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Systematics and biogeography of the southern African scincine genus *Typhlacontias* (Reptilia: Scincidae)

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Abstract. *Typhlacontias* is one of several fossorial skink genera of southern Africa, which are limbless or have degenerate limbs. It occurs in parts of the Namib Desert and the northern Kalahari Basin. In this generic revision six species, one with three subspecies, are recognised. The confused description of *T. punctatissimus* (Bocage, 1895) which has previously been addressed by Andersson (1916), is further discussed. *T. bogerti* Laurent is relegated to subspecies level of above species and *T. p. brainei* is described as a new and third subspecies. An apparently new species is recognised as one which was described as *T. johnsonii* in 1916 already. *T. rudebecki* is described as a new species and *T. gracilis* Roux, *T. rohani* Angel, as well as *T. brevipes* FitzSimons, are each treated as full species.

Key words. Reptilia, Scincidae, *Typhlacontias*, new species and subspecies, systematics, biogeography, southern Africa, Namib desert, Kalahari.

Introduction

The genus *Typhlacontias* was correctly identified as new by Bocage (1873) and only De Witte and Laurent (1943) attempted to split it when they proposed the genus *Fitzsimonsia* for *T. brevipes*. As the original syntypes of the type species *T. punctatissimus* were poorly preserved subadults, Bocage (1895) felt that the species description had to be amended when he received an assumed adult topotype in 1884. However, this was an aberrant specimen of a new species, later described as *T. johnsonii* (Andersson, 1916), and its supernumerary supranasal scales were considered species specific (Bocage 1895, pl.VII, Fig. 3; De Witte & Laurent 1943, Fig. 53). As a result *T. punctatissimus* became unidentifiable. Andersson (1916), recognising this confusion when he was supplied with seven additional specimens representing both species from the type locality, redescribed *T. punctatissimus* on the basis of a single juvenile and utilised the other six specimens to describe a new species, *T. johnsonii*, in a paper which was overlooked ever since its publication. A point of controversy is the presence of leg rudiments in this *T. punctatissimus* neonate (HB = 41 mm), in a supposedly limbless species (Bocage 1873; Boulenger 1887). To complicate matters further, Bocage's (1895) three original specimens were destroyed in a fire in the sixties, shortly after Dr D. G. Broadley was able to re-examine the third specimen (= *T. johnsonii*) and confirm the accuracy of Bocage's (1895) description (Broadley, pers. com.).

In 1907 Roux described *T. gracilis* from a single specimen from Barotseland in Zambia, the former Northern Rhodesia (vide "Rhodésie" in De Witte & Laurent 1943: 35). The drawings of the head scales (Roux 1907: 84, fig. 3 and 4) are not very accurate, suggesting the presence of only four upper and three lower labials and the parietal area in the dorsal view is inaccurate. In addition the type has a slightly

aberrant supraorbital area as the upper anterior temporal scale apparently fused with the third supraorbital (Fig. 4b).

Another new species, *T. rohani* (Angel 1924), was described from the Kalahari sand of south-eastern Angola, but was overlooked by FitzSimons (1932) when describing *T. ngamiensis*. As a consequence the latter has been relegated to a junior synonym (Auerbach 1987).

Unfortunately the origin of the type of *T. brevipes* was not known when FitzSimons (1939) described this species. The assumption that it came from Angola resulted in the omission of this species from his classic study "The Lizards of South Africa" in 1943. McLachlan (1984: 17) eventually restricted the type locality to Walvis Bay.

After the second World War a revival of the interest in faunal studies of southern Africa took place and possibly an improvement in funding provided a new impetus for exploring and collecting. Fresh material was produced from the central and northern Namib when Dr Charles Koch and Dr C. K. Brain of the Transvaal Museum and Dr G. Rudebeck of the Lund University Expedition visited those areas and *T. bogerti* was described from south western Angola by Dr R. F. Laurent in 1964. The author of this paper then started collecting during the sixties, intensively sampling the Namib Desert, as well as the Kalahari in north-eastern Namibia and Botswana. Dr D. G. Broadley in Rhodesia (now Zimbabwe) also entered the arena at that time and accumulated long series with the help of enthusiastic amateurs like Richard Japp in western Zambia and the Caprivi Strip of Namibia. Distribution gaps in south-western Zambia and south-eastern Angola still cast doubt at some of the conclusions drawn in this paper.

A special problem is provided by the single, mutilated type specimen of *T. rudebecki* sp. n., which does not quite fit into the biogeographic picture of *Typhlacontias* as produced by the other taxa. However it is hoped that this study is a step in the right direction.

Genus *Typhlacontias* Bocage

Typhlacontias Bocage, 1873. Journ. Sci. Lisboa 15: 213 (Type species: *Typhlacontias punctatissimus*). Boulenger 1887: 429; Bocage 1895: 56; Andersson 1916: 18; De Witte & Laurent 1943: 34; Greer 1970: 14; Welch 1982: 79.

A small genus of mostly apodal, fossorial skinks. The snout is flattened, protruding and covered by a large rostral scale. Nostrils pierced in the sides of the rostral, with a suture extending backwards to the edge of the rostral. A small to minute oblong postnasal scale is enclosed in this rostral groove. Three transversally enlarged azygous shields, i.e. internasal, frontonasal and frontal, cover the head between the rostral and the large subtriangular interparietal, in which a pineal eye is usually clearly visible. Eyes, small and completely exposed to partly covered, without eyelids, in contact with specific combinations of the second and third upper labials. Three pairs of temporal scales dorsally to the three posterior upper labials. No external ear opening. Body scales smooth, imbricate and in 18 rows around body. Tail length varies according to species from two thirds to one quarter of the body length. No preanal or femoral pores, sexes indistinguishable externally. The skull was discussed by Greer (1970: 14). Pectoral girdle strongly degenerate with no visible remnants of limbs, while the remains of the pelvic girdle may still have rudiments of the femurs. External leg rudiments consistently present in one species and occasionally so in another. Small conical teeth, palate toothless. Tongue squamous, anteriorly notched to slightly bifurcate.

Active sand swimmers patrolling leaf litter and decaying vegetable matter for termites, beetle larvae and other small invertebrate prey. Mostly active at night when soil temperatures allow near surface activity. Biology practically unknown but some species are ovoviviparous.

Range: The Namib Desert sands from north of Lüderitz into south western Angola and Kalahari sand of north-eastern Namibia, northern Botswana, western Zimbabwe and western Zambia. Although only one record exists from south-eastern Angola it is highly likely that these lizards are of common occurrence there.

Remarks: The original generic description was based on two poorly preserved syntypes (Bocage 1873) collected by the well-known naturalist J. O. Anchieta at the Curoca River mouth in the northern Namib Desert in Angola which were donated in 1867. A third, supposedly topotype, was added later and was used to expand the species description (Bocage 1895). It is now clear that the latter was an aberrant individual of *T. johnsonii* Andersson, 1916, a then still undescribed species, which caused confusion. All three specimens were destroyed by a fire in the Bocage Museum at the University of Lisbon during the seventies (D. G. Broadley, pers. com.). *T. punctatissimus* remains the type species and its original description (Bocage 1873; Boulenger 1887) was reviewed and updated by Andersson (1916: 21). Unfortunately the specimen, which the latter author considered to represent this species, is also aberrant as it has hindlimb rudiments.

Material

For this revision 616 specimens have been examined, including the types of *T. brevipes*, *T. gracilis*, *T. ngamiensis*, *T. rohani* and two syntypes of *T. johnsonii*. To save printed space only the specimens of new taxa and lectotypes are individually listed with catalogue number, while for every locality the institution in which a relevant voucher specimen is kept is listed. The following institutional abbreviations are used: CAS = California Academy of Science, San Francisco. EMUS = John Ellerman Museum, University of Stellenbosch. FMNH = Field Museum of Nat. Hist., Chicago. GMS = Gothenburg Museum, Sweden. IRB = Institut Royal des Sciences Naturelles, Brussels. LACM = Los Angeles County Museum, Los Angeles. MCZ = Museum of Comparative Zoology, Boston. MHNP = Museum of Nat. Hist., Paris. NDRS = Namib Desert Research Station, Gobabeb, Namibia. NMZ = National Museum, Bulawayo, Zimbabwe. SAM = South African Museum, Cape Town. SMF = Senckenberg Museum, Frankfurt on Main. TM = Transvaal Museum, Pretoria. ZFMK = Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

Key to the genus *Typhlacontias*

- 1a) A strongly enlarged second lower labial present 2
- b) No enlarged lower labials 7
- 2a) Rudimentary hindlimbs present 3
- b) No rudimentary limbs present 4
- 3a) Minute postnasal scale in short contact with 1st upper labial,
S of Kunene River *T. brevipes*
- b) Minute postnasal scale enclosed within rostral suture,
N of Kunene River (*T. punctatissimus* ssp.)
- 4a) Frontal shield subhexagonal to oval shaped, tail about one
quarter of head/body length *T. johnsonii*
- b) Frontal nearly halfmoon shaped with a strongly curved
anterior edge and a nearly straight posterior margin.
Original tail about two thirds head/body length (*T. punctatissimus* sspp.) 5
- 5a) Five upper labials with second usually reaching eye *T. p. brainei*
- b) Six upper labials with second plus third or third only
reaching eye 6
- 6a) Usually only third upper labial reaching eye *T. p. punctatissimus*
- b) Usually second and third upper labial reaching eye,
southern Angola *T. p. bogerti*
- 7a) Third upper labial entering eye *T. gracilis*
- b) Second upper labial entering eye 8
- 8a) Loreal in contact with second upper labial *T. rohani*
- b) Loreal not in contact with second upper labial *T. rudebecki* sp. n.

Systematic account

Typhlacontias johnsonii Andersson (Figs 1a, 2a, 7)

Typhlacontias johnsonii Andersson, 1916. Meddel. Göteborgs Mus. Zool. Afdel. 9: 19. Lectotype Re. ex. 1388a, Lectoparatypes Re. ex. 1388b-f in Gothenburg Museum of Natural History (Type locality: Porto Alexander = Tombua, coll. by D. F. d'Azinhaes, 3 July 1912, don. by H. Skoog).

Typhlacontias punctatissimus part. Bocage 1895: 56. Roux 1924: 164. Monard 1937: 86. De Witte & Laurent 1943: 34, fig. 53.

Material: 83 specimens examined. Types in Gothenburg Natural History Museum. Two lectoparatypes seen.

Type series: The description is based on six syntypes, all recorded under No. 1388 in the Zoological Department of the Gothenburg Museum (now 'Naturhistoriska Museet, Göteborg', Sweden). The largest and first mentioned specimen (HB = 123 mm) of this series, of which the measurements are listed (Andersson 1916: 20) is hereby designated as lectotype (1388a), while the remaining smaller individuals are lectoparatypes (1388b-f).

Etymology: Named in honour of Mr. C. O. Johnson, who financed Mr. Skoog's expedition to Angola.

Diagnosis: Tail shorter than in all other species, i.e. about 25 % of SV length. Eye smaller than in other species and partly overlain by edges of loreal and supraocular. Second upper labial about twice as long as tall and in contact with eye.

