



A review of the African red-flanked skinks of the *Lygosoma fernandi* (BURTON, 1836) species group (Squamata: Scincidae) and the role of climate change in their speciation.

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Abstract

We present an analysis of the morphometric and genetic variability of *Lygosoma fernandi*. Geographical variation and taxonomic consequences are discussed and *Lepidothyris* Cope, 1892 is resurrected as genus for the *L. fernandi* species group. The results show that *Lepidothyris fernandi* sensu lato is a species complex, which comprises an eastern and a western species. Each of them has a further subspecies of its own, and a third distinct species is present in southwestern Central Africa. The morphological and genetic differences between these taxa are analyzed resulting in the description of two new taxa, and the resurrection of two more taxa.

Key words. Squamata: Scincidae: *Tiliqua*, *Lygosoma*, *Riopa*, *Mochlus*, *Lepidothyris fernandi*, *Lepidothyris fernandi harlani*, *Lepidothyris striatus*, *Lepidothyris* sp. n., Africa, taxonomy, zoogeography

Introduction

Lygosoma fernandi was described as *Tiliqua fernandi* by Burton (1836) from the adjacency of Fernando Poo ('apud Fernando Po', type locality fide Burton [1836]) known today as Bioko Island, Equatorial Guinea. But soon it became clear that this African species had nothing to do with the true *Tiliqua* species that are restricted to the Papua–Australasian region. Thereafter, the species *fernandi* was alternately placed into several different genera by subsequent authors, e.g. Boulenger (1887) into *Lygosoma* Hardwicke & Gray, 1827 [with the type species *Lygosoma quadrupes* Linnaeus, 1766]; Cope (1892) into *Lepidothyris* Cope, 1892 [with the type species *Lepidothyris fernandi* Burton, 1836]; Bocage (1895) into *Lygosoma*; Mertens (1941) into *Riopa* Gray, 1839 [with the type species *Riopa punctata* Gmelin, 1799] and Mittleman (1952) into *Mochlus* Günther, 1864 [with the type species *Mochlus afer* Peters, 1854].

Mittleman (1952) was for many years the only author who tried a comprehensive revision of the scincid lizards and after he placed the species into the genus *Mochlus* Günther, 1864 he was followed by several authors e.g. Laurent (1964), Schmitz *et al.* (2000) and Veltum (2005). Mittleman (1952) differentiated the genus *Mochlus* from *Lygosoma* in having a well defined ear opening and from *Riopa* in lacking a transparent disc in the lower eyelid. At this time the genus *Mochlus* formed an endemic African genus with up to seven species assigned to it: *Mochlus afer* (type species of the genus), *M. brevicaudis*, *M. fernandi*, *M. guineensis*, *M. laeviceps*, *M. moquardi* and *M. sundevalli*. Broadley (1966) did not find any "clear divergence in adaptive trends" and therefore regarded *Mochlus* as a synonym of *Riopa*, placing all African *Mochlus* species back into the genus *Riopa*.

Greer (1977) tackled the systematics of the collective genus *Lygosoma* and came up with an even stricter view: because he found higher morphological similarities between *Lygosoma* and *Riopa* than between any of these two and other seemingly closely related genera (e.g. *Eumecia*, *Dasia*, *Lamprolepis*), he regarded both *Mochlus* and *Riopa* as synonyms of *Lygosoma* and accordingly placed *fernandi* back into the genus *Lygosoma*.

No further comprehensive revision of the relationships between the three genera has since been carried out, and modern research has often shown that species-rich skink genera with a very large distribution needed to be split into smaller taxonomic groups, often restricting them to specific biogeographical regions. Quite a few of these attempts have been convincingly proposed (e.g. *Mabuya* [Mausfeld *et al.* 2002; Mausfeld & Schmitz 2003]; *Eumeces* [Griffith *et al.* 2000, Schmitz *et al.* 2004], *Amphiglossus* [Schmitz *et al.* 2005a]; *Panaspis* [Schmitz *et al.* 2005b]) or are currently being reviewed (e.g. *Sphenomorphus*).

Lygosoma fernandi is often, probably wrongly, supposed to be a mostly dusk/dawn and nocturnal (Hauschild & Gaßner 1995; Laurent 1964) or partly nocturnal (Schmidt 1919) species which inhabits forest and woodland between 600 and 2100 m and it is proposed as a character species of the Guinea-Congolian forest belt with a disjunct distribution from Sierra Leone to Gabon and Kenya and from there to Angola and Zambia. Despite of this enormous distribution there exist no described subspecies until today. Therefore, it is the aim of the paper to find a directed geographic variation within the species.

Material and methods

The material examined was allocated to two groups from west and east Africa to analyse the differences between the populations. Localities for the distribution maps were taken from literature, from material of several scientific museum collections and from new material examined by us. For generating the distribution maps the program "Encarta Weltatlas 2000" was used.

As the holotype (respectively the iconotype) of *Tiliqua fernandi* is lost, topotypic material is part of the morphological analysis and a neotype is designated. Localities for the examined material are listed in the appendix in alphabetical order by country, (province if applicable) and locality, together with the acronyms of the holding institution and its respective catalogue number.

The following institutional acronyms were used: ANSP (Academy of Natural Science, Philadelphia, USA), IRSNB (Institut Royal des Sciences naturelles de Belgique; Brussels, Belgium); MCZ (Museum of comparative Zoology, Cambridge, USA); MHNG (Muséum d'histoire naturelle de la Ville de Genève, Geneva, Switzerland); MNHN (Muséum National d'Histoire Naturelle, Paris, France); NMK (National Museums of Kenya, Nairobi, Kenya); NMW (Naturhistorisches Museum, Wien, Austria); RM (Redpath Museum, Montreal, Canada); ZFMK (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany); ZMB (Museum für Naturkunde der Humboldt Universität, Berlin, Germany); ZMH (Zoologisches Museum der Universität Hamburg, Hamburg, Germany).

