HERPETOZOA 6 (1/2): 3-20 Wien, 30. Juli 1993

# Two new all-female lizard species of the genus Leiolepis CUVIER, 1829 from Thailand and Vietnam (Squamata: Sauria: Uromastycinae)

(Squamata, Sauria, Oromastychiae)

Zwei neue parthenogenetische Eidechsenarten der Gattung Leiolepis CUVIER, 1829 aus Thailand und Vietnam

(Squamata: Sauria: Uromastycinae)

# ILYA S. DAREVSKY & LARISSA A. KUPRIYANOVA

#### **ABSTRACT**

The Butterfly Lizard genus Leiolepis CUVIER, 1829 includes four bisexual (L. belliana, L. guttata, L. reevesii, L. peguensis) and three unisexual (triploid - L. triploida, L. guentherpetersi; probably diploid - L. boehmei) forms. The two latter, originating from Vietnam and Thailand respectively, are described as new in this paper.

Morphological, chorological and karyological analyses suggest that both triploid and probably diploid unisexual species originated from natural hybridization. The females of the triploid species display low fertility, some of them being totally sterile. It is supposed that reduced fertility in these females may be due to their hybrid origin and, as a consequence, to meiotic disturbances in the course of oogenesis, as is probably true in some other hybrids.

#### KURZFASSUNG

Die Schmetterlingsagamen-Gattung Leiolepis CUVIER, 1829 umfaßt vier bisexuelle (L. belliana, L. guttata, L. reevesii, L. peguensis) und drei unisexuelle (triploid - L. triploida, L. guentherpetersi; wahrscheinlich diploid - L. boehmei) Formen. Die letzteren beiden stammen aus Vietnam bzw. Thailand und werden hier neu beschrieben.

Morphologische, arealkundliche und karyologische Untersuchungen lassen vermuten, daß die triploiden Formen und auch die wahrscheinlich diploide unisexuelle Art durch natürliche Hybridisierung entstanden sind. Die Weibchen der triploiden Arten zeigen verminderte Fruchtbarkeit, wobei einige von ihnen völlig steril sind. Es wird vermutet, daß die verminderte Fertilität dieser Weibchen, wie dies wahrscheinlich auch für einige anderen Hybridformen zutrifft, auf ihren Hybrid-Ursprung und in der Folge auf Störungen der Meiose während der Oogenese zurückzuführen ist.

## **KEYWORDS**

Agamidae, Uromastycinae, Leiolepis, L. belliana, L. guttata, L. reevesii, L. peguensis, L. triploida, L. guentherpetersi sp. nov., L. boehmei sp. nov.; Vietnam, Thailand; new species, parthenogenesis, hybridization, sterility, fertility

# INTRODUCTION

The Butterfly Lizard genus Leiolepis CUVIER, 1829, widely distributed over south-eastern Asia, was formerly claimed monotypic (MERTENS 1961). However, according to a major thorough revision by PETERS (1971) this genus is represented by four bisexual species and one parthenogenetic triploid species, L. triploida PETERS, described from the south of the Malayan Peninsula. PETERS presumed an autotriploid nature of the unisexual L. triploida, which he thought, could have originated from reorganization of the initial

diploid karyotype in one of the bisexual ancestor forms, most probably L. belliana (GRAY, 1827). This was in particular deduced from the fact, that there were no unisexual diploid species in the area of the Malayan Peninsula that could have contributed to a possible hybrid origin of L. triploida. However, BÖHME later (1982) described a probably diploid unisexual population of Butterfly Lizards from Malaysia. He fancied that L. triploida could have originated from an interspecies hybridization between diploid partheno-

genetic females and males of the sympatric bisexual L. belliana. A similar origin was supposed for the majority of the other presently known triploid unisexual lizard species. BÖHME (1982) did not especially deal with the taxonomy of the examined parthenogenetic population. However, he stressed its obvious morphological distinctiveness from the triploid species described by PETERS (1971).

Carrying out herpetological studies in different parts of Vietnam, we discovered new triploid unisexual populations of Butterfly Lizards, and this required comparative studies of both L. triploida PETERS and the probably diploid parthenogenetic individuals described by BÖHME (1982). The results of our work and the description of two hitherto unknown unisexual Leiolepis species are presented below.

# MATERIAL AND METHODS

All in all, 58 individuals of the genus Leiolepis were studied which mainly originated from Vietnam and the Malayan Peninsula. Different species of the genus from other parts of its range were examined for comparison.

Acronyms used: MCZ - Museum of Compar-Acronyms used: McZ - Museum of Comparative Zoology, Cambridge, Massachusetts; NHRM - Naturhistoriska Riksmuseet, Stockholm. ZFMK - Zoologisches Forschungsinstitut und Museum Alexander KOENIG, Bonn; ZISP - Zoological Institute, Academy of Sciences, Saint-Petersburg.

a) MCZ 104381-85, 103695-97, 101922-29, 104376-80, 117552-77, 27 females, Malayan Peninsula; no further data available.

b) NHRM BJO/1939.099.3008/1-17, 17 females, central Vietnam, Thuan Luu; leg. B. BJORKENGEN, 4. II. - 2. IV. 1939.
c) ZFMK 24650, 24651, 25486, 27446-48, 6

females, S Thailand, Songkhla; leg. R. A. BRÜCK-NER, X. 1978.

d) ZISP 20326-29, 20331-34 (ZISP 20334 formerly ZFMK 52822), 8 females, central Vietnam,

Thuy Phu; leg. TRAN KIEN, II. 1988.
e) ZISP 20330, 1 female, central Vietnam,
Cu Lao Cham Island; leg. I. DAREVSKY, 29. IV.

f) ZISP 20336 (formerly ZFMK 24652), 1 female, S Thailand, Songkhla; leg. R. A. BRÜCK-NER, X. 1978.