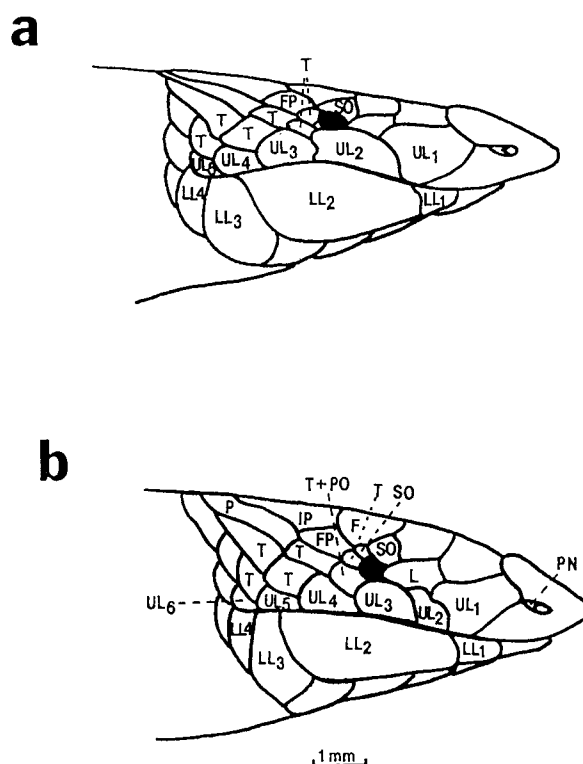


Fig. 1: a) *Typhlacontias johnsonii* Andersson, TM 63455, Ondondujengo River, Namibia; b) *Typhlacontias brevipes* FitzSimons, TM 31416, Unjab River, Namibia. Postoculars fused with temporals. (For abbreviations see Fig. 5).

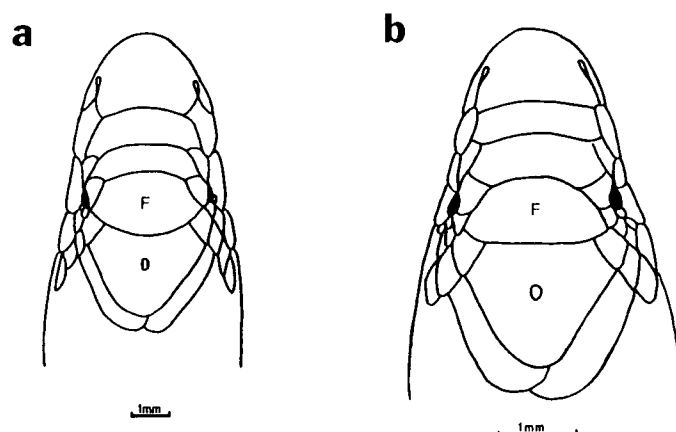


Fig. 2: a) *Typhlacontias johnsonii* Andersson, TM 63455. Data as above; b) *Typhlacontias punctatissimus bogerti* Laurent, NDRS-R 223, Curoca River crossing, Angola. Dorsal view to illustrate the difference in the shape of the frontal shield.

Description: Body relatively stout, underside of body flattened. Head wedge-shaped, snout depressed, rostral forming sharp horizontal edge. Relative size of laterally deeply notched rostral less prominent than in other species. Nostrils connected to rear edge of rostral by short suture, enclosing small oblong postnasal scale. Rostral followed by bandlike internasal and frontonasal, a suboval to hexagonal frontal, a large subpentagonal interparietal flanked by pair of striplike parietals which touch behind interparietal (Fig. 2a). Pineal eye in interparietal usually visible. Five upper labials, first largest, second very long and below eye, probably consisting of the fused second and third. Eye exposed but small, with a nearly straight posterior edge, partly covered by second upper labial and the single, large, triangular supraocular, resulting in a subtriangular appearance (Fig. 1a). Eye also in touch with loreal (= preocular according to Andersson 1916), occasionally a tiny single preocular, the upper anterior temporal which may have fused with the upper postocular and a tiny lower postocular, which may be missing. Frontoparietal in contact with upper anterior temporal. Large mental followed by large postmental, four lower labials of which the second is very large. Head scales show a certain amount of individual variation, s.a. subdivisions of dorsals (eg. frontonasal in TM 63344 and supernumerary postnasals in original specimen from Curoca River [Bocage 1895: 56]), minute preoculars may be present or partly obscured by loreal, labials may be split in two or scales may fuse.

Row of four preanal scales, subequal in size to the ventrals. Eighteen rows of tight-fitting smooth scales covering body.

Cleared specimen TM 63463 (Ondondujengo River) has 72 spinal vertebrae, remnants of pectoral and pelvic girdles present but no limb rudiments.

Ventrals: Range = 131–150, $n = 73$, $\bar{x} = 139.2$, $SD = \pm 5.1$. Subcaud.: Range = 35–42, $n = 50$, $\bar{x} = 38.4$, $SD = \pm 2.5$.

Size: Max SVL = 117 mm (TM 63461, Ondondujengo River). Max total = 139 (110 + 29) mm (TM 32569 56 km S of Orupembe). Min SVL = 39 mm (TM 63281 Hartmann's Valley). Min total = 51 (41 + 10) mm (TM 63373 Hartmann's Valley). Relat. tail length: Range = 23–33 %, $n = 53$, $\bar{x} = 26.8$ %, $SD = \pm 2.4$.

Colouration: Juveniles are pinkish pale yellow with only small sark spots on frontal and interparietal, an indication of a vertebral double line and a lateral line extends backwards through the eyes. The light dorsal areas on the snout may be light brown to golden yellow, with the tail pale blue. With maturity each scale's centre spot enlarges, black lines become more prominent and old individuals may become very dark. Apart from the unmarked lower jaw area every body and tail scale has a central dark spot. Size of spots variable and rows of

large spots create a dorsal band (2 rows), 1 dorsolateral line, a broad (3 rows) lateral band and often a black ventrum (4 rows). Dorsal band joins dark brown marks on top of head, lateral bands continue through eyes and join on snout.

Range: (Fig. 7) Wind blown sand of the Northern Namib Desert from the mouth of the Curoca River on the northern edge of the Curoca sand-sea in south-western Angola, southwards into the Kunene sand-sea in north-western Namibia. Documented as far south as the Sechomib River valley. In Namibia it avoids the coastal hummocks of the seaward side of the sand-sea where *T. brevipes* occurs. Although poorly documented in Angola it apparently occurs closer to the coast there. *T. brevipes*, which is of similar size and would therefore probably be in direct competition, has not been recorded from north of the Kunene River. On the inland edge of the Kunene sand-sea, it is usually sympatric with *T. punctatissimus* ssp., but only rarely with *T. brevipes* when the latter species extends that far inland along drainage valleys.

Distribution records: ANGOLA: Porto Alexander (= Tombua) 1511Dd (GMS); Curoca River (nr mouth) 1511Dd (Bocage 1895: 56); Lacrau 1711Bb (TM). NAMIBIA: Okotusu area 1711Bd, E edge of Kunene sand-sea 1712Ac and 1711Db, edge of Hartmann's Valley 1712Ac, 48 km NW of Ouhandjo 1712Ac (TM); Ondondujengo River at Hartman Valley — Cape Fria road crossing 1712Cc (SMWN, TM, ZMFK); Sechomib River valley 56 km SSW of Orupembe 1812Da (TM, ZFMK); nr end of Hartmann's Valley 1712Aa (TM, SMWN); Hartmann's Valley 1712Cb (TM).

Field notes: Active during summer evenings mostly around debris accumulations at the base on the leeward side of dunes. Individuals move just below the sand surface, out of sight, leaving a clear regular undulating track. Occasionally these tracks move across the slipface to the crest of the dune, over the top or down again. When moving, although not actually exposed, the position of the specimen is quite clear under the surface at the blunt end of the track and collecting is easiest at that moment. If disturbed they dive into the sand and become inaccessible. As this material was mostly collected during autumn, no gravid females were found. However, a number of young (about 40 mm HB length) were collected during April 1985. It is assumed that this species is live bearing and the young are born during late summer i.e. February to March.

Typhlacontias brevipes FitzSimons (Figs 1b, 6)

Typhlacontias brevipes FitzSimons, 1939. Ann. Transv. Mus. 20: 15, figs 14–17. Type S.A.M. 508 in South African Museum, Cape Town. (Type locality: Cape Division. Restricted to Walvisch (= Walvis) Bay, Namibia by G. R. McLachlan 1984: 17). Greer 1970. Welch 1982: 79. Branch 1988: 124.

Fitzsimonsia brevipes De Witte & Laurent 1943: 11. Haacke 1964: 8.

Material: 141 specimens examined. Type seen.

Etymology: Referring to the presence of limb rudiments.

Diagnosis: Rostral large and laterally strongly notched with the small enclosed postnasal scale making contact with the first upper labial, third upper labial in contact with eye, second lower labial very large. Minute hindlimb rudiments visible on either side of cloaca.

Description: Snout depressed and covered by a large rostral scale which extends beyond the lower jaw and forms a sharp horizontal edge, strongly notched laterally. Edges of nasal suture in rostral scale not touching as small postnasal scale is in contact with the first upper labial. The three bandlike scales i.e. internasal, frontonasal and frontal are subequal in width and breadth, large subpentagonal interparietal is posteriorly edged by a pair of striplike parietals, which slightly overlap. The pineal eye is usually clearly visible in the interparietal, but not so in the four most southern specimens from Groot Anigab (TM 44320-3). Six upper labials, first largest, third touching eye, sixth smallest. Eye small and round, bounded and partly overlain by the third upper labial, loreal, two supraoculars, the upper anterior temporal and a tiny lower postocular. Large mental and postmental, four lower labials with second very large. Body scales smooth, tight-fitting, imbricate in 18 rows. A minute rudimentary hindlimb, present on both sides of the vent. Cleared specimen TM 27450, Swakopmund, has 66 and TM

56876, Hoanib Oasis, has 68 vertebrae, remnants of the pectoral and pelvic girdles, with femur rudiments.

Ventrals: Range = 133–152, $n = 95$, $\bar{x} = 140.3$, $SD = \pm 4.6$. Subcaud.: Range = 45–56, $n = 56$, $\bar{x} = 52.0$, $SD = \pm 3.2$.

Size: Max SVL = 133 mm (TM 36886 Walvis Bay). Max total = 158 (125 + 33 dam.) mm (TM 42252 10 km SE of Torra Bay). Min SVL = 39 mm (TM 63349 Ondondujengo River). Min total = 54 (39 + 15) mm (TM 63349 Ondondujengo River). Rel. tail length: Range = 32–44 %, $n = 55$, $\bar{x} = 37.6$ %, $SD = \pm 2.7$.

Variation: A considerable amount of individual variation occurs amongst the head scales, especially the smaller ones around the eyes, which may be absent or fuse with adjacent scales. Fusions may be symmetrical or not. For example, TM 31529 (Munutum River) has both loreals fused to the internasal forming one wide halfmoon-shaped band. Amongst the specimens from just south of the mouth of the Kunene River, the size of the second upper labial, which is usually in touch with the loreal, is reduced to such an extent that the first and third upper labials are in contact above it. The development of the limb rudiments is fairly consistent. The total size, even in big adults, tends to be less than a millimetre in length, although the shape may vary from blunt triangular to slightly elongated.