All measurements are in millimetres and were taken with digital callipers to the nearest of 0.01 mm. The following morphological and scalation characters were obtained from each specimen: SVL, snout–vent length; TAL, tail length; RTAL, relative tail length; HL, head length; HB, maximum head width; HH, maximum head height; EMB, number of scales around midbody; VE, number of ventral scales from inguinal region to the mental scale; SL, number of supralabial scales; IL, number of infralabial (sublabial) scales; ED, ear lobuli; LFF, number of lamellae under forth finger; LFT, number of lamellae under forth toe.

Other characters were obtained only for the type series: TAH, tail height at the base of tail; TAW, tail width at the base of tail; FOOT, foot length from heel to the tip of the longest toe, excluding the claw; HAND, hand length from wrist to the tip of the longest finger, excluding the claw; FINGER, length of the fourth finger from the joint of the hand to the tip, excluding the claw; TOE, length of the fourth toe from the joint of the foot to the tip, excluding the claw.

Excel 2000 and SPSS (10.0) statistical packages were used to run the analyses. Hierarchical Cluster analysis and Principal Component Analysis (PCA) have been selected to evaluate the pholidosis and morphometric data and to explore relationships between the populations examined.

Molecular data were collected to support our morphological findings within the *Lygosoma fernandi* species group and to evaluate the phylogenetic position of the species within the repository genus *Lygosoma* sensu lato. To assess our morphological data we sequenced a portion of the mitochondrial 16S rRNA gene for 3 of the 4 taxa identified in this paper (no usable DNA could be extracted from the specimens of one of the East African taxa) (GenBank accession numbers AY308265–AY308268). The primers 16sar–L (light chain; 5' – CGC CTG TTT ATC AAA AAC AT – 3') and 16sbr–H (heavy chain; 5' – CCG GTC TGA ACT CAG ATC ACG T – 3') of Palumbi *et al.* (1991) were used to amplify a section of the mitochondrial 16S ribosomal RNA gene. Additionally a section of the mitochondrial 12S ribosomal RNA gene was amplified using the primers 12SA–L (light chain; 5' – AAA CTG GGA TTA GAT ACC CCA CTA T – 3') and 12SB–H (heavy chain; 5' – GAG GGT GAC GGG CGG TGT GT – 3') of Kocher *et al.* (1989). DNA was extracted from the tissue samples using QiAmp tissue extraction kits (Qiagen) or a modified Chelex–Protocol (Walsh *et al.* 1991; Schmitz 2003). PCR cycling procedure followed Schmitz *et al.* (2005b). PCR products were purified using QIAquick purification kits (Qiagen). Sequences (including complimentary strands for assuring the accuracy of the sequences) were obtained using an automatic sequencer (ABI 377).

The obtained 23 combined sequences for the phylogenetic analysis (tab. 1) comprised 975 bp (16S: 560 bp; 12S: 415 bp; lengths referring to the aligned sequences including gaps). Six short sections (together 43 bp) (34 bp from the original 16S data set and 7 bp from the 12S data set) were too variable to be reliably aligned, and were omitted from the analysis. *Psammodromus algirus* (Lacertidae) was used as outgroup. Sequences were aligned using ClustalX (Thompson *et al.* 1997; default parameters) and manually checked using the original chromatograph data in the program BioEdit (Hall 1999). This program was also used to calculate the similarity of each sequence pair within the *Lygosoma fernandi*–group.

We used the Bayesian (PP) reconstruction method. All Bayesian analysis were performed with MrBayes, version 3.0b4 (Huelsenbeck & Ronquist 2001), which approximated posterior probabilities of trees. For the Bayesian analyses parameters of the model were estimated from the data set using MrModeltest 1.1b (Nylander 2002). The exact parameters used for the Bayesian analyses followed those described in detail by Reeder (2003) and Schmitz *et al.* (2005b). Clades with PP \geq 95% were considered strongly (significantly) supported.

Acronyms: CAS for California Academy of Sciences, San Francisco, USA; LSUMZ for Louisiana State University, Museum of Zoology, Louisiana, USA; RM for Redpath Museum, McGill University, Montreal, Canada; ZFMK for Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

TABLE 1. List of voucher specimens for each species included in the present study, with their respective localities, collection numbers and accession numbers (12S, 16S).

