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New *Lygodactylus* taxa (Reptilia: Gekkonidae) from the Transvaal

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Abstract. This paper describes and compares three species and two subspecies of geckos of the genus *Lygodactylus* from the Transvaal. Their phylogenetic relationships to other *Lygodactylus* species belonging to the Austro-Oriental group or phylum are also discussed.

Key words. Reptilia, Gekkonidae, *Lygodactylus*, new taxa, Transvaal.

Introduction

The genus *Lygodactylus* Gray was revised by FitzSimons (1943), Loveridge (1947) and Pasteur (1964). Owing to the paucity of available material South African specimens and from the Transvaal in particular were lumped with existing recognised taxa. Pasteur (1964) recognised two distinct groupings or phyla extending into South Africa one of which he referred to as the Austro-Oriental phylum. This group he regarded as being relict, the species being separated by large distances. Such species included *L. methueni* FitzSimons, *L. rex* Broadley, *L. bonsi* Pasteur, *L. ocellatus* Roux and *L. bernardi* FitzSimons.

During a survey of the herpetofauna of the Transvaal (Jacobsen, 1989) a number of specimens were considered to belong to the *Lygodactylus ocellatus* and *L. methueni* complexes but could not be conveniently placed. These specimens were mostly characterised by a different colour pattern, size, preloacal pore count as well as occupying a wider range of habitats. In some areas sympatry between the other members of the complex and *ocellatus* sensu stricto was observed. It is evident that a grouping on morphological grounds between *ocellatus* s. s. and the other observed taxa was very tenuous as they differed in colour, pattern, body form and had a greater range in size and preloacal pore count. The only morphological similarities with *ocellatus* s. s. are the entire mental and four pairs of scansors per digit. It is apparent that neither of these characters are invariant as *L. bernardi*, considered by Pasteur (1964) to be closely related to *L. ocellatus* s. s. (an observation which I fully support), has both a tripartite mental and five pairs of scansors on the toes. In this case the distinctive body form and colour pattern are the most pronounced supporters of such a relationship. This, together with their mutual habitat of highveld or montane grassland above 1500 m a. s. l. establishes a clear link.

Jacobsen (in press) described *L. montisnimbi* and related it to *L. methueni* on the basis of five pairs of adhesive lamellae at the tips of the digits. The former differed from the latter in colour pattern which mostly included a lateral series of black blotches from the neck to midway between fore and hindlimb. Most of the unplaced

Table 1: Percentage frequency of some morphological characters of taxa belonging to the *Lygodactylus methueni* complex.

	Internasals				n	
	1	2				
<i>graniticolus</i>	100,0	0			9	
<i>waterbergensis</i>	100,0	0			7	
<i>nigropunctatus</i>	50,00	50,00			52	
<i>incognitus</i>	50,00	50,00			12	
<i>montiscaeruli</i>	60,00	40,00			25	
	Upper labials				n	
	6	7	8	9		
<i>graniticolus</i>	0	44,44	55,56	0	9	
<i>waterbergensis</i>	16,67	33,33	16,67	33,33	6	
<i>nigropunctatus</i>	9,43	41,51	39,62	9,43	53	
<i>incognitus</i>	16,69	41,67	41,67	0	12	
<i>montiscaeruli</i>	4,17	25,00	58,33	12,50	24	
	Lower labials				n	
	5	6	7	8		
<i>graniticolus</i>	10,00	80,00	10,00	0	10	
<i>waterbergensis</i>	0	57,14	28,57	14,28	7	
<i>nigropunctatus</i>	9,43	64,15	26,41	0	53	
<i>incognitus</i>	0	83,33	16,67	0	12	
<i>montiscaeruli</i>	4,17	37,50	58,33	0	24	
	Chin shields				n	
	2	3				
<i>graniticolus</i>	70,00	30,00			10	
<i>waterbergensis</i>	85,71	14,28			7	
<i>nigropunctatus</i>	58,49	41,51			53	
<i>incognitus</i>	100,00	0			12	
<i>montiscaeruli</i>	66,67	33,33			24	
	Precloacal pores					n
	7	8	9	10	11	
<i>graniticolus</i>	0	80,00	20,00	0	0	5
<i>waterbergensis</i>	0	0	100,00	0	0	2
<i>nigropunctatus</i>	0	5,00	45,00	45,00	5,00	20
<i>incognitus</i>	12,50	37,50	50,00	0	0	8
<i>montiscaeruli</i>	50,00	50,00	0	0	0	14
	Greatest SVL (mm)					n
	male	female				
<i>graniticolus</i>	37,5	39,5				7
<i>waterbergensis</i>	39,5	36,0				6
<i>nigropunctatus</i>	36,5	38,0				50
<i>incognitus</i>	36,0	37,0				12
<i>montiscaeruli</i>	35,0	37,0				24
	Greatest mass (g)					n
	male	female				
<i>graniticolus</i>	1,60	1,80				5
<i>waterbergensis</i>	1,35	1,40				6
<i>nigropunctatus</i>	1,15	1,25				49
<i>incognitus</i>	1,25	1,65				7
<i>montiscaeruli</i>	1,00	1,35				23

specimens referred to previously exhibited a similar colour pattern but differed in having only four pairs of scansors on each digit. These were therefore considered to be allied to *montisnimbi* but distinct according to the number of scansors on the digits. Such phena are widespread in the Transvaal from the Soutpansberg and Blouberg south to the Magaliesberg. In this paper five new taxa incorporating three species and two subspecies are described.

Material and Methods

During the course of this study 111 specimens were examined including all material in the Transvaal Museum (TM). Information collated included sex; snout-vent length (SVL); live mass; circumnarial scales; presence or absence of an internasal; number of supra- and infralabials; number of postmentals; number of gulars between posterior infralabials; number of scansors on the toes; precloacal pores in males; median subcaudal arrangement (following Pasteur 1964) and colour pattern including that of the gular and ventrum.

Character Analysis

Table 1 presents some of the character measures of the various forms under discussion.