Colouration: Juveniles have well developed dark lateral bands at an early age, a faint dorsal double line which starts on the head, down the yellow-grey back. With increasing size every scale develops a dark blotch to an extent that the specimen is more or less lined but then gets evenly speckled as the dark lines become less distinct. The background colour of back and body may be silver grey to pale straw yellow with the tail pale powder blue. Individuals from Gobabeb on the Kuiseb river are much lighter than the coastal specimens. Most of these specimens have an unmarked light sulphur yellow body with only a few vertebral rows of dark spots. The tails are darker marked with rows of dark specks on a blue-grey background.

Range (Fig. 6): Coastal Namib Desert from just north of Lüderitz to the Swakop and then the Omaruru River. No records are known from the Omaruru River to the southern tip of the northern sand-sea, where the road to Khorixas turns inland. Northwards from that point this species is quite common in vegetation islands and hummocks on the seaward side of the large sandbodies as far as the mouth of the Kunene River. It may extend inland along the drainage valleys of the dry rivers.

Distribution records: NAMIBIA: Cape Fria 1812Ac (TM); Cape Fria or Karlowa's Hut 1812Aa (SMWN, TM); 'Dunedin Star' Wreck 1811Bb (TM); Gobabeb 2315Ca (CAS, MCZ, SMWN, TM, ZFMK); Great Anigab Waterhole 2615Ac (TM); Hoanib River flood plain 1912Bd (SMWN); Hoanib River mouth 1912Bd, Hoanib/Mudorib River confluence 1913Ad, Hoanib River at 1913Ac (TM); Hoarusib River mouth 1912Ba (SMWN); 18 km NW of Hunkab River crossing 1913Ca (TM); Khumib River mouth 1812Cd (SMWN); Kuiseb River dunes at Rooibank 2314Ba (SMF); S of Kunene River 8 km from mouth 1711Bd, Möwe Bay area 1912Bc (SMWN, TM); Munutum River 16 km from mouth 1812Ac (SMWN); Munutum River 40 km from Cape Fria 1812Aa, 'Oasis' in Hoanib River 1912 Bc (TM); Omaruru River 16 km from mouth 2114Cd (SMWN, TM); Ondondujengo River 1712Cc (TM); Rocky Point 1812Cd (SMWN); Samanab River 2013Ab, Sandwich Harbour 2314Ad (TM); Sarusas in Khumib River 1812Cd, Sechomib River 1812Ad (SMWN, TM); Swakopmund 2214Da (LACM, TM); Swakop River 2214Da (TM, CAS); Terrace Bay 1913Cc (TM); Torra Bay 2013Ac (SMWN); 10km and 22km SE of Torra Bay 2013Ad, Unjab River at 2013Aa, Ab (SMWN, TM); 8 km E of Walvis Bay 2214Dc, 10 km S of Walvis Bay 2315Ba (TM).

Field notes: This species avoids large bare sand bodies and is usually found in the semistable sand of hummocks and sparsely vegetated dunes, as well as the edges and sandy vegetated banks of dry rivers. In general it does not share its habitat with other fossorial lizards. At Gobabeb, the furthest inland record, *T. brevipes* occurs along the banks of the Kuiseb River and although it is sympatric with *Typhlosaurus braini* there, the latter avoids direct competition by utilising the occasional hummocks on high dunes. However, near Groot Anigab, the currently documented southern range limit of both species, these two species were actually found in the same hummock. South of Torra Bay open valleys are crossed on shifting, barchan dunes which also carry *Meroles (Aporosaura) anchietae* and *Bitis peringueyi*. Only when

T. brevipes penetrates the northern sandseas along riverbeds towards the eastern side of the dunefields, has it been found to be sympatric with other legless lizards, such as *T. johnsonii* and *T. punctatissimus*. This species, like other congeners, tends to feed and be active just below the sand surface at night and during the twilight hours when the sand is of a suitable temperature. They leave their undulating tracks all over the windblown sand of dunes and hummocks, feeding on a variety of small insects, their larvae and occasional termites. Although dune slipfaces and debris accumulations are patrolled and frequented, *T. brevipes* appears to prefer vegetated hummocks and their leaf litter cushions. Most small juveniles (about 40 mm HB length), which appear to be neonates, were found during March to April. TM 44320, a large female (HB = 110 mm) from Groot Anigab, collected during January contained three well developed foetuses, which suggests that they were probably ready to be born during the latter part of summer, i.e. February to March.

Typhlacontias punctatissimus Bocage

The original description was based on a pair of poorly preserved subadult syntypes (Bocage 1873). Although referring to them as “limbless”, their state of preservation may have caused the author to overlook some of the finer details. Possibly due to a typographical error the presence of a subocular instead of a supraocular was described (Boulenger 1887). The species description was extended (Bocage 1895: 56) when an apparent adult topotype became available. An important aspect of this specimen was the presence of a pair of small supranasals, now recognized as an individual variation, as it has not been recorded again. This fact was considered as species specific and was used by Monard (1937: 84) and De Witte & Laurent (1943: 34) to differentiate *T. punctatissimus* from other species. Due to this compound description *T. punctatissimus* became unidentifiable. These three specimens were destroyed by fire in the Museo de Bocage at the University of Lisbon (acc. Prof. Saccarao, D. G. Broadley pers. com.) in the seventies, just after Broadley had the opportunity to re-examine the third specimen and confirm the correctness of its description (Broadley, pers. com.). Although the original syntypes have never been re-examined because of their poor condition, the description (Bocage 1873) contains a number of points, which are significant for the recognition of this species. The shape of the frontal scale was described as being “large and almost semicircular with the anterior edge rounded and posterior edge straight”. This shape is typical for *T. punctatissimus* (Fig. 2) and differentiates it from the assumed adult topotype which was actually a different species. The aspect providing absolute proof that another species was involved are the body ratios. The relative tail length of the longer of the former syntypes was equal to 51 % of HB length (Bocage 1873: 213), which is typical for *T. punctatissimus* (Table 1), whereas in the third or “adult” specimen the tail was only 26 % of the body length, which is diagnostic for *T. johnsonii* (Bocage 1895: Fig VII, 3+3a. Table 1). Seven new specimens from the type locality, donated by H. Skoog in 1912, were examined by Andersson (1916) and it was obvious to him that two species were involved. According to a single neonate (Re. ex. 1389, HB = 42 mm) he confirmed the original description of *T. punctatissimus* (Bocage, 1873) and redescribed

Table 1: Variation in size, body proportions and scalation.

Species	n	max SVL	% T/SVL		Ventrals		Subcaudals		Vertebrae
			Range	Mean	Range	Mean	Range	Mean	
<i>T. brevipes</i>	104	133	32–44	37.6	131–152	140.3	42–56	51.6	66, 67, 68
<i>T. johnsonii</i>	86	117	23–33	26.8	131–150	139.2	35–42	38.4	72
<i>T. p. bogerti</i>	29	86	46–55	51.9	114–135	122.7	59–69	62.3	62
<i>T. p. punctatissimus</i>	39	84	44–62	51.9	116–137	124.6	50–70	60.9	61
<i>T. p. brainei</i>	12	70	45–60	51.5	117–128	122.3	50–68	59.3	—
<i>T. gracilis</i>	112	84	40–61	50.2	122–147	134.7	60–65	62.5	68
<i>T. rohani</i>	233	90	48–73	57.0	124–146	134.3	64–84	69.4	62,63,66
<i>T. rudebecki</i>	1	82	—	—	157	—	—	—	—

it. He added to the controversy by recording the presence of tiny leg rudiments in this specimen, which has now been made available for re-examination and the presence of these limb rudiments is herewith confirmed. Only a single additional specimen with tiny hindlimb rudiments (R 224 Namib Desert Research Station, Gobabeb, from eastern edge of the Curoca Sand Sea, S of Curoca River near road crossing into Iona National Park, 1612Ad, Angola) has been traced amongst the 94 specimens of this species that have been examined for this revision. One of two cleared specimens has internal femur rudiments (TM 40727, Kakolo windmill 1612Cd, Iona Nat.Park, Angola), while the second (TM 63481) from the Ondondujengo River (1712Cc) in Namibia has no indication of any rudiments at all. According to other external morphological characteristics the specimens from the Curoca River mouth and the Ondondujengo River represent the typical subspecies, *T. p. punctatissimus*, while the other two specimens mentioned represent *T. p. bogerti*.

Under normal circumstances leg rudiments carry substantial weight in species recognition of fossorial skinks. At present not enough material is available from the type locality in the vicinity of the Curoca River to evaluate the taxonomic significance in this case and it is for the time being accepted as atavistic intraspecific or individual variation.

Unfortunately Andersson's (1916) paper has been overlooked since then in all studies dealing with *Typhlacontias*. *T. bogerti* Laurent (1964) is only subspecifically distinct from *T. punctatissimus* and trinomens must thus be used. In addition a third subspecies can be defined and is described below.

***Typhlacontias punctatissimus punctatissimus* Bocage (new status) (Fig. 3b)**

Typhlacontias punctatissimus Bocage, 1873. Journ. Sci. Lisboa 4: 213 (Type locality: Rio Curoca mouth, Moçâmedes district, Angola), 1887: 203 and 1895: 56 (Syntypes in 'Museo de Bocage', Lisbon, destroyed by fire). Boulenger 1887(3): 429. Andersson 1916: 21. Roux 1924: 164. Monard 1937: 86. De Witte & Laurent 1943: 34. Greer 1970: 14. Welch 1982: 79.

Typhlacontias bogerti, Haacke 1965: 22 (part. Namibian specimens). Mertens 1971: 70 (part. Namibian specimens).

Material: 39 specimens examined. Syntypes destroyed, not seen.

Etymology: Referring to its speckled colour pattern.

Diagnosis: The most slender of those species characterised by the enlarged second lower labial and the laterally strongly notched rostral, s. a. *T. brevipes* and *T. johnsonii*. Large frontal, nearly semicircular with straight posterior edge. In this subspecies usually only the third upper labial enters eye. Rudimentary hindlimbs may occur.

Description: The original description applies. Snout depressed, large rostral scale with horizontal edge, less strongly notched than in the above mentioned taxa. Nasal groove straight, enclosing minute postnasal scale. Rostral followed by a narrow striplike internasal, a slightly

Table 2: Variation in head scalation.