| Species | Locality | Collection number | Accession number |
|---------------------------------------|--|-----------------------|---------------------|
| <i>Psammodromus algirus</i> | Tanger, Cap Spartel, Morocco | GenBank | AF206588 / AF206588 |
| <i>Lepidothyris fernandi fernandi</i> | Mt. Nlonako, Cameroon | ZFMK 68959 | AY308417 / AY308265 |
| <i>Lepidothyris fernandi harlani</i> | Ghana | ZFMK, uncatalogued | AY308420 / AY308268 |
| <i>Lepidothyris hinkeli hinkeli</i> | S-Kivo: Irangi, Democratic Republic of Congo | ZFMK 58674 | AY308418 / AY308266 |
| <i>Lepidothyris hinkeli hinkeli</i> | Cymudongo / Nyungwe, Rwanda | ZFMK 55702 | AY308419 / AY308267 |
| <i>Lepidothyris striatus</i> | 3.7 km SE Boukoulibouali, PR Congo | RM 4671 | - / FJ807720 |
| <i>Lygosoma bowringii</i> | Thailand | GenBank | AB028775 / AB028786 |
| <i>Lygosoma koratense</i> | Malaysia | ZFMK 71715 | AY308421 / AY308269 |
| <i>Lygosoma koratense</i> | Thailand | GenBank | AB028805 / AB028817 |
| <i>Lygosoma lineolatum</i> | Rakhine State: Gwa Township, Myanmar | CAS 206647 | AY308422 / AY308270 |
| <i>Lygosoma lineolatum</i> | Mandalay Div.: Popa Mountain Park, Myanmar | CAS 210669 | AY308423 / AY308271 |
| <i>Lygosoma quadrupes</i> | Thailand | GenBank | AB028806 / AB028818 |
| <i>Lygosoma</i> sp. nov. | Pondok Sari, Permuteran, Bali, Indonesia | ZFMK 77822 | AY308415 / AY308263 |
| <i>Mochlus</i> sp. | Rift Valley Prov.: Kajiado Dist.: Elangata W.P., Kenya | CAS 198936 | AY308425 / AY308273 |
| <i>Mochlus afer</i> (I) | Kiyewetanga, Kenya | ZFMK 54317 | AY308412 / AY308261 |
| <i>Mochlus</i> sp. | Mombasa, Kenya | voucher not collected | AY308426 / AY308274 |
| <i>Mochlus sundevalli</i> (I) | Ke, Watamu, J. Ashe Farm, Kenya | ZFMK 77825 | AY308427 / AY308275 |
| <i>Mochlus sundevalli</i> (II) | Ke, Watamu, J. Ashe Farm, Kenya | ZFMK 77826 | AY308428 / AY308276 |
| <i>Mochlus sundevalli</i> (III) | Ke, Watamu, J. Ashe Farm, Kenya | ZFMK 32744 | AY308429 / AY308277 |
| <i>Mochlus sundevalli</i> (IV) | Ke, Watamu, J. Ashe Farm, Kenya | ZFMK 77827 | AY308430 / AY308278 |
| <i>Mochlus sundevalli</i> (V) | Ke, Watamu, J. Ashe Farm, Kenya | ZFMK 77828 | AY308431 / AY308279 |
| <i>Mochlus</i> cf. <i>sundevalli</i> | Katesh, Tanzania | ZFMK 77823 | AY308416 / AY308264 |
| <i>Riopa</i> cf. <i>albopunctatus</i> | near Ajur, Peryar-Trivandrum, India | ZFMK 73430 | AY308414 / AY308262 |
| <i>Riopa</i> sp. | Ooty-Bandypur, India | ZFMK 77814 | AY308424 / AY308272 |

Results

The partition homogeneity test for the combined 16S and 12S rRNA genes failed to detect significant incongruence between the two data sets ($P = 1 - (569/1000) = 0.431000$), suggesting that the two mtDNA fragments could be combined.

The comparison between the different likelihood scores for each model showed that the GTR + I + Γ model (Yang 1994) was determined to be the optimal model for the combined data set. This model incorporates unequal base frequencies [$\pi_{(A)} = 0.35080$, $\pi_{(T)} = 0.21860$, $\pi_{(C)} = 0.25350$, $\pi_{(G)} = 0.17710$], a proportion of invariable sites ($I = 0.4293$), and a gamma distribution shape parameter ($\alpha = 0.3952$).

In the resulting tree the included *Lygosoma fernandi* species group vouchers are placed together in an optimally supported monophyletic grouping (PP: 1.0). Furthermore, an obvious subdivision that is also supported by strong bootstrap values is seen: the eastern vouchers are placed together (PP: 1.0) and the western vouchers also form a strongly supported direct sister group in the analysis.

They are therefore not part of the same clade as *Lygosoma quadrupes* (the type species of the genus *Lygosoma* sensu stricto) which is placed as sister species to *L. koratense* (PP: 1.0) in the analyses. In the resulting tree this monophyletic clade is shown to be part of a group together with all other species excluding the taxa of the ‘*Mochlus*’ clade as well as *Lygosoma* sp. n. and *Lygosoma bowringi*.

Also all true *M. sundevalli* vouchers are placed together with *Mochlus afer* (which is the type species of the genus *Mochlus*) into a fully supported monophyletic group (PP: 1.0). Again it becomes clear that the taxa of the *fernandi*-clade are not part of this *Mochlus*-clade.

Within the monophyletic *fernandi*-clade the comparisons show a definite genetic differentiation between the specimens from East- and West-Africa. While the differences in-between the western and eastern localities differ on a comparatively low level (2.5 % and 1.9 %, respectively), there are pronounced differences between East and West African populations (3.5–5.2 %).

Resurrection of *Lepidothyris* Cope, 1892. The original description of *Lepidothyris* by Cope (1892) is within a key of scincid genera without determining a type species. In accordance to Opinion 46 of the ICZN (1999), *L. fernandi* is the type species of this genus, because Cope (1900) eight years later first associated this taxon with *Lepidothyris* and so it became *ipso facto* the type by this subsequent designation. As also the genetic analyses support different monophyletic clades, we follow this principal concept of the revision of Mittleman (1952) who differentiated the genera *Mochlus* and *Riopa* from *Lygosoma*. From these genera *Lepidothyris* differs as follows: from *Riopa* in having the lower eyelid scaly and lacking a transparent disc; from *Lygosoma* in ear opening present, tympanum visible; and from *Mochlus* in having strong and stout limbs instead partly reduced or very short limbs.

Regarding these results based on morphological and molecular aspects (comp. fig. 1) it becomes clear that the African species currently referred to ‘*Lygosoma*’ are different from true *Lygosoma* with its South-East Asian type species *Lygosoma quadrupes*. The African taxa show enough adaptive trends between the African and Asian clades that it is necessary to separate them from the Asian *Lygosoma* in African genera of their own. As the herein revised species group is distinct from the genera *Mochlus*, *Riopa* and *Lygosoma* in aspects of morphology, body proportions, habitats and behaviour, we revert back to the concept of Cope (1892) and regard the taxa of the *fernandi* species group as members of the African endemic genus *Lepidothyris* Cope, 1892.

Diagnosis of the genus *Lepidothyris* Cope, 1892. Nostril pierced in the nasal; palatine bones in contact on the median line of the palate; ear opening present, tympanum more or less deeply sunk, not concealed and visible; pterygoids in contact medially, the palatal notch not extending anteriorly to between the centre of the eyes; eyelids moveable, lower eyelid scaly; digits with non-retractile claws; supranasal plates present; two frontoparietal scales; limbs strong but stout.