Overlap in almost all characters is seen but on examining the character states, differences between species were observed. These are discussed in greater detail as follows:

Scutellation

1. Internasals: These range from 1–2. Only *graniticolus* and *waterbergensis* have exclusively one but sample sizes are small. The three forms of *nigropunctatus* show a uniformity in the frequency of one or two internasals, indicating a close relationship.
2. Upper labials: A similar picture is shown by the number of supralabials which in most species ranged from 6–9 with *graniticolus* exhibiting a relatively narrow range of seven or eight compared to the wide range shown by *waterbergensis*. The three forms of *nigropunctatus* again show a very similar frequency with seven or eight predominating.
3. Lower labials: The range of infralabials is more limited. In *graniticolus*, six has the highest frequency whereas *waterbergensis* ranges from 6–8 in decreasing order of frequency. Considering the three forms of *nigropunctatus*, the subspecies *incognitus* has predominantly 6, while the other two forms have a wider range of 5–7 but are mostly six or seven.
4. Chin shields: The frequency of chin shields in *graniticolus* and *waterbergensis* is similar with two predominating. Among the three *nigropunctatus* phena, *incognitus* stands out in having only two postmentals.
5. Precloacal pores: Considering the species pair *graniticolus* and *waterbergensis* the former has mostly eight and the latter nine although the sample size is small. The three forms of *nigropunctatus* show some divergence with typical *nigropunctatus* ranging from 8–11 but are mostly nine or ten while *incognitus* ranges from 7–9 and *montiscaeruli* seven or eight.

Size

1. Greatest snout-vent length (SVL): Absolute size is a useful measure should there be an adequate sample of each phenon but is of limited use if the converse is true. From Table 1 it is evident that the two taxa *graniticolus* and *waterbergensis* are very large while the *nigropunctatus* complex is smaller and similar in size to each other.
2. Mass: Greatest mass measured follows the tendency shown by greatest SVL.

Systematics

Lygodactylus nigropunctatus nigropunctatus sp. nov.

Type material. Seven specimens. Holotype: TM 58961, Farm Dientje 53KT, Pilgrims Rest district (2430DB), Transvaal, collector N. H. G. Jacobsen, 28 October 1980. Allotype: TM 58962, adult female, same data as holotype. Paratypes: TM 58953, 58956–7, 58967, adults with same data as holotype. Other material, 46 specimens as follows: TM 58972, 51929 Farm Bourke's Luck 454KT (2430DB), collector N. H. G. Jacobsen, TM 59017–8, 59035, Farm Nooitgedacht 345JS (2529DA), collector N. H. G. Jacobsen, 25 October 1981; TM 58992 Ntsweletau (2429DB), collector R. E. Newbery, 27 October 1980; TM 58996, 59020 Farm Leeuwfontein 188JR (2528BB), collector R. E. Newbery, 26 April 1981; TM 59005 Farm Rolle 235KU (2431CA), collector R. E. Newbery, 26 April 1981; TM 59012 Farm Mapochsgronde 500 JS (2529BB), collector N. H. G. Jacobsen, 25 March 1981; TM 59027, 59015, Farm Maslerooms Oude Stad 840KS (2429DD), collector W. Petersen, 25 May 1982; TM 59024, Farm Lolamontes 682KS (2429DC), collector W. Petersen, 26 May 1982; TM 59025 Farm Tivoli 98KT (2430AC), collector N. H. G. Jacobsen, 24 October 1980; TM 59028 Farm Dal Josaphat 461KS (2429BD), collector R. E. Newbery, 30 October 1980; TM 59036 Farm Klipfontein 256JS (2529CA), collector W. Petersen, 1 April 1982; TM 59037 Farm Diepkloof 44JS (2529BA), collector W. Petersen, 27 May 1982; TM 59060 Pilgrims Rest (2430DD), collector R. E. Newbery, 13 April 1985; TM 52550 Farm Klipfontein 498JR (2528DB), collector O. Prozesky, 16 October 1978; TM 58951–2, 58955, 58970, 59029 Farm Garatouw 282KT (2430CA), collector N. H. G. Jacobsen, 25 October 1980; TM 58963, 58966 Farm Maandagshoek 254KT (2430CA), collector N. H. G. Jacobsen, 25 October 1980; TM 59030 Farm Maandagshoek 254KT (2430CA), collector R. E. Newbery, 29 June 1982; TM 58965, 58973 Farm Holfontein 125KT (2430AD), collector N. H. G. Jacobsen, 26 October 1980; TM 58976, 58980, 59000, 59009, 59021, 59031 Farm Rietfontein 214JR (2528BC), collector W. van der Maelen, 25 July 1980; TM 58983, 58989, 58999, 59016, 59023 Farm Kuilfontein 324JP (2526CD), collector R. E. Newbery, 23 September 1980; TM 58990, 58994, 59004 Farm Zyferfontein 293JP, (2526CB), collector R. E. Newbery, 24 September 1980; TM 58988 Farm Nooitgedacht 392KT (2430CD), collector N. H. G. Jacobsen, 24 April 1981.

Type locality. Farm Dientje 53KT, 24 38' S, 30 47' E, Pilgrims Rest district, Transvaal.

Etymology. The specific name refers to the row of black spots usually observed dorsolaterally.

Diagnosis. *Lygodactylus nigropunctatus* differs from *L. ocellatus* in being primarily a larger gecko. Preloacal pores range from 7–11 in males. A different colour pattern with the total lack of typical *ocellatus* ocelli is noteworthy, coupled with the row of dorsolateral black spots on each side which characterise the species (Fig. 1a).

Description. Holotype: TM 58961, male, SVL 32,5 mm; tail 34,5 mm; mass 0,9 g.

Lepidosis. Head well developed, distinct from neck. Snout covered with heterogeneous rounded granular scales, smaller on the crown of the head and down the middle of the snout becoming larger dorsolaterally and laterally; canthus rostralis poorly developed. Nostril oval and slightly oblique, surrounded by the rostral, first upper labial, an enlarged nasorostral and two granular scales. Two scales posterior to nasorostral larger than surrounding scales. Two granular scales separate the nasorostrals behind rostral. Upper labials seven. Palpebral spines 12 from anterior of eye to dorsum of eye. Mental slightly wider than deep, roughly heptagonal; postmentals three (two large, separated by one small); infralabials seven. Ventrally scales very slightly overlapping; four rows of glandular scales under thighs; preloacal pores 9, arranged in a forward directed V with four rows of scales anterior to cloaca. Four pairs of adhesive lamellae under 4th toe and 11 non-adhesive enlarged subdigital scales; digits terminate in claws with three subdigital scales anterior to claw. Caudal scales in obscure whorls, with seven scale rows per verticil dorsally and four ventrally. Tail regenerating. Subcaudal scales smooth and overlapping, proximally in a median series of 2, 1, 1, 2, 1, 1.

Colour. Greyish-brown to brownish-grey dorsally and laterally, with a dorsolateral row of black spots extending from the shoulder to the sacrum. Tail indistinctly marked with two rows of black spots and offwhite spots. Ventrally the holotype has grey speckling on the lower labials and on the gular while the grey from the sides intrudes ventrolaterally and irregular

speckling also occurs ventrally. Lower abdomen, cloaca and subcaudals white without speckling, becoming grey distally.