Species	Enlarged 2nd L.L	Upper labials	UL below eye	Supra oculars	Prefront present	PF in contact with FP	Loreal in contact 2nd UL
<i>T. brevipes</i>	X	6	3	2	—	—	X
<i>T. johnsonii</i>	X	5	2	1	—	—	X
<i>T. p. bogerti</i>	X	6	2 and 3	2	—	—	X
<i>T. p. punctatissimus</i>	X	6	3	2	—	—	X
<i>T. p. brainei</i>	X	5	2	2	—	—	X
<i>T. gracilis</i>	—	6	3	2	X	X	X
<i>T. rohani</i>	—	5	2	2	X	—	X
<i>T. rudebecki</i>	—	5	2	2	X	X	—

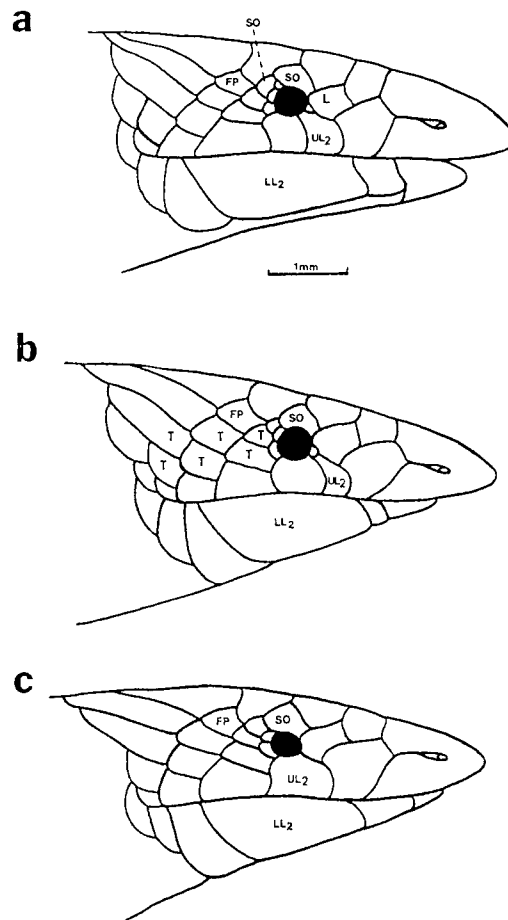


Fig. 3: a) *Typhlacontias punctatissimus bogerti* Laurent, topotype TM 40391, 34 km S of Namibé (= Moçâmedes), Angola, with supernumerary third upper postocular; b) *T. p. punctatissimus* Bocage, TM 63215, Munutum River crossing, Namibia; c) *T. p. brainei* ssp. n., holotype TM 68443, Khumib River, Namibia.

wider prefrontal and a fairly large semicircular frontal scale, which has a strongly convex anterior and nearly straight posterior edge (Fig. 2b). Eye round, completely exposed and bordered by one preocular, loreal, the anterior supraocular, two postoculars and the third upper labial, separated from second supraocular by upper postocular. Six, not five upper labials, first largest, second small and curving backwards but separated from eye by tiny preocular. The supposed presence of a subocular reported by Bocage (1873) appears to be due to a typographical error referring to a supraocular. No noticeably enlarged triangular preanal scales could be confirmed. The tiny hindlimb rudiments specifically mentioned by Andersson (1916) for the juvenile topotype (Re. ex. 1389), which was re-examined, are very distinct but could not be traced in any other specimens, except for one from further upstream along the Curoca River. In that case (D.E.R.U. R-224) the limb rudiments are even less well developed.

Cleared specimen TM 63481 (Ondondujengo River), has 61 vertebrae, remnants of pectoral and pelvic girdle, but no internal limb remnants.

Ventrals: Range = 116–137, $\bar{x}$ = 122.7, SD = $\pm$ 6.99, n = 27. Subcaud.: Range = 50–70, $\bar{x}$ = 62.3, SD = $\pm$ 2.99, n = 11.

Size: Max SVL = 84 mm (TM 24304 Nangolo Flats). Max total = 115 (77 + 38) mm (TM 63215 Munutum River). Min SVL = 38 mm (TM 63478 Ondondujengo River). Min total = 74

(49 + 25) mm (SMWN 8196 Hartmann's Valley). Rel. tail length: Range = 46–55 %, $\bar{x}$ = 51.9 %, SD = $\pm$ 6.21, n = 9.

Notes: The relative tail length of one of the original syntypes was 51 % (HB = 55 mm, tail = 28 mm). This matches the mean for this taxon (Table 1), which also applies to the topotype (SVL = 41 mm, tail = 20 mm, rel. tail length = 49 %) (Andersson 1916: 22). This ratio for the third specimen, presumed to be an adult topotype (Bocage 1895), was “measuring about a quarter of the length of the body,” i.e. 26.1 % (HB = 92 mm, tail = 24 mm) which is typical for *T. johnsonii* (Table 1, Range 23–33 %, $\bar{x}$ = 26.8 %).

As the two syntypes were destroyed by fire it is desirable to designate a lectotype. However as the Curoca River is the type locality for this taxon and at the same time appears to be the border between two subspecies, it seems important that any action is avoided which might further contribute to the confusion. It is therefore highly desirable that a topotype should be used for this purpose. At present the only specimen of this taxon from that site and from north of the Kunene River is the above mentioned juvenile with the atypical limb rudiments. Although this is viewed as being an intraspecific apparently atavistic individual variation, it may also represent a situation of taxonomic importance, for which reason this individual is unsuitable as a lectotype. As this problem can only be resolved once additional topotypes become available, it is abstained from designating a lectotype.

Colouration: The basic patterns of this taxon are created by the black centre spots of each scale which may be more or less emphasized, thereby creating the impression of lines. The broad (4 scales) dorsal band may be unmarked and of a rich golden brown, but may vary via straw yellow to pinkish grey, in which case two vertebral lines of brownish specks occur. Laterally two well defined black lines start as one near the nostril, pass through the eye and extend to the tail tip. Additional lines of specks may be present ventrally and on the underside of the tail. Scales in cloacal area usually unmarked. On the silvery blue tail the two vertebral dark lines are more prominent than on the body. The top and sides of the head may or may not be marbled with brown, have a few dark spots or an arrow-headed brown mark.

Variation: Within the range of *T. p. punctatissimus* odd specimens occur with individual variations to the labial formula, such as asymmetrical fusions of labial 1 and 2 (TM 31525) and of 2 and 3 (TM 31525), symmetrical fusions of 1 and 2 (TM 63259) and of 2 and 3 (TM 57556), vertical subdivision of labials 2 and 5 in TM 71475 on the left side created eight upper labials and of these the fourth is in touch with the eye. These variations might produce problems when keying out individual specimens, but similar variations occur in the other two subspecies as well. A relatively significant variation is the rare presence of external rudimentary hindlimbs.

Range (Fig. 8): Although the original type locality was the lower Curoca River on the edge of the Curoca Sand Sea, only one further specimen is known from there. At present the typical form is mostly known from south of the Kunene River in Namibia, where it occurs from the inland edge of the Kunene Sand Sea into the Marienfluss Valley and as far south as the Munutum River. It is not known from the immediate vicinity of the Namibian coast.

Distribution records: ANGOLA: Curoca River nr mouth 1511Dd (Bocage 1873) and nr Porto Alexander (= Tumboa) 1511Dd, which is nr mouth of Curoca River (= Type locality). NAMIBIA: Hartmann's Valley, several records from close proximity to one another within the q.d.s. 1712Aa (SMWN, TM); 1712Ac (TM, ZMFK) and 1712Cb (TM); Khumib River (SMWN); Marienfluss 1712Da (SMWN, TM); Munutum River 40 km from Cape Frio 1812Ab (SMWN, TM); Muntum River at Skeleton Coast Park border 1812Aa (TM); Nadas River 32 km from Cape Frio 1812Ac (SMWN); Nangolo Flats in Marienfluss Valley 1712Ad (TM); Ondondujengo River 1712Cc (TM, ZMFK); Okotusu area 1711Bd (TM); 16 km W of Orupembe 1812Ad (SMWN); Ouhandjo area 1712Ba (SMWN); 48 km NW of Ouhandjo 1712Ac (TM).

Field notes: This species is not normally associated with the major sand seas. Although their regular undulating tracks may be seen in the larger sand accumulations of their range, they are more often found in small patches of sand on stony hillsides and specimens may actually be found under stones in the inland part of their range. In the sandy parts of the Hartmann's Valley this taxon is sympatric with *T. johnsonii* and only capture will allow identifica-

tion of the species which produced the track. As most other fossorial skinks, these lizards move just below the sand surface and exposures, as when a stony area is crossed, only rarely happen. It is as yet unclear what predators this species may have. No information about reproduction is available. The smallest juvenile (TM 63478) of 38 mm HB length, tail broken was collected during April 1985 indicating that parturition takes place during late summer.

***Typhlacontias punctatissimus bogerti* (new status) Laurent (Figs 3a, 8)**

Typhlacontias bogerti Laurent 1964. Publ. cult. Comp. Diam. Angola 67: 82 (Type locality: '35 km S of Moçâmedes (= Namibé)', Angola. Types in Dundo Museum, Angola). Haacke 1965: 22 (part., Angolan specimens). Greer 1970: 14. Mertens 1971: 70. Welch 1982: 79.

Material: 29 specimens examined. Types not seen.

Etymology: Named in honour of renowned American herpetologist Dr Charles M. Bogert.

Diagnosis: A slender form with enlarged second lower labial scale and general characteristics described for the typical form but second and third upper labial in touch with eye.

Description: In general very similar to the typical form apart from the subspecific character, i.e. the second and third upper labial are in touch with the eye. This situation is fairly persistent amongst the series of 14 specimens from Moçâmedes (= Namibé), although individual variation occurs, such as the second upper labial being separated from the eye by the preocular as in the typical form (TM 24465, 24469, 24473), or the second upper labial may just be too short to reach (TM 24463, 24469). The Kakolo windmill sample (n = 7) may be seen as of an integrate population, as three are normal *T. p. bogerti*, but four have variations which do not allow the second upper labial to reach the eye. Usually two, rarely three postoculars.

Cleared specimen TM 40727 (Kakolo windmill), has 62 spinal vertebrae, remnants of the pectoral and pelvic girdles with tiny remnants of the proximal femur head, while R-224, in the collection of the Namib Desert Research Station, Gobabeb, from the eastern edge of the sand sea south of the Curoca River, has minute limb rudiments adjacent to the cloaca.

Ventrals: Range = 114–135, $\bar{x}$ = 122.7, SD = $\pm$ 6.99, n = 27. **Subcaud.:** Range = 59–69, $\bar{x}$ = 62.3, SD = $\pm$ 2.99, n = 11.

Size: Max SVL = 86 mm (TM 40725 Kakolo Windmill). Max total = 123 (83 + 40) mm (TM 40724 Kakolo Windmill). Min SVL = 40 mm (TM 40730 Kakolo Windmill). Min total = 58 (40 + 18) mm (TM 40730 Kakolo Windmill). **Relative tail length:** Range = 44–62 %, $\bar{x}$ = 51.9 %, SD = $\pm$ 6.21, n = 9.

Colouration: Similar to the typical form.

Range (Fig. 8): Northern Namib Desert of Angola in the Iona Park west of the Curoca Sand Sea and north to Moçâmedes (= Namibé).

Distribution records: ANGOLA: Curoca River crossing 1612Ad (NDRS); Kakolo Windmill 1612Cd, Moçâmedes (= Namibé) 1512Aa (EMUS, IRB, TM, ZMFK); 10 km S of Moçâmedes (= Namibé) 1512Ac, 34 km S of Moçâmedes (= Namibé) 1512Ca, (TM); 8 km SE of Pico de Azevedo 1512Da (SMWN).