From the other related genera *Lepidothyris* differs as follows:

from *Lygosoma* in having the ear opening present; and the tympanum visible;

from *Riopa* in having a lower scaly eyelid; and in lacking a transparent disc;

from *Mochlus* in having strong and stout limbs; instead partly reduced or very short limbs.

Morphological data. Significant differences in morphology were found between the western, eastern and southern populations. But also within the eastern and western populations differences which merit recognition

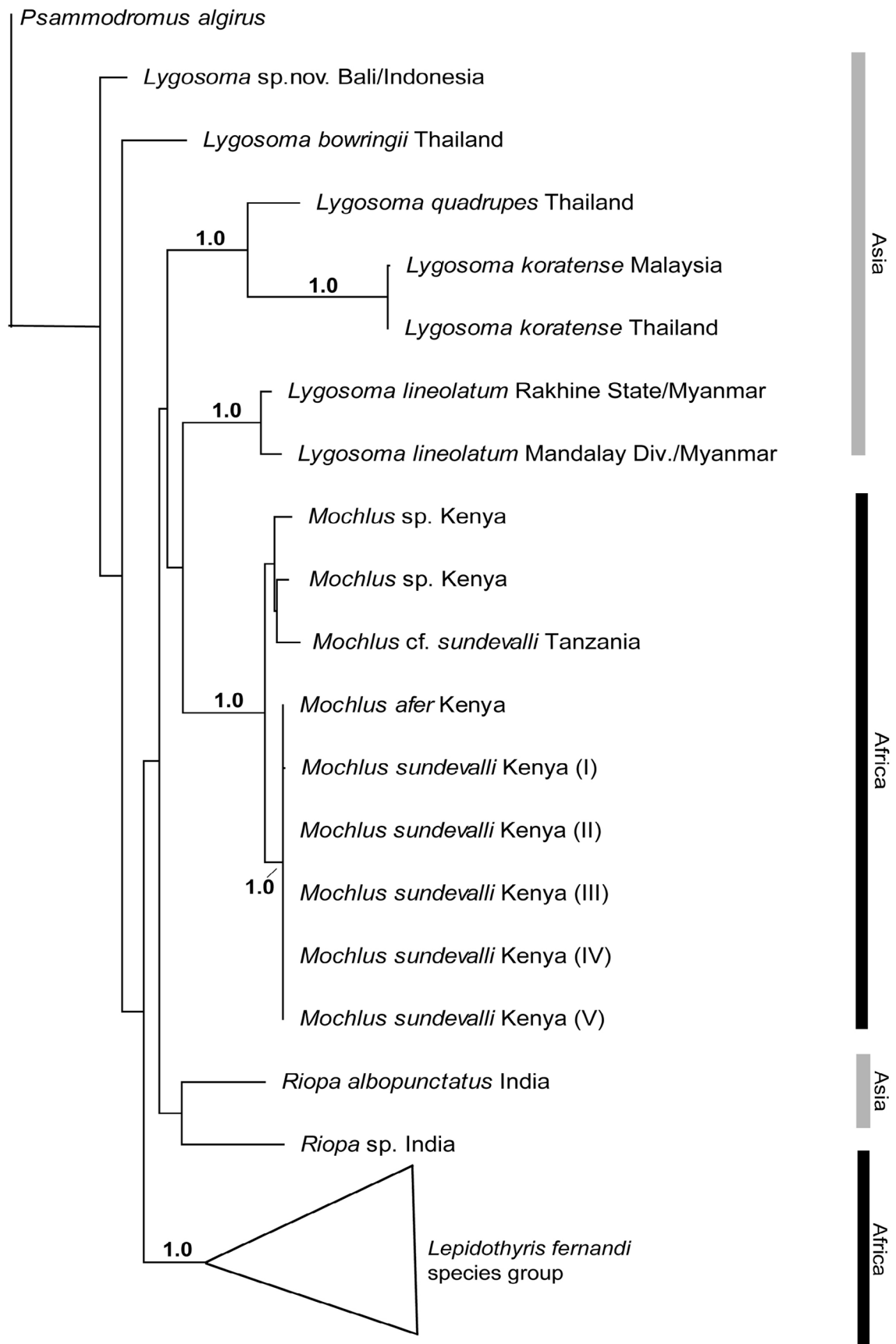


FIGURE 1. Cladogram of the Bayesian tree based on 975 bp of the combined mitochondrial 16S and 12S ribosomal RNA gene sequences. Values at the nodes are Bayesian posterior probabilities (values below 0.5 not shown).

on the subspecific level were recognized. The eastern and western species differ in pholidosis and colour pattern. Contrary to the nominate form the eastern specimens have visible ear digits and lower scale counts around midbody (see key to the species). They are easy to distinguish by their colouration. The western ‘nominate’ population has a white throat with dark stripes and lateral stripes not extending to the back. Eastern specimens have fully white throats and, apart from the new eastern subspecies, lateral stripes extending to the back. Both of these two recognized species are divided into different subspecies. Both not–nominate subspecies show the same differentiation in the colour pattern: they have a uniform coloured back instead of a black–red brown speckled one in the nominate form and a red–brown ground coloured with pale stripes in the eastern populations.

Additionally the specimens from populations in central and southwestern Africa show significant differences to both of the above mentioned eastern and western populations.

Therefore, also regarding the support from the genetical results (fig. 1), we herewith recognize three separate species (two of them with subspecies of their own) as follows:

***Lepidothyris fernandi fernandi* (Burton, 1836)**

1836 *Tiliqua fernandi* Burton, Proc. Zool. Soc. London 1836: 62. Type locality: Fernando Poo (today Bioko Island, Equatorial Guinea).

1895 *Lygosoma* nov. sp. Barboza du Bocage, J. Sci. math. phys. nat. Lisboa, 3: 272.