Paratypes. Lepidosis: TM 58953 and 58957 have a single granule separating the nasorostrals, while the other paratypes have two as in the holotype. TM 58962 has 10 eyelid spines. With respect to the upper labials TM 58953 and TM 58962 differ in having nine and eight respectively. Postmentals mostly two with the exception of TM 58953 and 58960 which have an additional granule, while TM 58957 has three.

Colour. Similar to holotype with dorsolateral spots variable in number and clarity.

Other material. 46 additional specimens examined. Considerable variation exists in the number of upper labials ranging from 6–9 and lower labials from 5–7. Preloacal pores in males range from 8–11 and glandular scales on underside of thighs in 3–4 rows.

Colour. Variable from brownish-grey to grey, dark grey-brown or blue-grey with very pronounced spots to almost none. These spots may be black or have adjacent pale spots posteriorly. However these spots do not form ocelli. Some specimens exhibit a second row of spots laterally extending from midbody to the inguinal region.

Ventrally the gular region may be heavily to lightly speckled while the chest and abdomen may be offwhite to yellowish, speckled ventrolaterally with grey, in some specimens more heavily than in others.

Size. Mean adult male SVL (>25,0 mm) = 31,71 mm \pm 2,73 (ISD), n = 17, mass = 0,79 g \pm 0,26 (ISD), n = 17. Largest male SVL = 36,5 mm, mass = 1,4 g. Mean adult female SVL (>25,0 mm) = 33,14 mm \pm 3,23 (ISD), n = 28, mass = 0,89 g \pm 0,25 (ISD), n = 28. Largest female SVL = 38,0 mm, mass = 1,25 g (truncated tail).

Reproduction. Like all other *Lygodactylus* species, *nigropunctatus* is oviparous laying two eggs at a time.

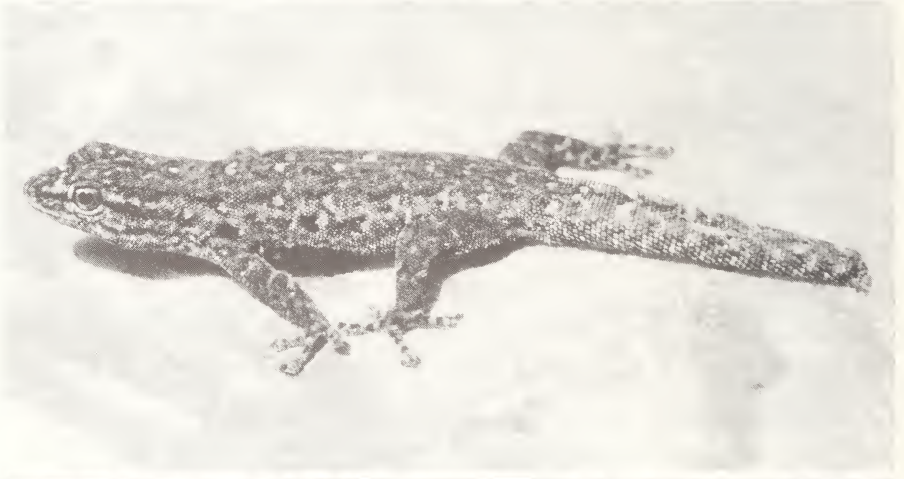
Habitat. *Lygodactylus n. nigropunctatus* is rupicolous usually found foraging on boulders, taking refuge in crevices or under rock on rock. Occurs on rocky outcrops in varying veld types at altitudes of 700–800 m a. s. l. Usually observed singly but pairs or small family groups are found.

Distribution. The species is widespread in the Transvaal, the nominate race absent from the Soutpansberg, Blouberg and the Waterberg (Fig. 2).

Remarks. Although in the past mostly incorporated in *ocellatus*, members of the *nigropunctatus* species group appear more closely related to *methueni/montisnimbi*. Reasons for this include the large size of the taxa (Fig. 3) as well as the arrangements of black spots or blotches and other aspects of the colour pattern. Populations of *nigropunctatus* sympatric with *ocellatus* sensu stricto have a greater number of preloacal pores than *ocellatus*. The current distribution patterns of *ocellatus* and *nigropunctatus* show that parallel evolutionary development may have taken place. The fact that a subspecies of *nigropunctatus* has reached the Blouberg an Makgabeng gives an indication that it is either an older or a more adaptive species than *ocellatus* which is apparently absent from these mountains, reaching according to current knowledge as far west as the Waterpoort in the Soutpansberg. The two species are found in sympatry on the farms Dientje 53KT, Flynn 217KS, Mapochsgronde 500JS and Nooitgedacht 392KT as well as in the Soutpansberg. On Dientje 53KT, *ocellatus* occurs on the crest or summit of the hills while *nigropunctatus* is found along the slopes.

Lygodactylus nigropunctatus incognitus subsp. nov.

Type material. 12 specimens. Holotype: TM 59058 Farm Outlook 789MS (2229DD), Soutpansberg district, Transvaal, collector R. E. Newbery, 3 November 1985. Allotype: TM 59056 adult female, same data as holotype. Paratypes: TM 59057 same data as holotype; TM 58947 Farm Bluegumspoort 779MS (229CD), collector N. H. G. Jacobsen, 30 January 1979; TM 59026 Farm New Gate 902MS (2229DD), collector R. E. Newbery, 26 June 1981; TM 59054 Farm Highfield 797MS (2229DD), collector N. H. G. Jacobsen and R. E. Newbery, 20 October 1984; TM 59055 Farm Peover 772MS (2229DC), collector R. E. Newbery, 6 November 1985;