Description of scutellation and coloration is largely based on the terminology suggested by MERTENS (1961) and PE-TERS (1971). The method used for chromosome preparation was published elsewhere (DAREVSKY & al. 1984; KUP-RIYANOVA 1984).

The following meristic and morphometric characters were used for comparison (abbreviations used in table 1 in parentheses):

Snout-vent length (SVL), tail length (TL), number of supralabials (SL), number of infralabials (IL), number of dorsal scales between the longitudinal dorsal stripes (DSC), number of ventral scales between the median line of the belly and the small dorsal scales (VS), number of enlarged scales across the lower part of the tibia (TS), number of femoral pores (PF), number of subdigital scales underneath 4th toe (SDS), number of oval spots in a transversal row between the dorsal stripes (DSP).

Leiolepis boehmei sp. nov. (fig. 1)

Holotype: ZFMK 24651, adult female; South Thailand, Songkhla. R. A. BRÜCKNER, October, 1978.

Paratypes: ZFMK 24650, 25486, 27446-48, same data as for the holotype; ZISP 20336 (formerly ZFMK 24652), same data as for the holotype.

Diagnosis: Medium sized unisexual (probably diploid) species. Differs from all other species of Leiolepis in the following combination of characters: SVL up to 123 mm; 17 - 19 ventral scales between the midline of the belly and the body sides; 12 - 14 enlarged scales across the lower part of the tibia; fourth toe with 29 - 35 subdigital scales; 17 - 19 femoral pores; 41 - 45 dorsal scales between the longitudinal dorsolateral stripes; median dorsal stripe absent; 6 - 7 light oval spots disposed in transverse rows between the

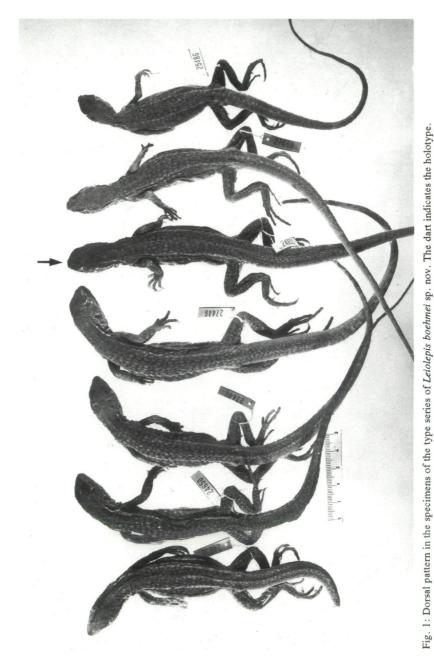
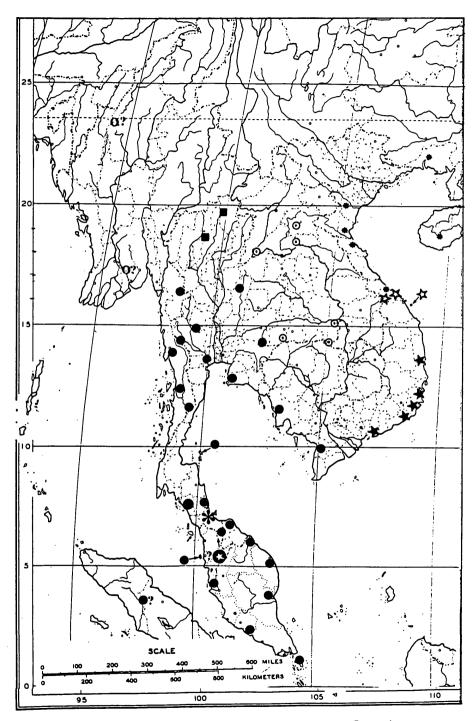


Abb. 1: Die Rückenzeichnung bei den Exemplaren der Typenserie von Leiolepis boehmei sp. nov. Der Pfeil bezeichnet den Holotypus.



●-1 ■-2 ★-3 •-4 ⊙-5 O-6 **┼**-7 **②**-8 **☆**-9

stripes produce a characteristic reticulum on dorsum.

Description of holotype: Rostral nearly three times as wide as high, bordered by 2 labials and 7 smooth postrostrals, followed by 10 feebly keeled scales. All other scales covering the snout and interorbital area distinctly keeled; 6 rows of scales between supraoculars; 9 -11 supra-, 11 - 12 infralabials; 45 - 46 rows of scales between the light dorsolateral stripes when counted in the middle of the body; 43 - 46 rows of scales between the median line of the belly and the small dorsal scales: 13 enlarged scales across the lower part of tibia; series of 19/19 femoral pores separated medially by 15 pubic scales; fourth toe with 31 bicarinate subdigital scales; 3 scales with enlarged triangular "spurs" at the base of third toe.

Snout-vent length 110 mm; tail length 245 mm.

Head olive with darker areas on the sides and a small yellowish spot on the lower eyelid. Dorsum blackish olive with two longitudinal lateral stripes, each 6 - 7 body scales wide. More or less distinct transverse rows formed by series of 6 - 7 grey oval spots between the dorsolateral stripes; indistinct light oblique stripes on the sides of the body. Chin, throat and breast grey with white vertical bars and indistinct marks.

The variability of morphometric and meristic characters within the paratype specimens and a comparison with related Leiolepis species are given in table 1.

