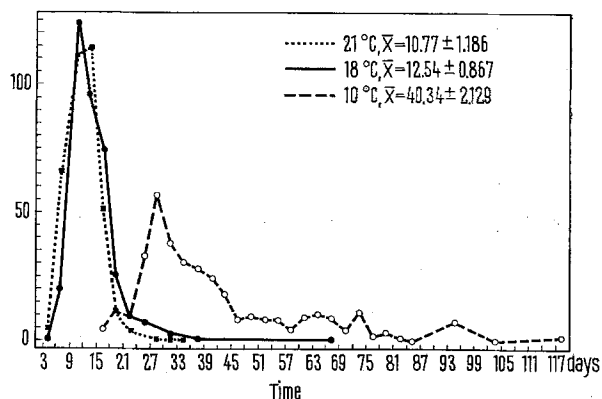


Fig. 2. The abscissae indicate the number of days required by the same individuals of Figure 1 to change from the male to the female sex phase.