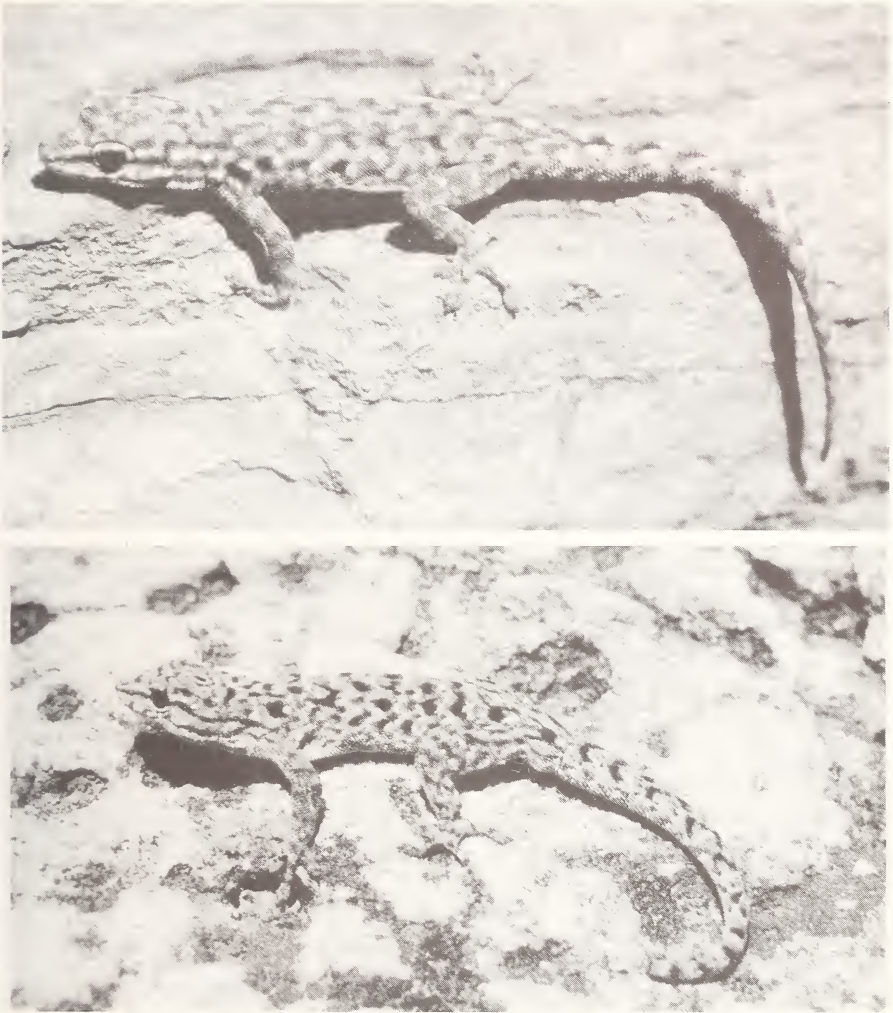


Fig. 1: New *Lygodactylus* taxa from the Transvaal. (Left top to bottom, right top to bottom). a. *L. n. nigropunctatus*; b. *L. n. incognitus*; c. *L. n. montiscaeruli*; d. *L. graniticolus*; e. *L. waterbergensis*.

TM 30450—1 4 mls (6,4 km) west of the Punchbowl Hotel (2229DD), collector W. D. Haacke, 16 January 1965; TM 19231—2 and 4, above Louis Trichardt (2229DD), collector V. Fitz-Simons, 9 October 1938.

Type locality. Farm Outlook 789MS, 22 59' S, 29 51' E, Soutpansberg district, Transvaal.

Etymology. The subspecific name refers to the poorly marked and difficult to recognise taxon.

Diagnosis. Very similar to typical *nigropunctatus*, differing in having exclusively two postmental scales, precloacal pores mostly (87,5 %) eight or nine and lower labials six, rarely five or seven. Apparently restricted to the Soutpansberg. The black dorsolateral spots are relatively indistinct (Fig. 1 b).

Description. Holotype: TM 59058, male. SVL 34,0 mm; tail 39,0 mm; mass 1,25 g.

Lepidosis. Head well developed, broader than neck. Snout covered with flattened, rounded scales larger on crown of head. Rostral much broader than high, subpentagonal; nostril oval, oblique posteriorly and surrounded by rostral, 1st upper labial, nasorostral and two elongate granular scales; nasorostrals separated by a single granule; nasorostrals in contact with a large scale posteriorly. Eyelod spines reduced and four in number; upper labials 7/7. Mental pentagonal, bordered posteriorly by two enlarged chin shields; lower labials 7/7; gular scales between posterior lower labials 28; gular scales round and imbricate. Dorsal scales granular, relatively homogeneous, along the spine juxtaposed gradually increasing in size laterally. Limbs well developed, pentadactyl, 1st digit greatly reduced. Distal part of digits expanded, with four pairs of adhesive lamellae and 10 non-adhesive subdigitally. Ventral scales imbricate and overlapping; three rows of glandular scales along thighs, preloacal pores eight arranged in an inverted V followed by four rows of scales anterior to the cloaca. Tail original, virtually non-verticillate, six supracaudals and four subcaudals per verticil; median subcaudals arranged aperiodically 2, 1, 2, 1, 2, 1 or 2, 1, 1, 2, 1, 1; scales on tail overlapping.

Colour. Grey dorsally, darker in a broad band from the tip of the snout over the eyes to the base of the tail. Irregular scattered pale, dark edged blotches are found paravertebrally. Limbs dark grey with irregular light and dark markings. Dorsal surface of tail grey with pale, dark edged wavy stripes extending from the base of the tail becoming indistinct distally. Dorsolaterally grey with irregular pale dark-edged blotches in a well defined row. Below this blotches less pronounced, but three black blotches prominent, one on the shoulder and two posteriorly. A dark stripe extends from the nostrils through the eye to the shoulder. Ventrally offwhite with irregular dark grey spots or blotches under the throat, and dark speckling on the belly.

Paratypes. Similar to holotype.

Lepidosis. TM 59056 has the nasorostrals separated by two granules and only six eyelid spines. TM 59057, 58947 and 59054 differ in having eight upper labials, while TM 30450 and 59026 have six.

Colour. Similar to holotype, males apparently having variable sizes and numbers of black spots or blotches laterally which may be absent in females. Ventrally colour may be offwhite to yellow. Inside of thighs may be heavily spotted with grey.

Size. Mean adult SVL = 33,87 mm \pm 1,7 (1SD), n = 12. Adult males reach 36,0 mm SVL and a mass of 1,25 g and adult females 37,0 mm and 1,65 g respectively. Mean male SVL = 33,5 mm \pm 1,70 (1SD), n = 4, mass = 1,25 g \pm 0,35 (1SD), n = 3.

Reproduction. Oviparous, two eggs measuring 8,34 x 6,63 mm (n = 14), range 7,6–8,8 x 6,3–6,9 mm, with a mass of 0,15–0,2 g, are laid separately under a rock on rock during mid- to late summer.

Distribution. This subspecies is apparently restricted to the Soutpansberg in the northern Transvaal (Fig. 2).

Habitat. These diurnal, rupicolous geckos are found on rocky outcrops along the summits of the southern range in veld types 8 and 20 (Acocks, 1975), and at altitudes of 1400–1600 m a. s. l. In habits very similar to other rupicolous *Lygodactylus* species, in that it also slips around the furthest side of a boulder if disturbed. They are highly cryptic and difficult to spot.