Distribution: All specimens

of the type series originate from Songkhla (province of Songkhla) situated at the Gulf of Siam in southern Thailand. From its external characters a female from Songkhla (Copenhagen University Zoological Museum: N 136130) also belongs to this species. According to PETERS (1971) this specimen shows some characters which are intermediate between L. triploida and L. belliana (comp. map fig. 2).

E t y m o l o g y: The species is named after Wolfgang BÖHME, author of numerous works on tropical lizards' taxonomy and on the unisexual diploid population of *Leiolepis* in particular.

Comments: BÖHMEs (1982) investigations were based on 12 mature female individuals. Six out of them (deposited in the ZFMK collection) and one (deposited in the ZISP collection) make up the type series; one female from Songkhla was at PETERS' (1971) disposal. As already stressed by BÖHME (1982), the absence of males among these 12 specimens, which were taken at the same time within a limited territory, may by itself testify unisexuality of the population in question. The individuals studied by BÖHME were fertile and different from the females of L. triploida (which are sterile in many cases) by their smaller size (see table 1). All this made BÖHME come to the undoubtedly correct conclusion that Songkhla is inhabited by a diploid parthenogenetic population which he regarded as an unisexual diploid clone of L. belliana. The possible origin of this parthenogenetic population is discussed below.

Fig. 2 (opposite page): Main locality records of seven Leiolepis species in SE Asia (after PETERS (1971), with additions and modifications).

1 - L. belliana belliana; 2 - L. belliana ocellata; 3 - L. guttata; 4 - L. reevesii revesii; 5 - L. reevesii rubritaeniata; 6 - L. peguensis; 7 - L. boehmei sp. nov.; 8 - L. triploida; 9 - L. guentherpetersi sp. nov.

Abb. 2 (gegenüberliegende Seite): Die Verbreitung von sieben Leiolepis-Arten in Südostasien (nach PETERS (1971), mit Ergänzungen und Veränderungen).

1 - L. belliana belliana; 2 - L. belliana ocellata; 3 - L. guttata; 4 - L. reevesii reevesii; 5 - L. reevesii rubritaeniata; 6 - L. peguensis; 7 - L. boehmei sp. nov.; 8 - L. triploida; 9 - L. guentherpetersi sp. nov.

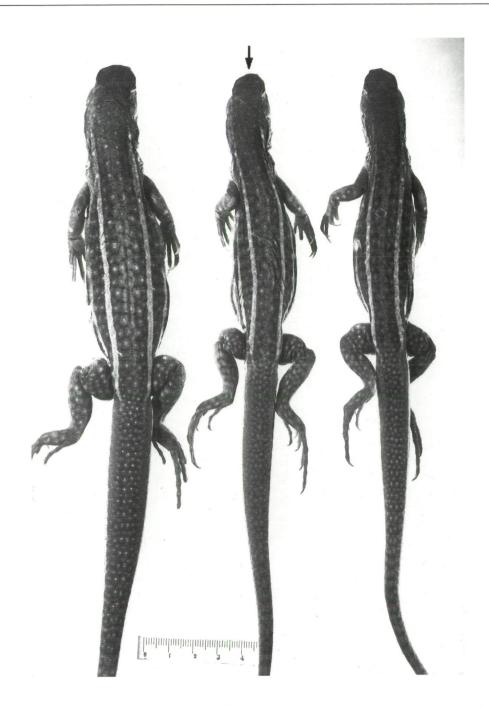


Fig 3: Dorsal pattern in three specimens of Leiolepis guentherpetersi sp. nov. from terra typica. The dart indicates the holotype.

Abb. 3: Die Rückenzeichnung dreier Exemplare von Leiolepis guentherpetersi sp. nov der terra typica. Der Pfeil bezeichnet den Holotypus.

# Leiolepis guentherpetersi sp. nov. (figs. 3, 4)

H o I o t y p e: ZISP 20326, adult female; central Vietnam, Thuy Phu, approx. 17 km SE of Hue, Binhtrithien Province, leg. TRAN KIEN, February, 1988.

Paratypes: ZISP 20327, 20328, 20329, 20331, 20332, 20333, 6 adult females, same data as for the holotype; ZISP 20330, 1 subadult female; Central Vietnam, Cu Lao Cham Island, Quangnam - Danang Province, leg. I. S. DAREVSKY, April 29, 1987; ZISP 20334 (formerly ZFMK 52822), 1 adult female, same data as for the holotype; NHRM BJO /1939.099.3008/1-17, 6 adult females, 11 subadult females; central Vietnam, Thuan Luu, approx. 50 km SW of Hue, Binhtrithien Province, leg. B. BJORKENGEN, February 4 - April 2, 1939.

Diagnosis: Large unisexual triploid (3n = 54) species. Different from all other Leiolepis species by the following combination of characters: Snout-vent length up to 156 mm; rostral 3 - 3,5 times as wide as high; 17 - 20 ventral scales between the median line of the belly and the small dorsal scales; 14 - 18 enlarged scales across the lower part of the tibia; fourth toe with 40 - 43 subdigital scales; femoral pores 21 - 23; 38 - 43 scales between the light dorsolateral stripes; median dorsal stripe absent; transverse stripes formed by rows of 4 - 5 light oval spots produce a characteristic reticulum between dorsolateral stripes.

Description of the holotype: Rostral nearly three times as wide as high, bordered by two supralabials and 6 smooth postrostrals, the latter being followed by 8 smooth scales. All other scales on the snout and in the interorbital area distinctly keeled; 6 rows of scales between supraocular areas; 8/9 supra-, and 9/10 infralabials; 42 - 44 scales between the dorsolateral longitudinal stripes, when counted in the middle of the body; ventral scales about as broad as two dorsals; 18 - 19 ventral scales between the median line of the belly and the small dorsal scales; 15 enlarged scales across lower part of tibia; the series of 21/22 femoral pores separated medially by 12 pubic scales; fourth toe with 42 bi- or tricarinate subdigital scales; four scales with enlarged triangular "spurs" at the base of third toe.