Lepidothyris fernandi was described by Burton (1836) as *Tiliqua fernandi* in the Proceedings of the Zoological Society of London as part of the report of William Yarell, Vice–President of the Society at this time. It is mentioned there, that a drawing ‘of a Saurian Reptile of the family Scincidae and of the genus *Tiliqua*, Gray’ was exhibited and ‘which forms part of the Museum of the Army Medical Department at Chatham, and which is regarded by Mr. Burton, Staff–Surgeon, in charge of the museum, as hitherto undescribed’. The thereupon following description and especially the description of the colouration refers to *Lepidothyris fernandi*: ‘Head, back, tail and upper surface of the extremities reddish brown, a blackish line intersecting each row of scales; sides lighter, marked by a series of irregular blackish streaks; belly and under surface of tail a brownish white; throat alternated longitudinally with light and dark–brown lines; submental scales whitish, bordered with a broad dark–brown edge.’

The Army Medical Department was based at Fort Pitt. We are sure that any possibly existing iconotype (see below) is lost because of the unstable history of this Fort which eventually even led to its complete destruction: the Fort was build between 1805 and 1819 on the high ground of the boundary between Chatham and Rochester in Kent, Great Britain. Later on, it became a hospital for invalid soldiers, with an asylum added in 1849. In 1860, the first Army Medical School was founded there by the great Florence Nightingale. The Fort was closed in 1920 and converted into a girls’ school but today nothing is visible of the original Fort. Nevertheless, the Fort had a close relation to African herpetology. Sir Andrew Smith, an authority on South African herpetology, and founder of the South African Museum, was stationed in South Africa from 1821 to 1837 (Adler 1989) and became a principal medical officer at Fort Pitt in 1837. Later he was the deputy inspector–general in 1845 and the director–general of the Army Medical Department from 1853 to 1858. Therefore it is not remarkable that a Medical Department had drawings and/or specimens of African reptiles. Smith had taken his collection of specimens and drawings with him to England to continue his work in England. Later on, his reptilian types were given to the collection of the natural history museums in Edinburgh and London (Adler 1989). But today the holotype is neither hosted in the collection of the British Museum in London (pers. comm. C. McCarthy) nor in the Royal Scottish Museum in Edinburgh (Herman *et al.* 1990).

The Army Medical Museum and its collections have moved to Netley in 1863 to the new Royal Victoria Army Hospital. This hospital was in use until the 1970s, but there was a lot of destruction by fire and water damage and later on the whole building was destroyed (pers. comm. A. Bauer). It is to assume that Burton

(1836) based his description of *Tiliqua fernandi* on a drawing rather than on a real holotype, making it an iconotype. Whatever the case, any possible types are very likely destroyed and therefore herein we designate a neotype of *Tiliqua fernandi* Burton, 1836 from the originally mentioned type locality, preserved in the collection of the Zoologisches Forschungsmuseum A. Koenig in Bonn, Germany and collected by Martin Eisentraut, a former director of the museum. The adult specimen was collected at a cacao plantation near San Carlos (Mertens 1964).

Neotype ZFMK 9362 San Carlos, Fernando Poo (today Bioko Island), Equatorial Guinea, leg. M. Eisentraut, 15.X.1962 (Fig. 2).

Diagnosis: *Lepidothyris fernandi fernandi* is a large skink, with a short but wide head and a rounded snout; eye relatively large with a round pupil; ear opening more or less oval and well visible, without lobuli; body stout and subcylindrical; four limbs, relatively short but strong, with five thin toes; tail just as stout as the body, about half of the total length and tapering smoothly, and despite its apparent stoutness easy to autotomize; body scales strongly keeled, with three keels on the dorsal scales up to five keels on the lateral scales; there are between 31 and 34 scale rows around midbody.

Colouration. Vividly red and black, above with darker shades because every scale is framed dark; lateral side of the head, between ear opening and forelimb, shows one to three brighter blotches, separated by darker lines or bars; flanks ground coloured red to orange, with irregular black V-shaped bars and blotches and speckled with white, yellow and blue; tail ground coloured black, speckled white in adult, in juveniles and subadults speckled or banded blue; no sexual dimorphism in colouration.

Size. Angel *et al.* (1954) gave a maximum total size of 420.0 mm. The maximum total size given by Spawls *et al.* (2002) is about 380.0 mm, with an average between 250.0 and 330.0 mm. But it is likely that this is a reference to the east African population, which is recognized as a new species in this publication. The maximum snout–vent length of the analysed specimens is 161.2 mm, average is 141.1 mm. Females are smaller than males (Dunger 1973).

Description of the Neotype: Snout–vent length: 142.2 mm; tail reduced, 130.6 mm; head length 27.3 mm; head wide 23.7 mm; head height 18.2 mm. Body stout, subcylindrical; there are 31 scales around the body and 57 scales longitudinal ventral scales; limbs short and strong with five toes, dark above, light brown-beige below; 4th fingers with eleven digits on both sides, 4th toe with 13 digits on both sides; ear opening oval, well visible, without ear lobules, its height ca. $\frac{1}{2}$ of the width of the eye opening, vertically higher than broad, tympanum visible only on the right side; lower eyelid with two scale rows; dorsal body scales keeled with two to three keels; dorsal tail scales moderately triple-keeled; lateral body scales and scales on the tail smooth; head distinctly set off from body; size of eye opening $\frac{3}{4}$ the length of the distance from the posterior edge of the eye to the ear opening; distance from tip of snout to anterior edge of eye as long as the distance from posterior edge of eye to ear; occipital scale lacking; no parietal organ visible; frontal scale twice as long as broad; two frontoparietal scales at the anterior side of the frontal scale; one frontonasal scale; two internasal scales; rostral scale broader than high; two nasal scales of equal size, nostril between the nasal scales; two loreal scales, anterior higher than the posterior on the right side, posterior very small on the left side; two preocular scales; four supraocular and seven supraciliar scales; eight supralabial and eight sublabial scales on each side; mental scale broader than high; three pairs of submaxillary scales, the first one is entire.