Remarks. *Incognitus* differs from the nominate race in several respects which together appear sufficient to elevate the phenon to subspecific rank. It is also apparently allopatric to the nominate race which in the future may further enhance the differences currently perceived. Differentiation is however limited possibly owing to relatively recent isolation, similar to that of sympatric *Lygodactylus ocellatus soutpansbergensis* and possibly at the same time.

Lygodactylus nigropunctatus montiscaeruli subsp. nov.

Type material. 11 specimens. Holotype: TM 58995, adult male, Farm Beuley 260LR (2329AA), Bochum district, Transvaal, collector N. H. G. Jacobsen und R. E. Newberry, 18

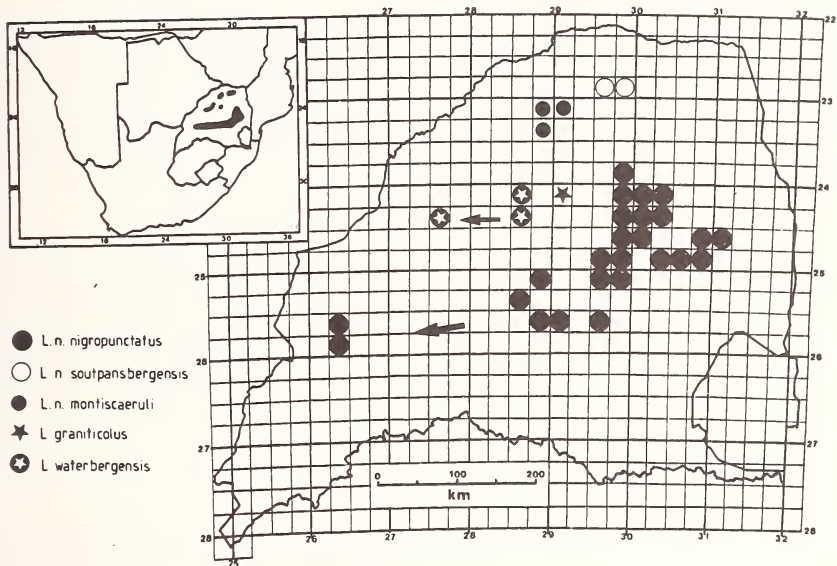


Fig. 2: Distribution of new *Lygodactylus* taxa in the Transvaal and in southern Africa.

May 1982. Allotype: TM 59014, adult female, same data as holotype. Paratypes. TM 58974, 58979, 58997, 59003, 59006, 59014, 59032, same data as holotype. TM 59013, 59033–4, same data as holotype except they were collected on the 19 May 1982.

Type locality. Farm Beauley 260LR, 23 4' S, 29 0' E, Bochum district, Transvaal.

Etymology. The subspecific epithet refers to the Blouberg (Blue mountain) which appears to form the centre of distribution of the taxon.

Diagnosis. Very similar to both *nigropunctatus* and *incognitus*, differing in having chin shields numbering two or three, preloacal pores seven or eight and median subcaudals arranged 2, 1, 1, 2, 1, while it appears to be restricted in range to the Makgabeng hills and Blouberg (Fig. 1c).

Description. Holotype: TM 58995, adult male. SVL 32,0 mm; tail 37,0 mm; mass 0,95 g.

Lepidosis. Head distinct from neck, snout blunt; rostral much broader than high, subhexagonal; nostril directed posteriorly and obliquely, surrounded by rostral, 1st upper labial, nasorostral and two granular scales; nasorostrals separated by a single rounded granular scale; nasorostral followed posteriorly by one enlarged scale; scales on snout larger than on crown of head; roughly eight spiny eyelid scales but somewhat obscure; upper labials 9/7. Mental subpentagonal, bordered posteriorly by two enlarged chin shields. Lower labials 6/6; gulars between posterior infralabials 25; gulars imbricate and overlapping. Dorsal scales granular, more or less homogeneous, not noticeably larger laterally. Limbs well developed but short, pentadactyl with the 1st digits greatly reduced. Distal parts of digits expanded with four pairs of adhesive and 11 non-adhesive lamellae subdigitally. Ventral scales imbricate and overlapping; four rows of glandular scales along underside of thighs; preloacal pores eight in a forward directed chevron with four scale rows of large scales and four rows granules anterior to the vent. Caudal scales faintly verticillate, 6–7 scales dorsally and four scales per whorl ventrally. Dorsally and ventrally caudal scales overlapping and median subcaudals aperiodic, and arranged in a series of 2, 1, 1, 2, 1, 1. Tail original and in a ratio of 1,15 : 1 with SVL.

Colour. Grey to greybrown dorsally with an interrupted blackish stripe from the neck to midway down the body. Dorsolaterally a row of blackish spots or blotches extend from the posterior margin of the head almost to the sacrum and fades on the tail. Laterally a dark stripe extends from the nostrils through the eye to the shoulder. A row of smaller spots is found between the fore and hindlimbs. Dorsolaterally a row of pinkish orange markings are found along the tail with darker markings laterally. Ventrally offwhite with irregular greybrown markings under the gular. Ventrolaterally the belly is spotted with grey but this diminishes towards midabdomen. Some spotting on underside of limbs and tail, pigmentation becoming more intense distally on the tail.

Paratypes. Similar to holotype but differ in that the upper labials range from 7–9 while the lower labials range from 5–7 and chin shields two or three. TM 59014 has 26 gular scales between the posterior lower labials. Preloacal pores in males range from 7–8. No glandular scales or pores in females. Original tail in ratios of 1,15–1,29: 1 to SVL.

Colour. Grey to greybrown, mostly similar to the holotype. TM 59003 distinctly spotted or blotched dorsolaterally, spots extending to, but fading in intensity on the base of the tail. Ventrally similar to holotype. TM 58974, a female without dorsolateral spots.

Other material. Incorporates additional 14 specimens examined. Very similar to the type series but original tail in ratios ranging from 1,06–1,44 ($X = 1,22$) to SVL.

Colour. Very similar to that of the type series.

Size. Mean adult SVL ($>26,5$ mm) = $32,0$ mm $\pm 2,79$ (ISD), $n = 23$, mass = $0,90$ g $\pm 0,22$ (ISD), $n = 22$. Adult males reach $35,0$ mm SVL and a mass of $1,4$ g. Mean male SVL ($>26,5$ mm) = $31,96$ mm $\pm 1,95$ (ISD), $n = 14$, mass = $0,88$ g $\pm 0,19$ (ISD), $n = 13$. Adult females reach $37,0$ mm SVL and a mass of $1,35$ g. Mean adult female SVL ($>26,5$ mm) = $32,06$ mm $\pm 3,91$ (ISD), $n = 9$, mass = $0,94$ g $\pm 0,26$ (ISD), $n = 9$.