Snout-vent length 130 mm, tail length 273 mm.

Head olive with darker areas on the sides and small yellowish spots on the lower eyelids and under the eyes. Dorsum blackish olive with two light dorsolateral stripes, each 7 - 8 scale rows wide, and with numerous whitish oval spots, their olive-grey edges forming a characteristic reticulum; rows of 4 - 5 oval spots between the dorsolateral stripes; two indistinct longitudinal whitish stripes between fore limbs and hind limbs and along the sides of the tail. Chin, throat, breast and the anterior part of the venter grey with indistinct round whitish spots and marks.

Variability within the paratypes and comparison with closely related species are presented in table 1.

Karyotype e: The triploid karyotype of L. guentherpetersi includes 18 metacentric and submetacentric macrochromosomes and about 36 acrocentric microchromosomes. It is difficult to count the exact number of the latter because of their small size, but the number of macrochromosomes clearly indicates triploidy. 3n = 54: 18 M (VSV) + 36 m (A) (see fig. 5).

D is tribution: At present two mainland populations and one insular population from the central Vietnam provinces of Binhtrithien and Quangnam-Danang are known. An isolated population of this unisexual species probably exists in South Vietnam in the coastal dunes of the Province of Thuanhai. From their external appearance these individuals (which were observed in 1987 by the first author of this paper but unfortunately were not taken) seem to belong to this species.

Field notes: In the area of the terra typica the lizards live in coastal dunes which are poorly anchored by sparse bushy and grassy vegetation.



Fig. 4: Dorsal pattern in six paratype specimens of Leiolepis guentherpetersi sp. nov. from Thuan Luu. Abb. 4: Rückenzeichnung bei sechs Paratypen von Leiolepis guentherpetersi sp. nov. aus Thuan Luu.

Their dwelling places are described at length by NGO DUC CHUNG & DANG CAO VAN (1986). The lizards were observed by the first author on the island of Cu Lao Cham (fig. 2) both on the coastal sands and among the bushy vegetation of the coastal slopes.

It is an important fact, that both known triploid unisexual species of Leiolepis are sterile to a considerable degree. Only 6 (= 30%) out of 20 mature individuals of L. triploida studied by PETERS (1971) were fertile to a variable extent. This was estimated from the developmental stage of their ovaries and oviducts.

According to the state of their internal genitals, only 5 out of 14 (= 35.7%) of our mature female *L. guentherpetersi* (snout-vent length no less than 90 mm) were fertile. As in the case of *L. triploida*, the much reduced state of the oviducts served as the diagnostic character. In the individuals investigated they represent almost straight flat formations devoid of any folds which indicates sterility (figs. 6-7).

Most of the adult females caught in February, the period of reproduction, had only 1 - 3 oocytes each (up to 3 mm in diameter) in their ovaries. Only two females had 1 - 3 big ova in their oviducts, ready to be laid. Corpora lutea were well noticeable in one case, indicating that three ova had already been laid. In four sterile females there was one (right) poorly developed ovary only. Reduced viability of the triploid females in comparison with their bisexual parental forms is noteworthy as well. When kept under absolutely equal conditions in a terrarium, the number of perished specimens was higher in triploid individuals than in bisexual ones. However, according to our field observations, the abundance of L. guentherpetersi is comparable with that of the bisexual species L. guttata. This means that a very small number of reproductive females is maintaining a stable population.

E t y m o l o g y: The species is named after Günther PETERS, author of numerous herpetological works, including the fundamental revision of the genus Leiolepis.

### The origin of the unisexual species of the lizard genus Leiolepis

More than 40 diploid and triploid parthenogenetic lizard species are known at present. For most of them it was shown with all certainty that they resulted from natural hybridization. As to the triploid unisexual species, they appear in the second stage of this process of hybridization as a result of back-crossing between diploid parthenogenetic females and males of their bisexual parental forms (see DA-REVSKY & al. 1985; DESSAUER & COLE 1989; MORITZ & al. 1989). Theoretically, the formation of triploid species is enabled by autopolyploidy, as a consequence of spontaneous reorganization of an originally diploid karyotype. According to HALL (1970) this very event happened when triploid parthenogenesis in the genus Leiolepis was formed. HALL assumed that autotriploid individuals occur incidentally in usually bisexual lizard populations, and that such triploids might become founders of triploid parthenogenetic clones. Relying on HALL's competent opinion, and considering the fact that no diploid unisexual species of *Leiolepis* was known within the Malayan Peninsula, PETERS (1971) also came to the conclusion that the appearance of *L. triploida* was originally based on autopolyploidy.

PETERS (1971: 87) did not completely preclude the possibility of the hybrid origin of this species, which could have resulted from mating between specimens of diploid bisexual forms of the kindred *L. belliana* group. Some evidence supporting the latter assumption resulted from BÖHME's (1982) discovery of a probably diploid parthenogenetic population in the south of Thailand (described as *L. boehmei* sp. nov. in the present paper).