Field notes: The types were collected under a stone and under a *Welwitschia* plant (Laurent 1964), as were those from 10 km S of Moçâmedes (= Namibé). In Moçâmedes specimens were found next to the trunk and amongst the roots of trees lining the streets (C. Koch, pers. com.). At the Kakolo Windmill the specimens were collected at night while they were active near the surface of red sand accumulations against a stony hillside. The large female paratype collected on 23 November 1949, contains embryos with well developed eyes (Laurent 1964: 84).

***Typhlacontias punctatissimus brainei* ssp. n. (Figs 3c, 8)**

Etymology: Named after Mr Steve Braine, former ranger of the Skeleton Coast Park, Namibia, for his contribution towards the knowledge of the fauna of that area during his term of office there.

Holotype: TM 68443, collected by W. D. Haacke, 11. 4. 1989.

Paratypes: 15 specimens. TM 31497–8, Sehomib River Valley 29 km SW of Orupembe

(1812Ad) coll. W. D. Haacke, 4. 10. '65. TM 32375, same as previous specimens but 7. 5. '66. TM 56863, Hoanib River 2 km E of Amspoort, 19°20'S 13°12'E, coll. S. Braine 18. 9. '83. TM 68437–68442, ZFMK 57532, same data as holotype. SMWN 2011, Khumib River 16 km E of Sarusas East (1812Ba), SMWN 2014(3), 29 km SW of Orupembe 1812Ad, coll. W. J. Steyn 4. 10. 65.

Type locality: Khumib River 25 km from the coast, Skeleton Coast Park, Opuwo District, Namibia, 18°44'S 12°36'E (1812Da).

Diagnosis: In general appearance and characteristics similar to the typical form but upper labials 2 and 3 appear to have fused, resulting in five, instead of six upper labials and the large second upper labial is in contact with the eye. Preocular absent or minute and partly covered by loreal. Eye usually in touch with the least number of scales of all taxa, namely second upper labial, loreal, anterior supraocular and two postoculars.

Description: Holotype TM 68443, sex undetermined, 112 (70 + 42) mm, tail 60 % of HB length, 18 scale rows round middle, 120 ventrals, 68 subcaudals, five upper labials of which the large second (fused 2 + 3?) is in contact with eye, preocular absent or minute and covered by large loreal, two supraoculars form lateral edge of frontal and larger, anterior also in contact with upper edge of eye, two small postoculars, four lower labials of which the second is very large (Fig. 3c).

Variation: Similar to holotype with minor individual variations, s. a. second and third upper labials not fused on both sides (SMWN 2014c) and on right side only (SMWN 2011).

Ventrals: Range = 117–128, $n = 12$, $\bar{x} = 122.3$, $SD = \pm 2.64$. Subcaud.: Range = 50–68, $n = 6$, $\bar{x} = 61.8$, $SD = \pm 5.63$.

Size: Max SVL = 70 mm (TM 31498, holotype). Max total = 112 (70 + 42) mm (TM 31489, holotype). Min SVL = 41 mm (TM 56863, near Amspoort, neonate). Min total = 9 (41 + 18) mm (TM 56863, near Amspoort, neonate). Relative tail length: Range = 45–60 %, $\bar{x} = 51.5$ %, $n = 6$, $SD = \pm 4.86$.

Range: Recorded from the Sechomib to the Hoanib River valleys, just outside the border of the Skeleton Coast Park, Namibia, and not above an altitude of about 600 m a.s.l.

Field notes: Wind-blown sand accumulations on rocky hillsides, flat stone desert, hummocks and vegetated banks along and in drainage valleys.

Remarks: The fact that fusion of the 2nd and 3rd upper labial is part of the individual variation within the range of *T. p. punctatissimus*, is good supporting evidence that these taxa are only subspecifically distinct.

***Typhlacontias gracilis* Roux (Figs 4b, 7)**

Typhlacontias gracilis Roux, 1907. Rev. Suisse Zool. 15: 83, Fig. 3–4 (Type locality: 'Zambezi'. Type in Neuchatel Nat. Hist. Museum). Angel 1920: 617 (Lealui). Pitman 1934: 306. De Witte & Laurent 1943: 35, fig. 54–55. Greer 1970: 14. Broadley 1971: 58. Welch 1982: 79. Branch 1988: 125.

Typhlacontias gracilis gracilis, Broadley 1971: 58.

Material: 113 specimens examined. Type seen.

Etymology: Referring to its gracile or slender body shape.

Diagnosis: Least tendency for head scales to fuse, as a consequence has more than other taxa. Four normal sized lower labials with the fourth slender and horizontal, six upper labials with third entering orbit, prefrontal separated from frontoparietal by third supraorbital (In type antero-upper temporal fused with third supraorbital Fig. 4b). Eye usually in touch with third upper labial, two preoculars, two of three supraoculars and three postoculars.

Description: Large rostral not strongly notched laterally. Dorsal head scalation as typical for this genus with frontonasal slightly larger than internasal and frontal. Narrower frontal allows space for a prefrontal wedged between frontonasal and two supraoculars. Frontoparietal fits into notch between frontal and interparietal. Two supraoculars in touch with eye are followed by a third scale, here referred to as third supraocular, separated from eye by upper postocular, but in touch with the frontal thereby separating frontoparietal and prefrontal. All

other taxa, except *T. rohani*, have two supraoculars of which at least one is in touch with the lateral edge of the frontal. Usually two preoculars and one to three postoculars occur.

Type has anterior upper temporal fused with third supraocular and this enlarged scale touches frontal laterally, thereby separating prefrontal from frontoparietal (Fig. 4b). NMZ 7894 from Kalabo has labial one and two fused, with that enlarged scale on the left side showing a slight dorsal notch. Accordingly only five upper labials exist and "second" enters the orbit. Nevertheless, frontoparietal and interparietal are still separated by third supraocular and two preoculars exist, thereby distinguishing it from Kalabo *T. rohani*. Opinions of what constitutes a labial scale appear to differ. This reviewer considers *T. gracilis* to have six upper labials and usually four lower labials. The fourth lower labial is narrow and horizontal, sometimes only visible when the mouth is opened and it extends to below the sixth upper labial.

Body covered with 18 tight-fitting scale rows. Anal scales not markedly enlarged.

Cleared specimens TM 33866 and TM 33880, both from Kalabo, have 68 and 60 spinal vertebrae, remnants of pectoral and pelvic girdles but no limb rudiments.

Ventrals: Range = 122–147, $\bar{x}$ = 134.66, n = 43, SD = $\pm$ 4.74. Subcaud.: Range = 60–65, $\bar{x}$ = 62.5, n = 14, SD = $\pm$ 3.88.

Size: Max SVL = 84 mm (NMZ 7875 Kalabo). Max total = 93 (64 + 29) mm (NMZ 6799 Kalabo). Min SVL = 38 mm (NMZ UM 10060 Kalabo). Min total = 79 (53 + 26) mm (NMSR 3406 Kabompo). Rel. tail length: Range = 40–61 %, $\bar{x}$ = 49.34 %, n = 29, SD = $\pm$ 4.39.

Colouration: Buff to straw coloured. Each scale is dark centred, with dark spot varying in size and equal sized spots may form lines, s.a. two faint vertebral lines which start in some dark marks on top of the head. A lateral line, which, when well developed, may be dark brown and include the snout, starts in the eye area extending to the tail tip. The intensity of the lined pattern varies extensively.

Range (Fig. 7): Western Zambia, i.e. Barotseland in the upper Zambezi Plains.

Distribution records: ZAMBIA: Kabompo 1324Ca (NMZ); Kalabo 1422Dc (NMZ, TM, ZFMK); Lealui 1523Aa (MHNP, Angel 1920); Lyumba 1430Ca (FMNH, Broadley 1971).

Field notes: Found in high rainfall area in Kalahari sand together with other fossorial skinks s.a. *Typhlosaurus lineatus jappi*, *Lygosoma sundevallii* as well as several amphisbaenian taxa and their snake predators of the genera *Amblyodipsas* and *Xenocalamus*. This taxon occurs in an area with a higher average annual rainfall than any of the other *Typhlacontias* taxa and as a consequence may have to cope with flooding of the Barotse Plains and associated hazards.

Remarks: The re-examination of the long series of specimens from Kalabo provided proof that at that site *T. rohani* occurs sympatrically with *T. gracilis* and therefore these two taxa are here reinstated as full species.

Typhlacontias rohani Angel (Figs 4a, 7)

Typhlacontias rohani Angel, 1923. Miss. Rohan-Chabot Angola-Rhodesia (Paris) 4: 162, figs 6–8. (Type locality: Lwankundu, south-east Angola. Type in Paris Nat. Hist. Museum). Angel 1942: 109. De Witte & Laurent 1943: 35. Welch 1982: 79.

Typhlacontias ngamiensis FitzSimons, 1932. Ann. Transv. Mus. 16: 37 (Type locality: Mothlatlogo = Bothatogo, Botswana. Type in Transvaal Museum, paratype in Field Museum, Chicago), and 1935: 374, figs 17–19, also 1943: 239. De Witte & Laurent 1943: 35. Mertens 1955: 77 and 1971: 71. Broadley 1962: 805. Haacke 1965: 20. Welch 1982: 79. Griffin 1985: map 51.

Typhlacontias gracilis ngamiensis, Broadley & Blake 1979: 7. Branch 1988: 125.

Typhlacontias gracilis rohani, Auerbach 1987: 103. Broadley 1988: 376.

Material: 233 specimens examined. Type seen.

Etymology: Named in honour of M. de Rohan-Chabot who led an expedition in 1914 into the south-eastern part of Angola, an area which is herpetologically still unexplored.

Diagnosis: No enlarged lower labial scales, five upper labials with second entering orbit, frontoparietal and prefrontal in contact with one another.

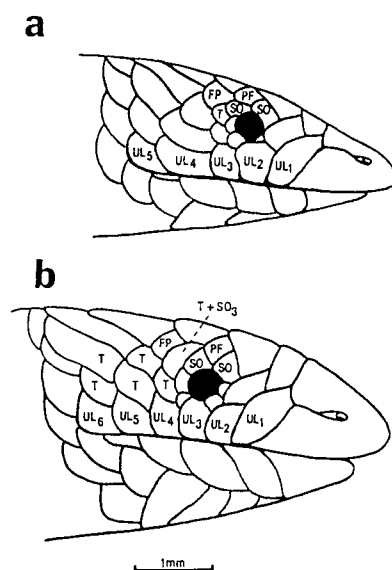


Fig. 4: a) *T. rohani* Angel, holotype MHNR 1923.1.1, Lwankundu River, Angola; b) *T. gracilis* Roux, holotype, unnumbered. Upper Zambezi River, Zambia (For abbreviations see Fig. 5.)