Reproduction. Oviparous, two eggs measuring $7,0$ – $8,3 \times 4,5$ – $6,2$ mm (mean $7,8 \times 5,7$ mm, $n = 8$) with a mass of $0,1$ – $0,15$ g (mean $0,13$ g, $n = 6$), are laid at a time under rock on rock. Three pairs of ova were collected in a pocket under rock on the farm Urk 10LS in late summer.

Distribution. This subspecies is only known from the Blouberg and a low-lying plateau-like offshoot, the Makgabeng (Fig. 2).

Habitat. Almost exclusively rupicolous, occupying rocky outcrops and cliffs along the Blouberg and Makgabeng. Occasionally climbs trees. Usually takes refuge in vertical and horizontal crevices on boulders or rock faces. Mixed vegetation in veld types 18, 19 and 20 (Acocks 1975) at altitudes of 950 – 1300 m a. s. l. Usually observed singly, occasionally in pairs.

Remarks. Allopatrically separated from both the nominate form and *incognitus*, differing from both of these in the number of preloacal pores and median subcaudal scale ar-

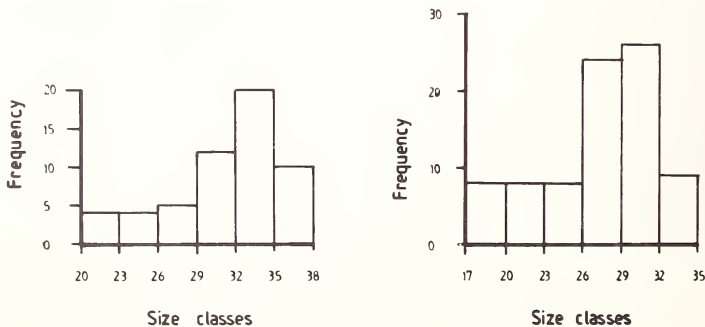


Fig. 3: Comparative frequency of SVL of *L. nigropunctatus* (left) and *L. ocellatus* (right).

rangements. *Montiscaeruli* appears to be the most northwestern form of *nigropunctatus* and at the end of a ring cline with gradually increasing number of preloacal pores from northwest to southwest. Viewed on its own this character would be insufficient to justify subspecific status for these populations. However, the aperiodic arrangement of the median subcaudals is such that *montiscaeruli* is closer to the nominate *nigropunctatus* than to *incognitus* and vice versa in the case of the preloacal pores. Table 1 provides a comparison of these taxa.

Lygodactylus graniticolus sp. nov.

Type material. 10 specimens. Holotype: TM 5940, adult male, Percy Fyfe Nature Reserve (2429AA), Potgietersrus district, Transvaal, collector R. E. Newbery, 28 November 1979. Allotype: TM 58942, adult female, same data as for holotype. Paratypes: TM 58941, 58943—4 same data as for holotype, TM 41732—3, same locality as holotype, collector N. H. G. Jacobsen, 22 May 1972, TM 64763—4, 64767, same locality as holotype, collector N. H. G. Jacobsen, 29 May 1986.

Type locality. Percy Fyfe Nature Reserve, 24° 2' S, 29° 5' E, Potgietersrus district, Transvaal.

Etymology. The species appears to be exclusive to the granitic hills in the area.

Diagnosis. A large gecko (Fig. 1d) distinguished by the ovate expanded portion of the digits and rounded dorsal scales (Fig. 4), as well as its restricted habitat and distribution (Fig. 2).

Description. Holotype: TM 58940, adult male. SVL 37,5 mm; tail 37,5 mm; mass 1,6 g.

Lepidosis. Head well developed and slightly wider than the neck. Snout slightly rounded, rostral wider than high, roughly hexagonal; nostril oval and directed slightly posteriorly; circumnarians include rostral, 1st upper labial, nasorostral and two granular scales; nasorostrals separated by a single granular scale; nasorostrals followed posteriorly by two enlarged scales; no spiny eyelid scales; upper labials 8/8. Mental subhexagonal bordered posteriorly by three postmentals. Lower labials 7/6; gulars between posterior infralabials 20; gulars imbricate and slightly overlapping. Dorsal granular scales roughly homogeneous but larger ventrolaterally. Limbs well developed but short, pentadactyl; 1st digits greatly reduced; distal portions of remaining digits expanded (broadly ovate) and covered with four pairs of adhesive lamellae; ventrally 10 enlarged subdigital scales occur proximally. Four rows of glandular scales under each thigh; preloacal pores 9 arranged in a curved row with roughly four scale rows posteriorly. Caudal scales whorled with seven scale rows dorsally and four ventrally. Dorsally, scales appear juxtaposed with some overlap between adjacent scale rows. Ventrally scales subhexagonal, imbricate and overlapping. Tail regenerating, median subcaudal arrangement obscured.

Colour. A greybrown to brownish band paravertebrally from snout to tail, tapering off on the base of the tail. A row of pale centred ocelli extends dorsolaterally from behind the eye onto the base of the tail. Laterally grey with a row of pale centred ocelli extending from the neck over the shoulder to the groin. Limbs grey variegated with offwhite. Regenerated tail irregularly streaked with greybrown longitudinally. Ventrally, grey spotting on gular, more extensive on lower labials. Chest and belly white to creamy; glandular rows on underside of thighs straw coloured. Underside of tail white becoming pigmented ventrolaterally.

Paratypes. Similar to holotype but with a range in SVL of 35,0—39,5 mm and a mass of 1,55—1,8 g. TM 58942 has four circumnarial scales. Upper labials range from 7—8. TM 41733 has only five lower labials. Chin shields mostly two (70%). Subdigital lamellae 10—11. Preloacal pores in males eight (TM 58941, 41733, 64764). Glandular scales and preloacal pores absent in females. Median subcaudal scales of TM 58942 arranged roughly 1, 2, 1, 2, 1, 2. Ratio of tail to SVL 1,14 : 1 in TM 58942.

Colour. As for holotype with dark spotting and occasional ocelli down the back. Dark blotches may be found laterally behind the shoulders and midway between fore and hind limbs (Fig. 1d). Females lack the straw-coloured glandular scales under the thighs.