The probable presence of diploidy and parthenogenesis in this lizard made BÖHME formulate the working hypothesis

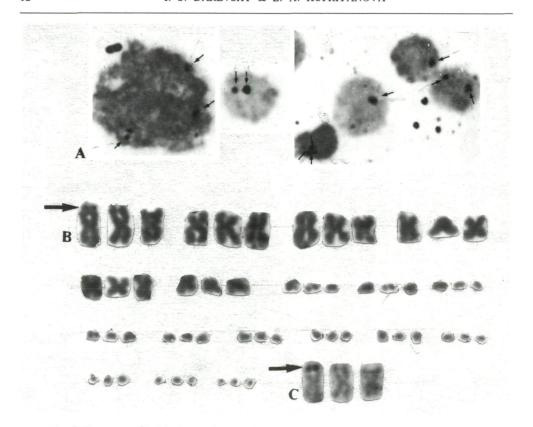


Fig. 5: Karyotype of Leiolepis guentherpetersi sp. nov.

A - Interphase and prophase nuclei. Darts point to nucleoli.

B - Karyotype 3n = 54: 18 M (V + SV) + 36 m (A). Dart points to Giemsa-stained secondary constriction in the despiralized zone of chromosome no. 1.

C - Chromosome trio no. 1. Dart points to despiralized silver-stained NOR-bearing zone.

Abb. 5: Der Karyotyp von Leiolepis guentherpetersi sp. nov.

A - Interphase- und Prophasekern. Die Pfeile bezeichnen die Nucleoli.

B - Karyotyp 3n = 54: 18 M (V + SV) + 36 m (A). Der Pfeil bezeichnet die Giemsa-gefärbte sekundäre Einschnürung in der entspiralisierten Zone von Chromosom Nr. 1. C - Triplett von Chromosom Nr. 1. Der Pfeil bezeichnet die entspiralisierte, durch Silberfärbung

sichtbar gemachte NOR-tragende Zone.

that L. triploida could have originated from hybridization of parthenogenetic diploid females and males of the widely distributed Thailand species L. belliana.

Hypothesizing on potential parental couples which could have participated in the formation of the parthenogenetic species, the present day distribution of all bisexual and parthenogenetic forms that might hybridize is of great importance. According to the data of PETERS (1971) the geographic distribution of L. triploida is not clear, but terra typica of this species, which apparently inhabits northern Malaysia, is the region of the Malaysian-Thailand boundary. This suggests that L. triploida occurs also in the south of Thailand, from where the diploid L. boehmei sp. nov. is known. The characteristics of coloration (fig. 8) and some morphological characters, which are intermediate between L. boehmei and L. belliana in L. triploida, also speak in favour of BÖHME's hypothesis. In particular, L. triploida adopted the bright lateral and dorsomedian stripe as well as the characteristic reticular pattern from the unisexual maternal species.

The origin of the probably diploid parthenogenetic species L. boehmei remains an unsolved problem so far. There is every probability to assume that this species is also of hybrid nature and resulted from hybridization between various diploid bisexual forms formerly united under the common specific name *L. belliana*. Based on the small sample at his disposal BÖH-ME (1982) showed that there are some marked distinctions in size and coloration between the individuals from Pattani in southern Thailand and Kuantan from the neighbouring regions of Malaysia. It is quite possible that actually two different bisexual species are involved, representing the parental forms of the parthenogenetic *L. boehmei*.

Let us now consider the mechanism that could have led to the origin of the Vietnam triploid species L. guentherpetersi. According to cytogenetic features and to analogies with L. triploida, there is every reason to believe that L. guentherpetersi is also of hybrid nature, and that the bisexual forms L. reevesii and L. guttata have taken part in its formation. As shown in the map (fig. 2) the former of the probable parental species is distributed north, the latter south of L. guentherpetersi. An answer to the question on the hybrid origin of the Vietnam triploid species is, however, complicated by the fact that possible maternal diploid parthenogenetic forms similar to L. boehmei have not yet been found within Vietnam. By analogy with examples of hybridogenesis in other parthenogenetic lizard species (MORITZ & al. 1989), one could surmise that such an intermediate diploid unisexual form once existed somewhere in central Vietnam in the area of L. guentherpetersi. In this case, the origin of this latter triploid species may be hypothesized as follows: At the first stage, as a result of hybridization between the bisexual species L. reevesii and L. guttata, a now extinct diploid unisexual form appeared. Its backcross hybrids with one of the parental species may have become the ancestors of L. guentherpetersi. It is difficult to say now, from which parental form this triploid species received two genomes. In this connection it should be noticed that L. guentherpetersi possesses a type of coloration and dorsal pattern which is clearly

intermediate between both parental forms.

The northern species L. reevesii is notable in particular for its broad reticulation and spots, forming ocelles with light centres and greyish edges (fig. 9). As to the southern species L. guttata, its distinguishing character is the presence of two dorsolateral stripes as shown in fig. 3. In its dorsal pattern L. guentherpetersi combines both types of pattern described above. Some pholidotic characters are also intermediate. To elucidate the relations of L. guentherpetersi with more certainty, some special nuclear and mitochondrial DNA analyses, as well as biochemical studies should be made, as was done in other parthenogenetic lizard species.

As far as we know L. guentherpetersi is allopatric referring to both presumable parental species at present. It should be noted that the gap between their areas is not great (less than 20 - 30 km between L. guentherpetersi and L. reevesii in the Trang province) (fig. 2).

The presence of an insular population of *L. guentherpetersi* in the Island of Cu Lao Cham, situated about 20 km off the shore in the Danang Province, was already mentioned. Separation of island and mainland happened as a result of the last transgression about 10 - 12 thousand years ago. This may represent indirect evidence on the fact that the origin of the hybrid *L. guentherpetersi* occurred no later than 10 millenia ago.