Colouration. Head and back red to red–brown; on the back every scale is bordered dark, leaving a dorsal surface with uniform dark rows of pentagons; supralabial scales red, bordered black posteriorly; mental scale red, sublabial scales black with a white dot in each scale; colouration of the lateral sides of the body mainly dark especially between ear opening and forelimb, between the limbs black and red stripes are visible, most scales with white dots; lateral side of tail lined horizontally white and black, where the white lines are made up of black scales with white dots; belly dirty white to brownish; scales on the throat dark with a white dot, leaving the surface of the throat with uniform black and white longitudinal lines.

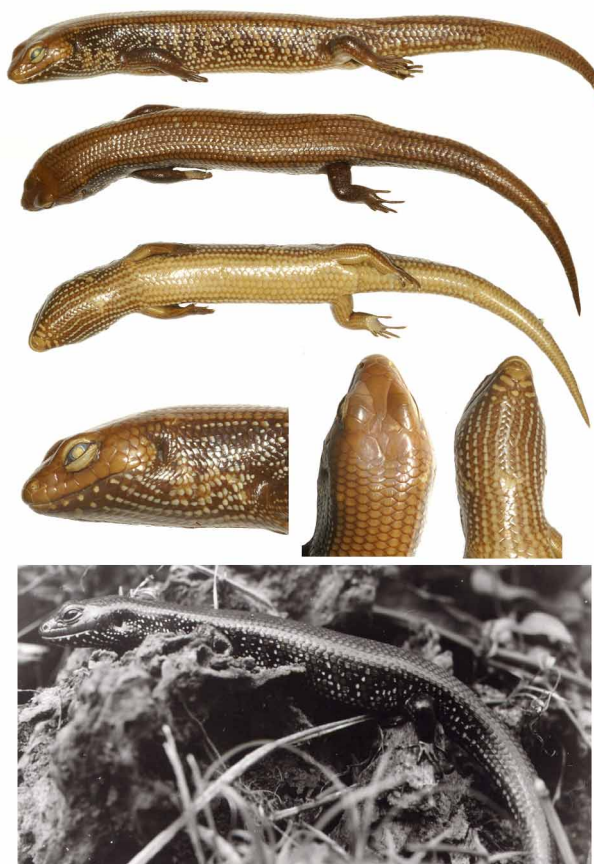


FIGURE 2. Neotype of *Tiliqua fernandi* Burton, 1836 from Bioko Island, Equatorial Guinea (ZFMK 9362).

Lepidothyris fernandi harlani (Hallowell, 1844)

1844 *Plestiodon harlani* Hallowell, Proc. Acad. Nat. Sci. Phila., p. 170. Type locality: Liberia.

1885 *Tiliqua nigripes* Müller, Verh. Ges. Basel, VII, p. 704. Type locality: Gold Coast.

This taxon was described by Hallowell (1844) from Liberia and later regarded as a synonym of *L. fernandi* by several authors (e.g. Boulenger 1887; Schmidt 1919; Taylor & Weyer 1958). We found differences in colouration, scale counts and genetics and regard it as a valid subspecies of *L. fernandi*.

Diagnosis: Differs from the nominat form in having more scales around midbody, invariably 34 instead of 31 to 34; head only sparsely set off from body, shorter than in nominate form; and in the very different colouration.

Colouration. Head and back red–brown to orange; colour changing in the first third of the tail to brown; supralabial scales red–orange, sublabial scales black with a white dot on each scale; lateral body colouration between ear opening and forelegs dark without visible bars; in average, nine to ten dark bars between the limbs on the lateral sides of the body (instead of more than ten in *L. fernandi fernandi*), some of them ‘V’-shaped, on a red ground colour; dorsum is vividly red to red–orange, without darker shades; throat more or less dark striated, always lighter than in the nominat form; belly also with darker lines but always lighter than in *L. fernandi fernandi*; ventral part of the tail creamish white with light black lines, lateral side of tail mottled white and black.

Size. The maximum snout–vent length of the analysed specimens is 154.0 mm, average is 122.8 mm.

Remarks. The species was named by Hallowell after his contemporary Dr. Harlan. The types were collected by the Dr. Goheen expedition and were put in the possession of Mr. J. J. Haldemann, Esq. of Columbia, Pennsylvania.



FIGURE 3. *Lepidotyphris fernandi harlani* from Ghana. Photo by Wolfgang Böhme.

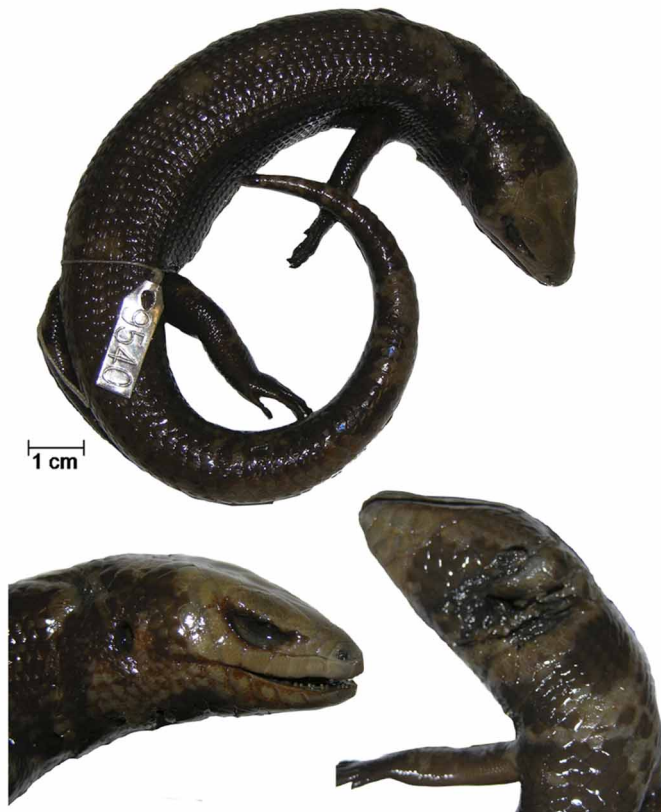


FIGURE 4. Holotype of *Lepidothyris fernandi harlani* (HALLOWELL, 1844).