Size. Mean adult SVL = 36,64 ± 1,52 (1SD), n = 7, mass = 1,62 g ± 0,19 (1SD), n = 5. Adult males reach 37,5 mm SVL and a mass of 1,6 g. Mean male SVL = 36,33 ± 1,04 (1SD),

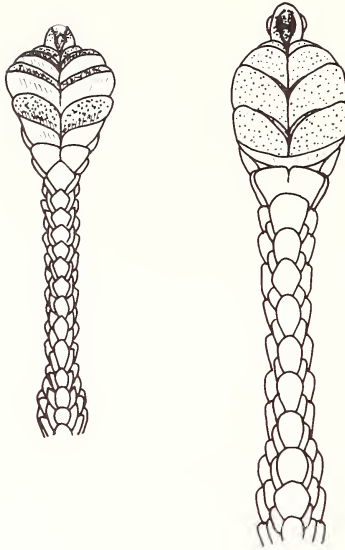


Fig. 4: Comparative morphology of the 4th toe of *L. graniticolus* (right) and *L. waterbergensis* (left).

$n = 3$, mass = $1,47 \pm 0,17$ (ISD), $n = 2$. Adult females reach 39,5 mm SVL and a mass of 1,8 g. Mean female SVL = $36,87 \text{ mm} \pm 1,93$ (ISD), $n = 4$, mass $1,72 \text{ g} \pm 0,14$ (ISD), $n = 3$.

Reproduction. Oviparous, two full term ova measuring $8,1 \times 5,4-5,6$ mm were measured in situ in a female during November. Another female was also gravid with two developing ova at this time.

Distribution. This species is only known to date from the granite outcrops and hills on the Percy Fyfe Nature Reserve (Fig. 2).

Habitat. This gecko appears to be exclusively rupicolous inhabiting crevices between boulders on rocky outcrops in veld type 20 (Acocks 1975) at an altitude of 1500 m a. s. l. They appear to be solitary but on rare occasions two may be found together.

Remarks. An isolated species but presumably more widespread on granite boulders in the Lunsklip area than the collecting suggests. A distinct endemic species which resembles other large species such as *rex* and *methueni* in size but appears to be more closely related to the *bonisi* group according to morphology and colour. This tends to contradict the evidence of lineage proposed by Pasteur (1964). Relationships need to be re-evaluated on the basis of morphological features including colour pattern.

Lygodactylus waterbergensis sp. nov.

Type material. Seven specimens. Holotype: TM 58939, Farm Sterkrivier Nedersetting (SRNS) 253KR, Potgietersrus district (2428BA), Transvaal, collector R. E. Newbery, 20 March 1980. Allotype: TM 58969, same data as holotype. Paratypes: TM 58998, 64842, same data as holotype except that the latter were collected on 2 April 1986. TM 59002, Farm Buffelshoek 277KR, Potgietersrus district (2428BC), Transvaal, collector R. E. Newbery, 20 March 1980; TM 59040-1, Farm Groothoek 278KQ, Thabazimbi district (2427BC), Transvaal, collectors N. H. G. Jacobsen and R. E. Newbery, 27 November 1984.

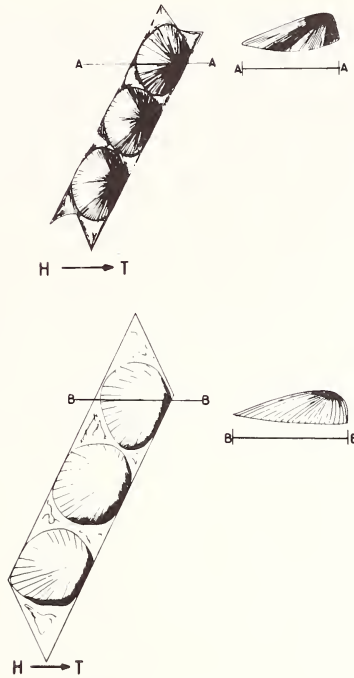


Fig. 5: A comparison of the dorsal granules of *L. waterbergensis* (top) and *L. graniticolus* (bottom).

Type locality. Farm Sterkrivier Nedersetting 253KR, 24 12' S, 28 42' E, Potgietersrus district, Transvaal.

Etymology. Apparently endemic to the Waterberg, hence the specific name.

Diagnosis. *Lygodactylus waterbergensis* is closely related to *L. graniticolus* differing in colour pattern (Fig. 1 e), the round to obovate distal expansions of the digits and the conical dorsal granular scales (Fig. 5). Median subcaudals are aperiodically arranged 2, 1, 1, 2, 1, 1, 2, 1, 1.

Description. Holotype: TM 58939, adult male, SVL 39,5 mm; tail 42,5 mm; mass 1,35 g.

Lepidosis. Head not distinct from the neck. Snout rounded, rostral subhexagonal, much wider than high; nostril round and laterally directed; circumnaries include rostral, 1st upper labial, an enlarged nasorostral and two granular scales; nasorostral separated by a single granular scale; nasorostral followed posteriorly by two enlarged scales. Scales on snout twice as large as on crown of head. Spiny eyelid scales reduced or absent. Upper labials 6/6. Mental large, subpentagonal followed posteriorly by two chin shields; lower labials 6/6. Dorsal scales small, juxtaposed, raised posteriorly. Ventrally gular scales in 20 rows between posterior lower labials; gular scales subimbricate and overlapping. Chest and abdomen scales hexagonal, imbricate and overlapping. Four rows of glandular scales on inside of thighs and nine preloacal pores arranged in a shallow forward directed curve. Digits obovately expanded at the tip with four pairs of adhesive lamellae distally and 11 enlarged subdigital scales proximally. Caudal scales whorled and overlapping. Tail regenerating, and in a ratio of 1,14 : 1 with SVL. Subcaudals irregular as tail regenerating but does appear to indicate a median series arrangement of 2, 1, 1, 2, 1, 1. Tail verticillate with 6–7 supracaudals and 3–4 subcaudals per verticil.

Colour. Grey dorsally with irregular rows of dark spots and interrupted bars extending posteriorly from the snout. Tail with spaced dark, white margined crossbars becoming pointed posteriorly. Tail variably spotted with offwhite. A dark eye stripe extends from the nostril through the eye to the ear and onto the shoulder. A second stripe extends from the angle of the jaw to the shoulder. Laterally brownishgrey with irregular black spots between fore and hindlimbs. Limbs greybrown with variable dark spots and blotches. Ventrally gular speckled with grey. Median chest and belly offwhite with dark speckling ventrolaterally. Underside of thighs brownish- to straw yellow. Underside of tail offwhite with intermittent speckling becoming denser ventrolaterally.

Paratypes. Lepidosis. Similar to holotype but circumnarians four in TM 58969. Variation found in the upper labials which range from 7–9; lower labials range from 6–8; Gular scales between posterior lower labials 21 in TM 58969; TM 59040 has three chin shields. Preloacal pores and glandular scales absent in females. Tail to SVL ratio range from 1,09–1,17 : 1. Median subcaudals in TM 58969 arranged in a series of 2, 1, 1, 2, 1, 1.