Some karyological data suggest the hybrid origin of L. guentherpetersi. The structure of the karyotype of this species does not differ from that of the diploid species L. reevesii, L. belliana and L. guttata (KUPRIYANOVA 1984; SHOU-BAI & al. 1987; SOLENDER & SCHMID 1988) and that of the triploid L. triploida (HALL 1970). All these species are characterized by 12 (2n) / 18 (3n) metacentric and submetacentric macrochromosomes and 24/36 acrocentric microchromosomes. Like in all species listed above, in L. guentherpetersi a secondary constriction is located in the distal zone of the long arm of chromosome no. 1 (fig. 5). It should be noted that a despiralized zone in this region is present only in one of the chro-



Fig. 6: Ventral pattern in five specimens of Leiolepis guentherpetersi sp. nov. from Thuan Luu.

Abb. 6: Zeichnung der Bauchseite bei fünf Exemplaren von Leiolepis guentherpetersi sp. nov. aus Thuan Luu.

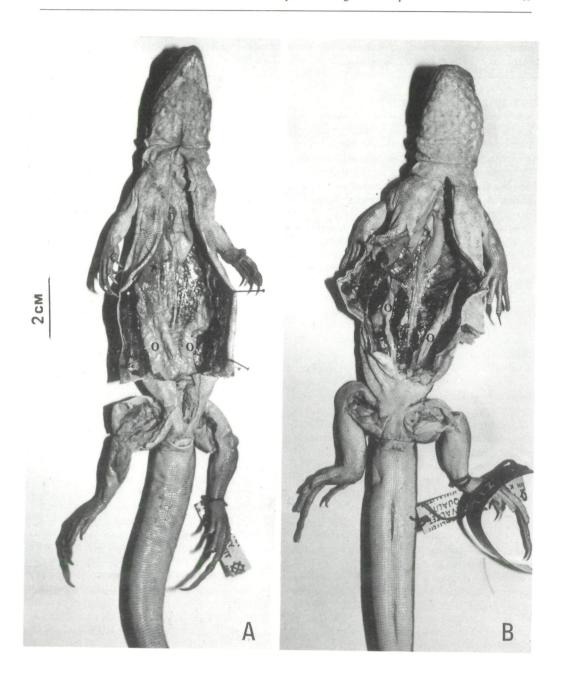


Fig. 7: Fertile (A) and sterile (B) adult female of *Leiolepis guentherpetersi* sp. nov. O - oviducts; normally developed in specimen A (ZISP 20327), and much reduced in specimen B (ZISP 20326).

Abb. 7: Fertiles (A) und steriles (B) adultes Weibchen von *Leiolepis guentherpetersi* sp. nov. O - Ovidukte; normal entwickelt bei Tier A (ZISP 20327) und stark reduziert bei Tier B (ZISP 20326).

mosomes of the triplett. The size of the chromosomes of trio 7 is too small to determine whether they belong to those of medium size as in L. belliana, or to the microchromosomes as in L. reevesii (see SOLENDER & SCHMID 1988), whether the chromosomes of trio 7 are heteromorphic. However, some differences in size of chromosomes no. 1, the presence of a despiralized zone, of a secondary constriction in only one of three chromosomes no. 1, and the silver-stained nucleolar organizers in it suggest heteromorphism of these chromosomes (fig. 5 B, C). Variability in size and number of interphase and prophase nucleoli has been studied: 36% of the cells contain one nucleolus, 42% two nucleoli, 14% three nucleoli, and 8% of the cells 0 or 4 nucleoli (fig. 5 A). Such heterozygousity concerning NOR activity and intensity of rRNA genes has observed different hybrid in parthenogenetic lizards in comparison with bisexual species (WARD & COLE 1986; KUPRIYANOVA 1989, 1989a, 1992; SITES & al. 1990). Unfortunately we have not yet studied these characters in the caryotypes of the bisexual parental species. The morphology of the chromosomes and the structure of the karyotype are similar in L. guentherpetersi and L. triploida and do not permit a judgement on their origin with certainty. However, structural-functional specificy of karyotype and genome may suggest the hybrid origin of L. guentherpetersi.

Like in other hybrids, hybridization may result in disturbances which, in return, may lead to reduced fertility. In one or another degree a pronounced sterility of hybrids, triploid ones included, is a rather widespread phenomenon both in the animal and plant kingdom. One of the well studied examples of this kind are the Rock Lizards of the Lacerta saxicola group, where triploid hybrid females, resulting from cross breedings between parthenogenetic females and males of closely related bisexual forms, are fully sterile (DA-REVSKY & KULIKOVA 1961). Such Rock Lizard hybrids represent an evolutionary "cul-de-sac" and therefore have no taxonomic rank. However, among twenty known triploid parthenogenetic hybrid lizard species only those of the genus Leiolepis demonstrate low fertility and perhaps low viability.

Questions on systematics and taxonomy in parthenogenetic species have been discussed by several authors (DAREVSKY) 1967; MASLIN 1968; BÖHME 1975, 1982; COLE 1985; WALKER 1986; FROST & WRIGHT 1988). As far as unisexual lizards are concerned in particular, we think that the most acceptable hypothesis is that of COLE (1985). According to his opinion morphologically different parthenoforms of hybrid origin which are self-supporting, genetically unique, and independently evolving entities should be regarded as separate species. Parthenoforms which have different ploidy and result from hybridization of different parental forms should be regarded as separate species, irrespective of the degree of their morphological differences. Whenever parthenoforms have the same origin and ploidy but differ in other features, they should be regarded as separate clones within one unisexual species. According to COLE's (1985) point of view the semifertile but self-supporting triploid lizards L. triploida and L. guentherpetersi have to be considered as indepedent unisexual species.