FIGURE 5. *Lepidothyris fernandi harlani* from Ghana (without detailed locality). Photo by Philipp Wagner.

***Lepidothyris hinkeli* sp. n.**

Holotype: ZFMK 55701 Cyamudongo, Nyungwe, Rwanda, leg. Paçome & H. Hinkel (Fig. 7).

Paratopotype: ZFMK 55702 same locality as holotype, patata field next to primary forest, subadult, leg. H. Hinkel, 15.–20. XI 1990.

Paratypes: ZFMK 55704 South Kivu, Station Irangi, DR Congo.

ZFMK 58674 South Kivu, Station Irangi, DR Congo, leg. H. Hinkel.

MHNG 2699.51 South Kivu, Station Irangi, DR Congo, leg. H. Hinkel.

ZFMK 50354 South Kivu, Station Irangi, Dem. Rep. Congo, juvenile, leg. H. Hinkel.

IRSNB 2643 Musosa, District Tanganyika, Congo Belge (=DR Congo), leg. H.J. Bredo, 1939.

Diagnosis: The new species is distinguishable from *L. fernandi* by different aspects of morphology and colouration: *L. hinkeli* sp. n. is smaller in size than its sister taxon from West Africa; unlike *L. fernandi* the new species has small but distinct ear lobuli; there are between 34 and 38 scale rows around midbody, which is much higher than in *L. fernandi* with 31 to 34 rows; number of longitudinal ventral scales also higher (61 to 77) than in *L. fernandi* with 56 to 67 scales.

Colouration. Throat and belly white, without any markings; light patches, framed dark, on the sides of the head between ear opening and forelimb, the dark framing is lacking at the lower border of the typical black patch; laterally between the limbs there are seven to nine dark stripes reaching the dorsal side of the body.

Size. The maximum snout–vent length of the analysed specimens is 145.0 mm, average is 115.3 mm.



FIGURE 6. *Lepidothyris hinkeli hinkeli* from Ituri Forest, DR Congo. Photo by Reto Kuster.

Description of Holotype: Snout–vent length: 143.9 mm, tail is broken behind 46.5 mm, head length 30.2 mm, head wide 23.2 mm, head height 17.7 mm. Body stout, sub–cylindrical; there are 34 scales around the body and 67 scales longitudinal ventral scales; limbs short and strong with five toes, dark above, light below; 4th fingers with twelve digits on the right and eleven on the left side, 4th toe with nine digits on both sides; ear opening, well visible, oval, with two small ear lobules, little less in diameter than the half of the width of the eye opening, little less broad than high, tympanum visible; lower eyelid with two scale rows; dorsal body

scales moderately keeled with three, sometimes four keels; dorsal tail scales moderately triple-keeled to smooth; lateral body scales and tail scales smooth; head distinctly set off from body; size of eye opening half the length of the distance from the posterior edge of the eye to the ear opening; distance of tip of snout from anterior edge of eye a little shorter than the distance from posterior edge of eye to ear; occipital scale lacking; parietal organ set in the posterior edge of the interparietal scale; frontal scale twice as long as broad; two frontoparietal scales at the anterior side of the frontal scale; two frontonasals instead of only one in the paratype series; two internasal scales; rostral scale broader than high; two nasal scales, nostril inside the postnasal scale, the anterior nasal scale smaller than the postnasal scale; two loreal scales, the anterior higher than the posterior; two preocular scales; four supraocular and seven supraciliary scales; eight supralabial scales on each side; eight sublabials on the right, seven on the left side; mental scale broader than high; three pairs of submaxillary scales, the first one is entire.

Colouration. Head and back red to red-brown; on the back lateral black bars are visible, the last two before the hindlimb continue across the back; supralabial scales red; first two sublabial scales red, the following white with a black dot in each scale; colouration of the lateral sides of the body between ear opening and forelimb with a dominant red spot, which is framed by a white line which is itself again bordered by a wider black line above and behind. The red spot is subdivided by one vertical broken black, white framed line; between the limbs nine black bars which are white framed, some of which V-shaped, on a red ground colour; lateral side of tail lined with white and black bars; belly and throat white without any stripes.



FIGURE 7. Holotype of *Lepidothyris hinkeli hinkeli* sp. n.

Variation of paratypes: The paratypes agree generally well with the given description of the holotype. All of them have, contrary to the holotype, only one frontonasal scale. Some of them show a black line from the end of the jaw straight downwards. Juveniles (ZFMK 50354, 55704) show the typical reddish colouration

only on the back and the head; between the lateral black bars they are white in colour. The lateral bars continue across the back. The tail is striated black and blue, black is dominant. The two subadult individuals (MHNG 2699.51, ZFMK 55702) show mostly the typical characteristics of the holotype; the bars on the back are more distinctly visible and the tail shows more blue than in adult specimens. The only adult paratype (ZFMK 58674) shows the typical characteristics of the holotype.

Etymology: We dedicate the new species to Dr. Harald Hinkel, the collector of the type specimen, in admission of his work on the herpetology of the eastern Congo and Rwanda.

***Lepidothyris hinkeli joei* ssp. n.**

Holotype: ZFMK 64410 Oyo, Bokouélé, Peoples Rep. Congo, leg. E. Fischer & H. Hinkel, 1993.

Paratypes: MNHG 2539.71 Kasai–Occidental, Dekese, Dem. Rep. Congo, leg. S. Battoni, 1959.