Description: Snout depressed with a horizontal edge. Rostral only as long as the narrow internasal plus the broad fontonasal. Rostral with only slight lateral notches but fairly long nasal sutures enclosing minute postnasals. Five upper labials with the second (2 and 3 fused?) entering the orbit. Usually one or two small preoculars. In the Kalabo series these two scales have fused into a narrow vertically elongate scale separating the loreal from the eye, while in the type the loreal enters orbit above a small preocular (Fig. 4a) and in the type of *T. ngamiensis* no preocular is apparent, as it is often the case in other specimens when the minute scale is covered by the loreal. Frontoparietal and prefrontal in contact, separating the two large supraoculars from contact with frontal, usually two postoculars of which the lower prevents contact between lower anterior temporal and upper labial in contact with eye. Four lower labials of which the last is narrow, horizontally elongate and sometimes invisible unless the mouth is opened. Midbody scale rows 18, four anal scales not significantly different from ventrals.

Ventrals: Range = 124–146, $n = 193$, $\bar{x} = 134.26$, $SD = \pm 4.57$. Subcaud.: Range = 64–84, $n = 73$, $\bar{x} = 69.4$, $SD = \pm 11.3$.

Size: Max SVL = 90.0 mm (TM 30971, Tsodilo Hills). Max total = 125 (83 + 42) mm (TM 38347, 50 km W of Tsumkwe). Min SVL = 33.0 mm (TM 39313, nr Katima Molilo). Min total = 50 (33 + 17) mm (TM 39313, nr Katima Molilo). Rel. tail length: Range = 48–73 %, $n = 69$, $\bar{x} = 56.95$ %, $SD = \pm 5.98$.

Colouration: Similar to *T. gracilis*, but in some areas, such as the Kwando River in the Caprivi Strip, Namibia, exceptionally dark specimens occur, as the dark centre blotches of each scale are larger and better developed than usual. In these specimens the body sides are dark brown and the head, especially the snout, is also very dark.

Discussion: *T. rohani* and *T. gracilis* are very similar in general characteristics, s.a. size, scalation, colouration, etc. which justifies the idea that they are only subspecifically distinct. However, there are some differences of which the main features are very consistent, nl. the facial scalation. *T. rohani* has a fairly wide geographical range in north-eastern Namibia, northern Botswana, western Zimbabwe and probably south-eastern Angola. Throughout this range the available specimens have five upper labials with the second (2 and 3 fused?) in contact with the orbit. Furthermore the frontoparietal and prefrontal are in contact with one another. In contrast *T. gracilis* has six upper labials and the third enters the orbit while the

frontoparietal and prefrontal are separated by a third supraocular scale. As the main range of *T. gracilis* lies in Barotseland of western Zambia with a collecting gap of about 300 km between Kalabo and the Caprivi Strip of Namibia the subspecies status was probable and difficult to dispute. However, a re-evaluation of a large number of the sample from Kalabo proved that 18 specimens have the characteristics of *T. rohani* from further south with no significant variation in the main features. A local variation of that sample is a slender, upright preocular, separating the loreal from the orbit. A single *T. gracilis* specimen (NMZ 7894) has only five upper labials as the first and second fused. Of these the left one has a slight dorsal notch, indicating that that large scale is indeed a result of fusion. Two preoculars are present and the supraoculars are divided by the upper of the first temporals. This means, although it suggests a relationship with *T. rohani*, it is a *T. gracilis* with a slight aberration. Greer (1970: 14) compared a skull of *T. gracilis* with one of *T. rohani* (= *T. ngamiensis*) and found a difference in the palatal rami between the two taxa. To further test the relationship between *T. rohani* and *T. gracilis*, especially with reference to Kalabo, some statistical tests were carried out. The ventral scale counts vary significantly and show up differences. Furthermore the subcaudal counts and relative tail lengths of *T. rohani* from Kalabo and *T. rohani* from elsewhere, were compared but no difference was found, indicating conspecificity. However, when the data for the Kalabo *T. rohani* were subjected to a T-test in comparison to the data of *T. gracilis*, in both the cases, i.e. subcaudals (sig. level = 5.01784E-4) and tail/body ratio (sig. level = 3.19417E-3) were found to be highly significant, providing additional evidence that two species are involved. As a consequence of proven sympatry of these two taxa at Kalabo, they are accepted as full species of which the ranges overlap in western Zambia.

Range (Fig. 7): Kalahari sand with an average annual rainfall above 400 mm p.a. in NE Namibia including the Caprivi Strip, northern Botswana, western Zimbabwe, SE Angola and western Zambia as far as the Zambezi Valley.

Distribution records: ANGOLA: Lwankundu River 1620Ad (MHNP); BOTSWANA: Bothatogo 2022Db (TM, FMNH); Dibejama 1821Ad (FMNH); Dodo Crossroads 1825Cb (NMZ); near Gubatsha Hills 1824Ca (TM); Kasane 1725Cc, Maun 1923Cd, Ngwezumba Bridge 1824Bd (NMZ); Savuti Camp 1823Db, Shakawe 1821Bd (TM); Tamafupi 1926Ac (NMZ); Tsoe 2024Cb (LACM); Tsodilo Hills 1821Db (TM). NAMIBIA: near Grootfontein 1919Bc (TM); Kanovlei 1919Ab (SMW); Katima Mulilo 1724Cb (TM); 15 km and 65 km WSW of Katima Mulilo 1724Ca (NMZ, TM); Kwando River 1723Cd (TM); Kwetche (Mahango Reserve) 1821Ba, Leeupan 1820Bd, 10 km S of Leeupan 1820Db (SMW); Makambu 1718Ad, Mangetti Forest 1818Da (TM); Mpungu 1718Ca (SMW); Odila Dam 1716Bd (TM); Rundu 1719Dd (TM, SMW); Samangeigai 1920Aa (TM); 25 km NW of Tamsu 1820Ba; Tsumkwe 1920Da (SMW); 50 km W of Tsumkwe 1920Ac, 55 km NW of Tsumkwe 1920Aa, Verskyn 1919Aa, Wenela 1723Cb (TM); Western Veterinary Fence 2120Ac (SMW). ZAMBIA: Kalabo 1422Dc (NMZ 6766-7, 6769, 6780, 6782, 6787, 6791, 6793, 6795, 7894, 10048, 10050, 10052-4, TM 33868, 33887, 35580). ZIMBABWE: Bembesi Vlei 1826Dc (NMZ); 10 km NW of St. Martin's Mission 1927Bb (TM); Dahlia 1827Ca, Dandari 1826Cc, Dett 1826Db, Dina Pan 1826Cd, 6 km S of Dina Pan 1926Ab, Dopi Windmill 1826 Dd, Good Luck Ranch 1827Ca, Gubalala 1826Dc, Kennedy 1827Cc, Lupane 1827Dd (NMZ); Main Camp, Hwange 1826Db (TM); Manzimbomvu Pan 1826Cc, Maraposa, Nyamandlovu 1928Cc, Shapi Pan 1826Dc, Somavundhla Pan 1927Aa, Teaklands 1927Bd, Tibukai Pan 1825Dd, Verney's Pan 1826Dd, Victoria Falls 1725Dd, Westwood Ranch 1725Dd (NMZ).

Field notes: Active sandswimmers which forage just below the sand surface at night, leaving thin, regularly undulating tracks. As more vegetated environment is utilised these tracks are not as obvious as those occurring in desert sand. May be found by raking in leaf litter under bushes and elsewhere or by turning over logs, as no stones occur. Feeding on small insects s.a. beetle larvae and termites. Biological information is limited. Appears to be ovoviviparous as a specimen from 15 km W of Katima Molilo (NMZ-UM 22889) contains three full term young. However, a specimen from Kalabo (NMZ-UM 6766) is gravid with four large eggs (each about 3.5 x 5.5 mm) which show no sign of development. Unfortunately no collecting dates exist which would allow deductions relating to the season. Other sandswimmers which share the range are *Typhlosaurus lineatus lineatus* in Namibia and Botswana and *T. l. jappi* in western

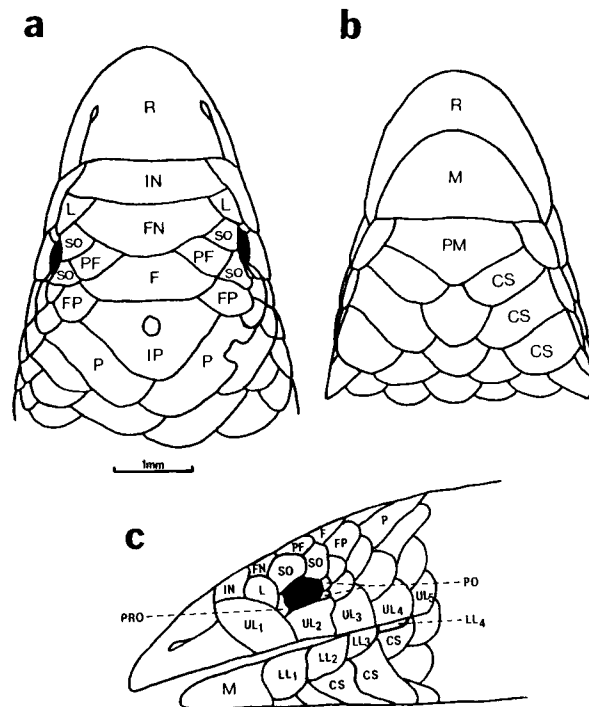


Fig. 5: *Typhlacontias rudebecki* sp. n., holotype TM 25465, São Nicolau, Angola; a) dorsal, b) ventral, c) lateral view. CS = chin shield, F = frontal, FN = frontonasal, FP = frontoparietal, IN = internasal, IP = interparietal, L = loreal, LL = lower labial, M = mental, P = parietal, F = prefrontal, PM = postmental, PO = postocular, PRO = preocular, R = rostral, SO = supraocular, T = temporal, UL = upper labial.

Zambia. Several amphisbaenians also share this moist environment s.a. *Zygaspis quadrifrons*, *Monopeltis anchietae*, *M. leonhardi*, *M. sphenorhynchus*, *Dalophia pistillum* and *D. longicauda*. Several burrowing snakes are specialised predators of these sandswimmers and will also consume *Typhlacontias rohani* and *T. gracilis*. The most probable predators are *Amblyodipsas ventrimaculata*, *Xenocalamus mechowii* and *X. bicolor*.

***Typhlacontias rudebecki* sp. n. (Figs 5a, b, c, 7).**

Etymology: Named after the collector Dr G. Rudebeck, who was a member of the Swedish Lund University Expedition to South Africa at that time.

Holotype: TM 25465, sex undetermined, collected during September 1956 by G. Rudebeck.

Type locality: São Nicolau, Moçâmedes (= Namibé) district, Angola (1412 Ad).

Diagnosis: Lower labials not fused, number of ventrals higher than of related *T. gracilis*. Rostral not notched laterally, five upper labials with first (= fused 1 and 2?) very large, extending to below anterior edge of eye, loreal separated from second upper labial which is in touch with the eye.