### **ACKNOWLEDGEMENTS**

We take the opportunity to express gratitude to the following colleagues for valuable opinions, for sending material and for help during our field work in Vietnam: Wolfgang BÖHME (Museum Alexander KOENIG, Bonn); Ivan INEICH (Muséum National d'Histoire Naturelle, Paris); C. J. COLE (American Museum of Natural History, New York); Tran KIEN (Pedagogic Institute, Hanoi); V. V. YAKUSHEY

(Institute of Evolutionary Morphology and Ecology, Moscow); Eric AHLANDER (Naturhistoriska Riksmuseet, Stockholm); Jose P. ROSADO (Museum of Comparative Zoology, Cambridge). Partly supported by the grant "The previledged trends in genetic research" provided by the Russian Academy of Sciences.

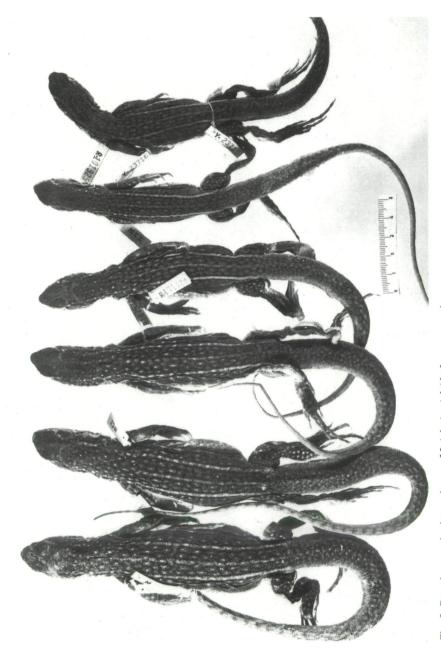


Fig. 8: Dorsal pattern in six specimens of Leiolepis triploida from terra typica.

Abb. 8: Rückenzeichnung bei sechs Exemplaren von Leiolepis triploida der terra typica.



Fig. 9: Dorsal pattern in three specimens of *Leiolepis r. reevesii* from Thuan An (15 km SE Hue). Abb. 9: Rückenzeichnung bei drei Exemplaren von *Leiolepis r. reevesii* aus Thuan An (15 km SE Hue).

Table 1: Comparison of pholidosis and metric characters in 6 related species of the genus *Leiolepis*. Entries for characters (explanation of abbreviations see "MATERIAL AND METHODS"): 1 - range, 2 arithmetik mean, 3 - standard deviation, 4 - coefficient of variability, 5 - sample size.

Tabelle 1: Vergleich verschiedener Beschuppungsmerkmale und Maße bei 6 verwandten Arten der Gattung Leiolepis. Die angeführten Werte zu den Merkmalen (Abkürzungserklärungen siehe "MATERIAL AND METHODS") sind: 1 - Spannweite, 2 - arithmetisches Mittel, 3 - Standardabweichung, 4 - Variationskoeffizient, 5 - Stichprobenumfang.

Taxon		DSC	vs	SL	IL	SDS	тs	PF	SVL max.	TL max.	TL/SVL in adults
L. triploida	1 2 3 4 5	-	17-22 19.35 1.26 6.5 26	8-12 9.30 0.57 6.6 30		34-39 35.8 1.22 3.4 28	9-13 11.38 0.84 7.4 40(2n)	17-21 18.66 9.96 5.2 58(2n)	14.8	29.9	2.16-2.31 2.24 0.05 2.58 6
L. guenther- petersi	1 2 3 4 5	37-43 41.52 1.74 4.19 25	17-20 17.9 0.84 5.91 25	8-10 8.9 0.53 5.91 25			14-18 15.8 1.38 8.73 25	21-24 22.18 0.82 3.69 50(2n)	15.6	28.2	1.64-2.47 2.11 0.23 10.9
L. boehmei	1 2 3 4 5	42-46 43.89 1.45 3.30 9	17-19 18.0 0.86 4.7		10-12 10.56 0.88 8.33 9	31.89 1.76	12-14 12.67 0.70 5.52	15-19 18.1 1.18 6.51 18(2n)	12.3	24.5	2.04-2.31 2.19 0.13 5.1
L. guttata*	1 2 3 4 5	-	18-27 22.5 2.27 10.1 30	8-11 9.52 0.84 8.8 29	9-13 10.9 1.05 9.6 29	37-45 40.58 2.27 5.6 19	13-25 19.67 2.81 14.3 60(2n)	18-26 22.48 1.31 5.8 60(2n)	18.4	36.9	2.00-2.40 2.14 0.11 5.1
L. r. reevesii*	1 2 3 4 5	-	13-18 15.96 1.03 6.6 48	6-9 7.96 0.61 7.7 49		29-38 32.86 1.99 6.1	7-12 9.28 1.37 14.8 98(2n)	12-18 14.45 1.14 7.9 98(2n)	15.1	34.0	-
L. b. belliana*	1 2 3 4 5	-	10-18 15.1 1.33 8.2 81	7-11 9.0 0.9 10.0 79	8-11 9.0 0.72 7.8 61	32-41 36.7 2.19 5.96 80	7-14 9.69 1.27 11.45 168(2n)	13-20 16.09 1.37 8.5 168(2n)	15.6	33.7	2.00-2.35 2.16 0.04 1.94 20

from PETERS (1971)

#### LITERATURE

BÖHME, W. (1975): Indizien für natürliche Parthenogenese beim Helmbasilisken, Basiliscus ba-Salamandra, Frankfurt am Main; 11(2): 77-83.

BÖHME, W. (1982): Über Schmetterlings-

agamen, Leiolépis b. belliana (GRAY, 1827) der Malayischen Halbinsel und ihre parthenogenetischen Linien (Sauria: Uromastycidae).- Zool. Jb. Syst.; 109: 157-169.