Colour. As for holotype. TM 58969 darker with a regular row of dorsolateral dark centered ocelli extending from the neck to the sacrum and diminishing on the base of the tail. TM 59002 shows some resemblance to *L. graniticolus*, in colour and colour pattern.

Size. Mean adult SVL = 35,1 mm \pm 3,24 (ISD), n = 5, mass = 1,15 g \pm 0,32 (ISD), n = 5. Largest male SVL = 39,5 mm, mass = 1,35 g. Largest female SVL = 36,0 mm, mass = 1,40 g.

Reproduction. Not known but probably oviparous.

Habitat. A rupicolous gecko found basking on sandstone boulders in grassland or scrub, taking refuge in crevices between rocks. Found in veld type 20 (Acocks 1975) at altitudes of 1500–2000 m a. s. l.

Distribution. Widespread but endemic to the high-lying scarp of the Waterberg from Thabazimbi in the southwest to Hanglip in the northeast (Fig. 2).

Remarks. This species differs from *graniticolus* but appears to be closely related both with regard to size as well as colour pattern. This species which is allopatric to *graniticolus* has separated from the latter long enough to have evolved into a separate taxon. It represents the most westward form of what Pasteur (1964) calls the Austro-Oriental phylum retaining the altitudinal preferences which were probably the normal habitat of the ancestral stock.

Discussion

From the foregoing it appears that there are four separate species groups found in the Transvaal all apparently related according to the paucity of distinguishing morphological characters. These groups include *methueni*, *ocellatus*, *nigropunctatus* and *graniticolus*.

According to Pasteur (1964) these groups would form part of the Austro-Oriental phylum which originated in Central Africa and dispersed southwards reaching maximum extension in the Transvaal. Subsequent isolation, possibly of climatic origin, left relict populations widely separated, such as *L. rex* in Malawi and *L. methueni* in the Woodbush 1000 km apart or in the other evolutionary line, with *L. bonisi*, *L. bernardi* and *L. ocellatus* separated from each other by 400–600 km. In this paper it is evident that the *methueni* complex, although a geographical relict is in the process of diversification.

Pasteur (1964) also distinguished the *rex/methueni* group from the *bonisi* group on the basis of size (exceeding 40,0 mm SVL), sexual dimorphism with males larger than females, and a tail which is 1,2 times longer than SVL, dorsal colouration and a range of 9–11 preloacal pores. Many of the taxa described in this paper show

characters which overlap with those discussed by Pasteur (op. cit) for the *rex* and *bonsi* complexes. What are the true relationships ? A retention of the lineages suggested by Pasteur (1964) are feasible but distinguishing characters difficult to define. Should this approach be upheld, the relationships would follow those suggested in fig. 6.

All species with the exception of *L. rex* and to a lesser extent *L. methueni* are rupicolous indicating a common ancestry and distinct from the remainder of *Lygodactylus* species. These are all arboreal although many species are found on the walls of houses and even on rocks away from trees.

The transition to a rupicolous way of life is of considerable significance and possibly relates to a paucity of trees as the ancestral stock moved south. Pasteur (1964) mentions in this context an adaptive zone which according to Simpson (1953) refers to a way of life and not a place where life is led. This adaptive zone must have been along the eastern escarpment of Africa which experienced considerable climatic

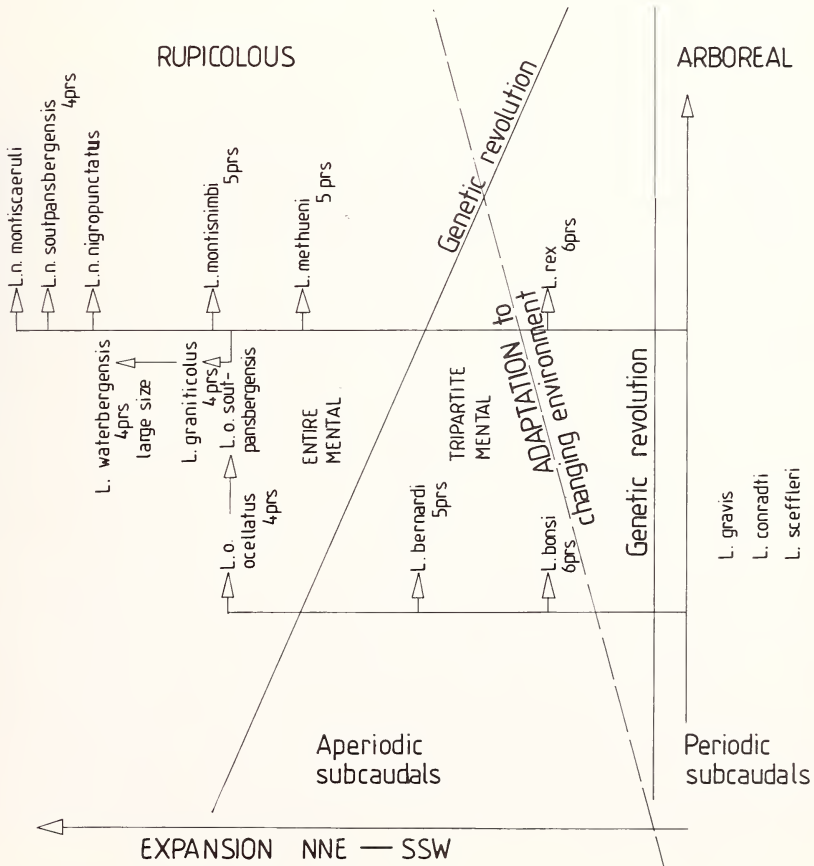


Fig. 6: Evolution of the Austro-Oriental phylum (adapted from Pasteur 1964).

fluctuations during the Pleistocene with resultant expansion and contraction in the number of trees (Cooke 1964).

The two evolutionary lines proposed by Pasteur (1964) for the Austro-Oriental phylum reach their southern limit in the Transvaal where a further adaptive zone developed enabling species to live in more arid environments and at lower altitudes. This change is no doubt correlated to their change to a rupicolous lifestyle. Subsequent isolation from parent stock produced the large number of taxa described in this report.

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Zusammenfassung

Die Arbeit beschreibt und vergleicht drei Arten und zwei Unterarten von Geckos der Gattung *Lygodactylus* aus dem Transvaal. Ihre phylogenetischen Beziehungen zu anderen süd- und ostafrikanischen Arten von *Lygodactylus* werden ebenfalls betrachtet.

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