Description: TM 25465, Holotype. Tail incomplete and body cut into two parts, 49 mm and 33 mm long with a total of about 152 ventrals and 18 scale rows around the body. Rostral laterally not notched and subequal in length to first three azygus scales on the top of the head i.e. internasal, frontonasal and frontal (Fig. 5a). Nostrils, followed by tiny oblong nasal scale, pierced in sides of rostral with short straight suture connecting them to back edge. Eye round, exposed but with slight overlap by second upper labial and supraoculars. First upper labial

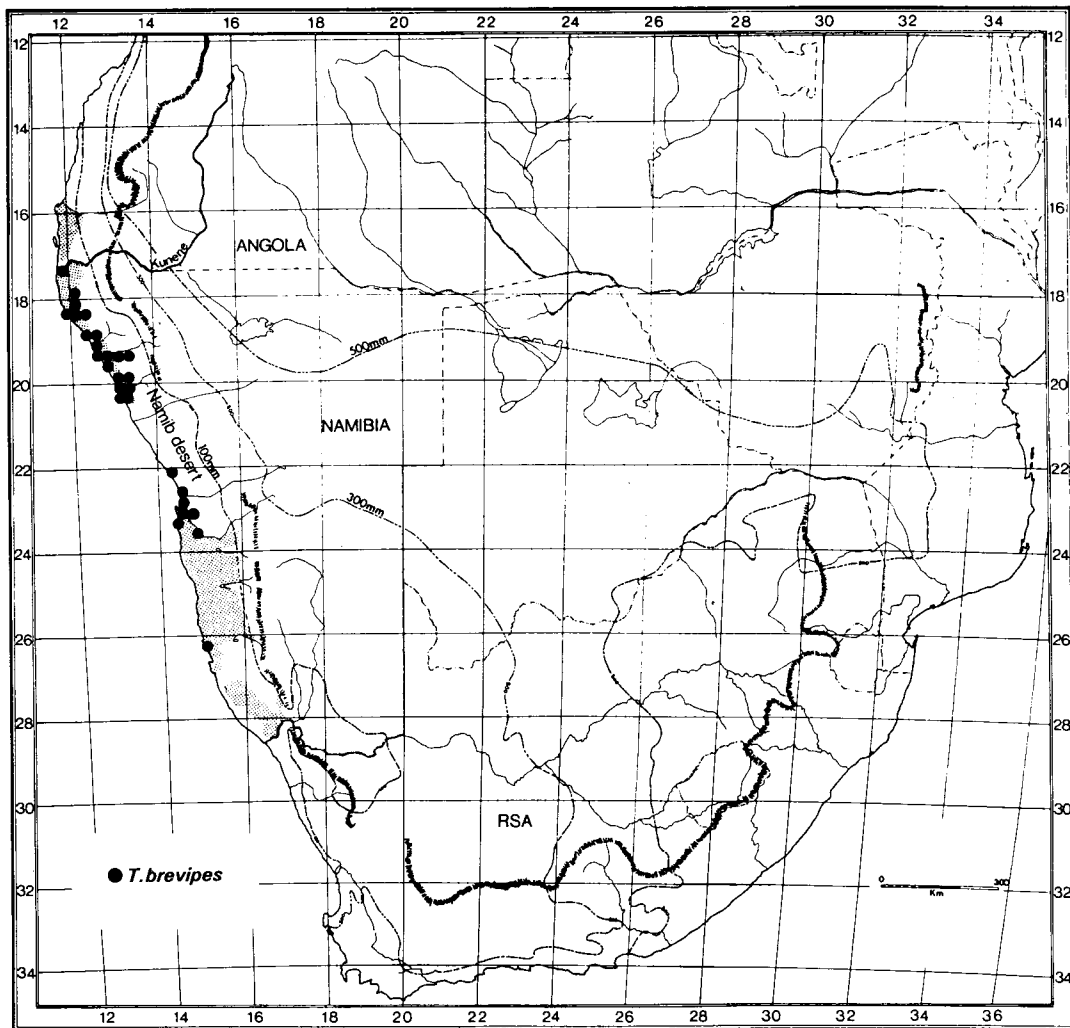


Fig. 6: Distribution of *Typhlacontias brevipes* in the Namib Desert.

large (1 & 2 fused?), anteriorly extending to above level of eye and posteriorly past anterior edge of the eye. Loreal separated from eye and second upper labial by single preocular. Five upper labials of which second is in broad contact with eye, two small postoculars, two large supraoculars in touch with prefrontal, posterior supraocular in touch with frontal, thereby separating similar-sized prefrontal and frontoparietal. Pineal eye clearly visible in the relatively small subpentagonal interparietal. Frontonasal larger than internasal or frontal. The large mental is followed by a large postmental (Fig. 5b), four lower labials of which the narrow horizontal fourth scale is difficult to see when the mouth is closed.

Colour: Dorsum pale with a light brown vertebral stripe two half scales wide, bordered by a dark lateral line three scales wide which extends forward through the eye to the nostril. Ventrally each scale of four rows bears a light brown spot.

Discussion: According to the unfused lower labials this taxon is closer to *T. rohani* and *T. gracilis*, than to the Namib species. However, the general proportions differ and the habitat, although not specifically recorded, is coastal Namib Desert. *T. gracilis* and *T. rohani* are restricted to Kalahari sand at a fairly high altitude with a fairly high average annual rainfall.

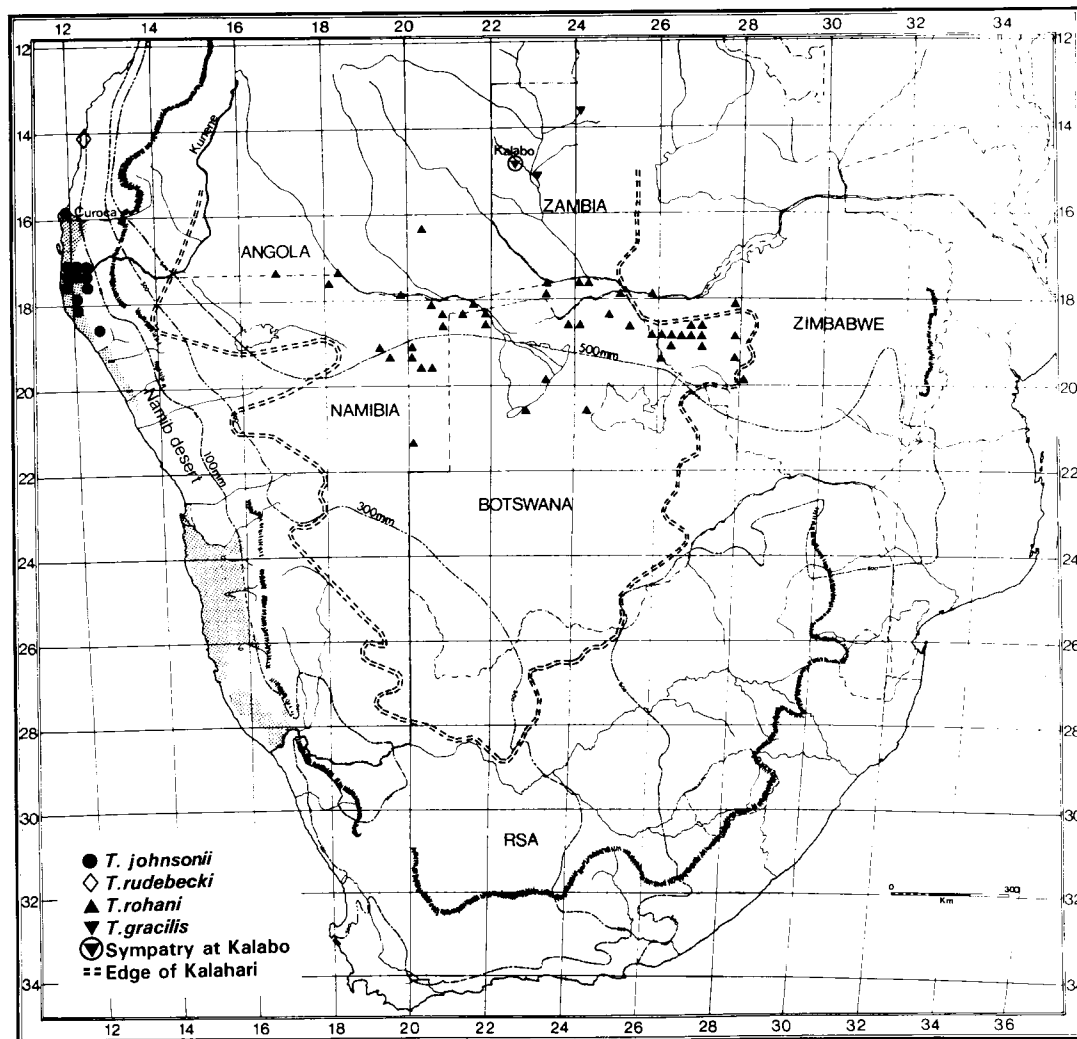


Fig. 7: Distribution of *T. johnsonii* and *T. rudebecki* sp. n. in the northern Namib Desert and *T. rohani* and *T. gracilis* in the northern Kalahari sands.

Discussion

Character analysis: Greer (1970: 14) gave a description of the general characteristics of the genus. He discussed the skull of *T. brevipes*, *T. gracilis* and *T. rohani* (= *T. ngamiensis*) and their general external characters. His identification of head-scales differs from that of this author. The supraoculars of Greer, in touch with the sides of the interparietal, are here considered to be frontoparietals as these scales do not reach the eye, but are in touch with frontal and interparietal in all species and usually the parietals as well. The extra scale wedged laterally between frontal and frontonasal and two supraoculars are here referred to as prefrontals. Scales in contact with the dorsal aspect of the eye are referred to as supraoculars, as was done when describing *T. brevipes* (FitzSimons 1939: 15). Greer (op. cit.) interprets the presence of a large interparietal and a single transverse internasal (postrostral) as an indica-

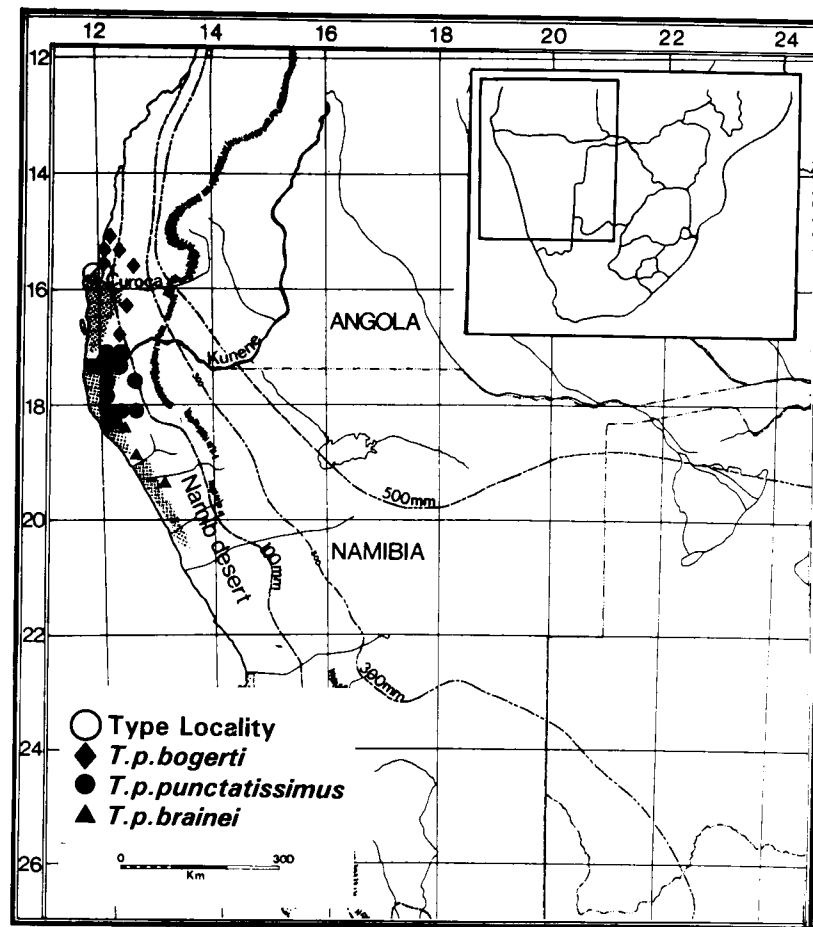


Fig. 8: Distribution of the three subspecies of *Typhlacontias punctatissimus* in the northern Namib Desert.