COLE, C. J. (1985): Taxonomy of parthenogenetic species of hybrid origin.- Syst. Zool.; 34: 359-363.

DAREVSKY, I. S. (1967): Rock Lizards of the Caucasus (Systematics, Ecology and Phylogene-sis in the polymorphous groups of Caucasian Rock Lizards of the subgenus Archaeolacerta); Leningrad (Nauka Press) (in Russian).

DAREVSKY, I. S. & KULIKOVA, V. N. (1961): Natürliche Parthenogenese bei der Kaukasischen Felseidechse (Lacerta saxicola EVERS-

MANN).- Zool. Jb. Syst.; 89: 119-176.

DAREVSKY, I. S. & KUPRIYANOVA, L.
A. & ROSHCHIN, V. (1984): A new all-female tri-

A. & ROSHCHIN, V. (1984): A new all-remaie triploid species of gecko and karyological data on the bisexual Hemidactylus frenatus from Vietnam.- J. Herpetology; 18(3): 274-284.

DAREVSKY, I. S. & KUPRIYANOVA, L. A. & UZZELL, T. (1985): Parthenogenesis in Reptiles; In: GANS, C. & BILLET, F. (Eds.): Biology of the Reptilia; Vol 15 (Development B), :412-526. New York (Wiley Interscience).

DESSAUER, H. C. & COLE, C. J. (1989): Diversity between and within nominal forms of unisexual teiid lizards; In: DAWLEY, R. & BOGART,

J. (Eds.): Evolution and Ecology of Unisexual Vertebrates .- The university of the state of New York

Mus. Bull.; 366: 49-71.

FRÓST, D. R. & WRIGHT, J. W. (1988): The taxonomy of uniparental species, with special reference to parthenogenetic *Cnemidophorus* (Squamata, Teiidae). Syst. Zool.; 37: 200-209.

HALL, W. P. (1970): Three probable cases of parthenogenetic in ligantic (Against Against Against Chaptelon).

parthenogenesis in lizards (Agamidae, Chameleonidae, Gekkonidae).- Experientia; 26(11): 1271-

1273.

KUPRIYANOVA, L. A. (1984): Karyotypes of three species of the agamid lizards; In: BORKIN, L. (Ed.): Ecology and Faunistics of Amphibians and Reptiles of the USSR and adjacent countries.- Proc.

Zool. Inst. Acad. Sci., Leningrad; 124: 115-118.

KUPRIYANOVA, L. A. (1989): Advances in the cytogenetics of unisexual lacertid lizards.-Abstracts, First World Congress of Herpetology,

Canterbury, GB.
KUPRIYANOVA, L. A. (1989a): Modern cytogenetical studies of some lizards (Family Lacertidae).- Abstracts, Fourth National Congress on Cy-

tidae).- Adstracts, Fourth National Congress on Cytogenetics, Vratca, BG, pp. 198-199.

KUPRIYANOVA, L. A. (1992): Diversity in parthenogenetic lacertid lizards: cytogenetic studies. In: KORSOS, Z. & KISS, I. (eds.): Proc. Sixth Ord. Gen. Meet. SEH, Budapest 1991, pp. 273-279.

MASLIN, T. P. (1968): Taxonomic problems in acathenogenetic yeartheres. Syst. Zool. 17: 210.

in parthenogenetic vertebrates. - Syst. Zool.; 17: 219-231.

MERTENS, R. (1961): Die Rassen der Schmetterlingsagame, Leiolepis belliana.- Senckenbergiana biologica, Frankfurt am Main; 42: 507-510.

MORITZ, C. & DONNELLAN, S. &

ADAMS, M. & BAVERSTOCK, P. R. (1989): The

origin and evolution of parthenogenesis in Heteronotia binoei (Gekkonidae): extensive genotypic diversity among parthenogens.- Evolution; 43: 994-1003.

NGO DUC CHUNG & DANG CAO VAN (1986): Some data about ecological and biological peculiarities of two subspecies of Leiolepis belliana GRAY and Leiolepis guttata CUVIER (Agamidae, Reptilia) in some regions in Binhtrithien Province.-Tap Chi Sinh. Hoc.; 8 (2): 34-37. (In Vietnamese with English summary).

PETERS, G. (1971): Die intragenerischen Gruppen und die Phylogenese der Schmetterlingsagamen (Agamidae: Leiolepis).- Zool. Jb. Syst.; 98:

11-130.

SHOUBAI, R. & QINHONG, L. & SCHOXIONG, D. (1987): The karyotypes of Leiolepis belliana belliana.- Zool. Research; 8: 184 (In Chinese).

SITES, J. & PECININI-SEALE, D. & MO-RITZ, D. & WRIGHT, C. & BROWN, W. (1990): The evolutionary history of parthenogenetic Cnemidophorus lemniscatus (Sauria, Teiidae). 1. Evidence

for a hybrid origin.- Evolution; 44: 906-921. SOLENDER, E. & SCHMID, M. (1988): Cytogenetic studies on Sauria (Reptilia). Mitotic chromosomes of the Agamidae.- Amphibia-Reptilia;

9: 301-310.

WALKER, J. W. (1986): The taxonomy of parthenogenetic species of hybrid origin: Cloned hybrid populations of *Cnemidophorus* (Sauria: Tei-

idae). Syst. Zool.; 35: 427-440.

WARD, O. G. & COLE, C. J. (1986): Nucleolar dominance in diploid and triploid parthenogenetic lizards of hybrid origin.- Cytogenetics, cell genetics; 42: 177-182.