tion of a relationship with *Scelotes* and he assumes that *Typhlacontias* evolved in arid areas of southern Africa, with *T. brevipes*, due to the presence of external limb rudiments and a relatively large postnasal scale, as the most primitive form. In the light of Broadley's (1968) evaluation of evolutionary trends in the acontine scincid genus *Typhlosaurus*, one may have to re-evaluate Greer's suggestion. A number of morphological characters of the eight taxa are listed in Tables 1 and 2. The presence or absence of the very large second (= fused second and third?) lower labial in combination with the presence of prefrontals separates this genus into two groups.

T. brevipes, *T. johnsonii* and *T. punctatissimus*, have this large second lower labial, but no prefrontal and are Namib Desert endemics (Figs 6, 7, 8), while *T. gracilis*, *T. rohani* and *T. rudebecki* sp. n. have no fused lower labials but a prefrontal above the supraoculars. The first two species of the latter group are widespread in Kalahari sand with high rainfall at fairly high altitude above sea level (Fig. 7). In contrast the presence of *T. rudebecki*, of which the range is still unknown, on the northern Namib coast at sea level is not yet understood.

Broadley (1968: 18) lists three trends in *Typhlosaurus* Wiegmann (Acontinae), which imply degrees of evolutionary advancement or a greater degree of specialisa-

tion to a fossorial lifestyle. These might be applicable to *Typhlacontias* as well, nl. a) a reduction in the number of headshields, b) progressive attenuation of the body, and c) simultaneous increase in the number of ventrals. The latter trend in fossorial lizards is usually correlated with a reduction in tail length. All these changes are obviously related to greater specialisation as sand swimmers. Applying these parameters, *T. gracilis* with the most numerous headshields and long tail has retained with *T. rohani* a number of primitive characters, although the latter has started to reduce its tail length. *T. rudebecki* might rate as the most specialised or advanced in this group due to the amount of head scale reduction and the apparent attenuation of the severed body. Although primitive characters persist, limb loss (one cleared *T. gracilis* and three *T. rohani* checked), an advanced feature, is complete.

The Namib Desert endemics with the enlarged second lower labials, i.e. *T. brevipes*, *T. punctatissimus* and *T. johnsonii* show a similarly involved picture. *T. brevipes* with its externally visible limb rudiments and enlarged postnasal, which supposedly are retained ancestral characters, is the most primitive species in the eyes of Greer (1970: 15). However, some features appear to be specialised or advanced, such as the high number of ventrals, a relatively short tail and a wedge-shaped head with a reduced number of head scales. *T. punctatissimus* has retained a gracile body shape and a long tail similar to *T. gracilis* and *T. rohani* but, although it has a reduced number of head scales, internally it may still have minute femur and occasionally even externally visible limb rudiments. Within the three subspecies of this species small variations in the reduction of head scales exist.

T. johnsonii, with its high number of ventral scales, the relatively shortest tail, the most depressed wedge-shaped head and with the greatest reduction of head scales, is according to these criteria the most specialised or advanced taxon of this group and the genus.

To test these deliberations a data matrix for 14 characters was generated for the 8 recognised taxa with *Scelotes brevipes* as an outgroup (Tables 3 & 4). The phylogenetic systematics computer program Hennig86, version 1.5 (Farris 1988), was used to generate a phylogenetic hypothesis, expressed as a cladogram.

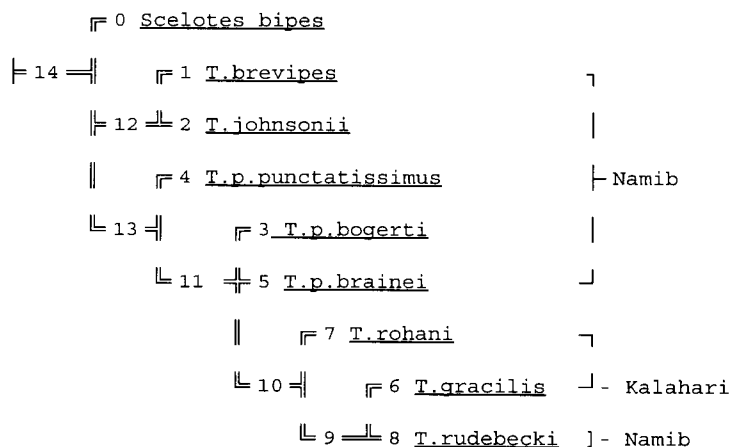


Table 3: Data list for *Typhlacontias* taxa and *Scelotes bipes* as outgroup.

1. Tail/SVL %	>50 % = 0, <50 % = 1, <40 % = 2, >30 % = 3.
2. Max SVL	<100 mm = 0, >100 mm = 1.
3. Ventrals	<125 = 0, <135 = 1, <145 = 2, >145 = 3.
4. Vertebrae	60–65 = 0, 65–70 = 1, 70–75 = 2, >75 = 3.
5. Enl.lab2	Absent = 0, present = 1.
6. Upl./eye	3 = 0, 2 = 1, 2 &/or 3 = 2.
7. Lor./upl.2	Contact = 0, no cont. = 1.
8. Supraocul.	3 = 0, 2 = 1, 1 = 2.
9. Hind limb	Ext. = 0, ext/int. = 1, absent = 2.
10. Prefrontal	Present = 0, absent = 1.
11. Rostr. sut.	Shrt & pstn = 0, Ing & pstn = 1, no pstn = 2.
12. Supoc/frnt.	3 = 0, 2 = 1, 0 = 2, 1&2 = 3, 1 = 4.
13. Supoc/eye	2 = 0, 1 = 1, 0 = 2.
14. Eye lid	Present = 0, absent = 1.

Table 4: Data matrix for eight *Typhlacontias* taxa and *Scelotes bipes* as outgroup.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>T. brevipes</i>	2	1	2	1	1	0	0	1	2	0	0	3	0	0
<i>T. johnsonii</i>	3	1	2	2	1	1	0	2	0	2	0	4	1	0
<i>T. p. bogerti</i>	0	0	0	0	1	2	0	1	1	1	1	3	1	0
<i>T. p. punctat.</i>	0	0	0	0	1	0	0	1	1	1	1	3	1	0
<i>T. p. brainei</i>	0	0	0	9	1	1	0	1	1	1	1	3	1	0
<i>T. gracilis</i>	0	0	1	1	0	0	0	0	0	2	1	0	0	0
<i>T. rohani</i>	0	0	1	0	0	1	1	1	0	2	1	2	0	0
<i>T. rudebecki</i>	9	0	3	9	0	1	0	1	9	2	1	1	0	0
<i>Scel. bipes</i>	3	0	0	0	0	0	0	0	2	0	0	3	2	1

A single tree (Length 30 steps, consistency index 0.67, retention index 0.62) was generated, confirming the basic clustering as viewed by the author.

T. brevipes, *T. johnsonii* and *T. puntatissimus* of the Namib Desert with the enlarged second lower labial, no prefrontal scales and leg rudiments in two taxa form the more ancestral group. *T. gracilis*, *T. rohani* from Kalahari sand and *T. rudebecki*, from the Namib coast, with normal-shaped lower labials, prefrontal scales, slender long-tailed bodies and no indication of limb rudiments, form an apparently more advanced group. In this context the status of *T. rudebecki* is slightly compromised, as that single tailless specimen could not be cleared, reducing its data content by three.

In addition the same data matrix was run using PAUP version 3.1.2d5 (Swofford 1985). PAUP generated two most parsimonious trees, 56 steps in length with a consistency index of 0.46. The measure of phylogenetic content in the data set as measured by the gl-statistic (=0.36) showed a significant phylogenetic signal. A strict consensus analysis of these two trees produced an unresolved trichotomy between *T. brevipes*, *T. johnsonii* and *T. rudebecki*. This situation lacks credibility and is probably due to the fact that the type specimen contributed three less data points to the matrix. A bootstrap analysis of the two trees indicated a 100 % frequency in all internal branches.

It seems essential to increase the data set for a thorough phylogenetic analysis, which is only possible once more material, in particular of *T. rudebecki*, becomes

available. Until such time the Hennig86 must serve as a preliminary hypothesis of phylogenetic relationships.

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Zusammenfassung

Typhlacontias ist eine der zahlreichen, sandwühlenden Skinkgattungen mit degenerierten Gliedmaßen. Die Verbreitung der sechs bekannten Arten ist auf die Namib-Wüste und das zentrale Kalahari-Becken des südlichen Afrikas begrenzt. Die Gattung wurde an Hand von zwei schlecht konservierten Exemplaren von Bocage (1873) beschrieben, so daß der Autor 1895 nach Erhalt eines dritten Exemplares von der Terra typica die Art nachbeschrieb. Letzteres Exemplar repräsentierte jedoch eine unbeschriebene Art, dazu mit abnormaler Beschuppung, wodurch die Art *T. punctatissimus* unidentifizierbar wurde. Die drei Exemplare wurden bei einem Brand zerstört. Als Andersson sieben weitere Exemplare vom selben Fundort bekam, erkannte er das Problem, revalidierte 1916 die Originalbeschreibung und beschrieb die Art *T. johnsonii* neu. Das einzige Exemplar in dieser Serie, das zu *T. punctatissimus* gestellt werden konnte, hatte sichtbare Beinrudimente, die bisher nur bei einem weiteren Exemplar der Art festgestellt werden konnten, weshalb es nicht als Neotypus geeignet ist. Anderssons Arbeit wurde leider bis jetzt völlig übersehen. Inzwischen wurde sehr viel neues Material gesammelt und neue Arten beschrieben, die aber erst nach dem Wiederauffinden von Anderssons (1916) Arbeit zugeordnet werden konnten. In der vorliegenden Arbeit werden dazu eine neue Art und Unterart beschrieben, die Verbreitung aller acht Taxa dokumentiert und ein Versuch gemacht, die verwandtschaftlichen Beziehungen in dieser Gattung zu verstehen.

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