IRSNB 2644 Yangambi, Distr. Stanleyville, Congo Belge (=DR Congo), leg. G. Gilert, 18.IV.1946

IRSNB 2645 Ibembo (forêt), Uele, Congo Belge (=DR Congo), leg. H. Siméons, 20.II.1940.

IRSNB 2646 Ibembo (forêt), Uele, Congo Belge (=DR Congo), leg. H. Siméons, 20.II.1940.

Diagnosis: The new subspecies differs from the nominotypic form in having a monochromatic back, without lateral bars continuing on the back. Lateral bars in most cases smaller and lower in number than in the nominate form, not bordered with white dots; lower lip is lighter than in *L. hinkeli hinkeli* and without any black markings on the first sublabial scales; body scales in most cases stronger keeled than in the nominate form.

Colouration. Throat and belly white, without any markings; dark framed light patches on the sides of the head between ear opening and forelimb, dark framing is lacking towards ventrally; laterally between the limbs there are eight to eleven dark stripes, not reaching the dorsal side of the body.

Size. The maximum snout–vent length of the analysed specimens is 146.0 mm, average is 115.5 mm.



Fig. 24 — *Mochlus fernandi*, exemplaire de Dundo (Ang. 6122). A: montrant l'ornementation latérale; B: glissant dans l'herbe (Photo A. de B. MACHADO).

FIGURE 8. *Lepidothyris hinkeli joei*, original published in LAURENT (1964).

Description of Holotype: Snout–vent length: 111.9 mm, tail is broken behind 38.9 mm, head length 23.4 mm, head wide 15.2 mm, head height 10.8 mm. Body stout, sub-cylindrical; there are 36 scales around the body and 65 longitudinal ventral scales; limbs short and strong with five toes, dark above, light below; 4th fingers with eleven digits on both sides, 4th toes with 15 digits on the left and 16 digits on the right side; ear opening visible, oval to round, with two small ear lobules, little less in diameter than half of the length of the

eye opening, little less broad than high, tympanum visible; lower eyelid with two scale rows; dorsal body scales moderately keeled with three keels; lateral body scales smooth to moderately keeled with three small keels; dorsal tail scales moderately keeled to smooth with three keels, lateral tail scales relatively smooth with three keels; head not distinctly set off from body; eye opening as long as the distance between the posterior edge of the eye to the ear opening; distance from tip of snout to anterior edge of eye little shorter than distance from posterior edge of eye to ear; occipital scale lacking; parietal organ set in the posterior edge of the interparietal scale; frontal scale a bit longer than broad; two frontoparietal and prefrontal scales at the anterior side of the frontal scale; one frontonasal scale; two internasal scales; rostral scale broader than high; two nasal scales equal in size, nostril in the middle of the scales; two loreal scales, equal in size; two preocular scales; four supraocular scales; eight supralabial and sublabial scales on each side; mental scale broader than high; three pairs of submaxillary scales, the first one is entire.

Colouration. Head and back red to red-brown; on the back no darker bars visible; supralabial and sublabial scales the same colour as the head; lateral body colouration between ear opening and forelimb light, framed by a darker undulate bar on the upper side from ear opening to the forelimb; ground colour of the lateral body sides is red to red-brown, contrary to the paratype series only a few dark bars are visible between the limbs (artefact due to preservation); incomplete tail light red to red-brown, also an artefact due to preservation, without any markings or darker bars; belly and throat whitish to reddish, without any stripes.



FIGURE 9. Holotype of *Lepidothyris hinkeli joei*.

Variation of paratypes: The paratype series agrees in morphology with the given description of the holotype. They differ slightly in aspects of the colouration: 8 to 11 small to medium sized black stripes on the lateral body sides, stripes not bordered with dots; the not autotomized tails have broader lateral stripes than the body, stripes cross the ventral part of the tail; incomplete tail diffuse black and red.

Etymology: We dedicate the new subspecies to Dr. Rüdiger (Joe) Wagner, the father of the senior author, to acknowledge his valuable work over many years.



FIGURE 10. Syntype (ANSP 9535) of *Lepidothyris striatus* (HALLOWELL, 1854).

Lepidothyris striatus (Hallowell, 1854)

1854 *Euprepis striatus* Hallowell, Proc. Acad. Nat. Sci. Phila., p. 98. Type locality: „Liberia“ (sic; corrected by Hallowell (1860) to Gabon).

1883 *Euprepes (Tiliqua) elegans* Fischer, Jahresber. Naturhist. Mus. Hamb. 1–16, fig. i–xv. Type locality: Sierra Leone.

1884 *Euprepes leoninus* Fischer, Abh. Geb. Naturw., 8 (2): 43–51. Type locality: Sierra Leone.

Syntype: ANSP 9535 Gabon, leg. Ford, 1854

Syntype: ANSP 9536 Gabon, leg. Ford, 1854

Diagnosis: *L. striatus* is distinguishable from the other taxa of the genus *Lepidothyris* by different aspects in morphology and colouration:

L. hinkeli is smaller in size and also has an ear opening with two lobule scales. *L. hinkeli* has 34 to 38 scale rows around midbody instead of 32 to 35 in *L. striatus*; longitudinal ventral scales differs from 61 to 77 in *L. hinkeli* instead of 57 to 67 in *L. striatus*, colouration of the throat is speckled black instead of the pure white throat of *L. hinkeli*.

L. fernandi has the same size but lobule scales as in *L. striatus* are lacking. *L. fernandi* has 31 to 34 scales rows around midbody and 56 to 67 longitudinal ventral scales.

Colouration. Both taxa differ in colouration from *L. striatus*: both have distinct lateral dark bars and stripes, which are lacking in *L. striatus*, who is speckled black, red and white. The belly of both *L. hinkeli* and

L. striatus is white, and only more or less white in *L. fernandi*, who shows consistently pale red stripes; *L. fernandi* and *L. striatus* have a throat speckled with darker spots, *L. hinkeli* has a pure white throat.

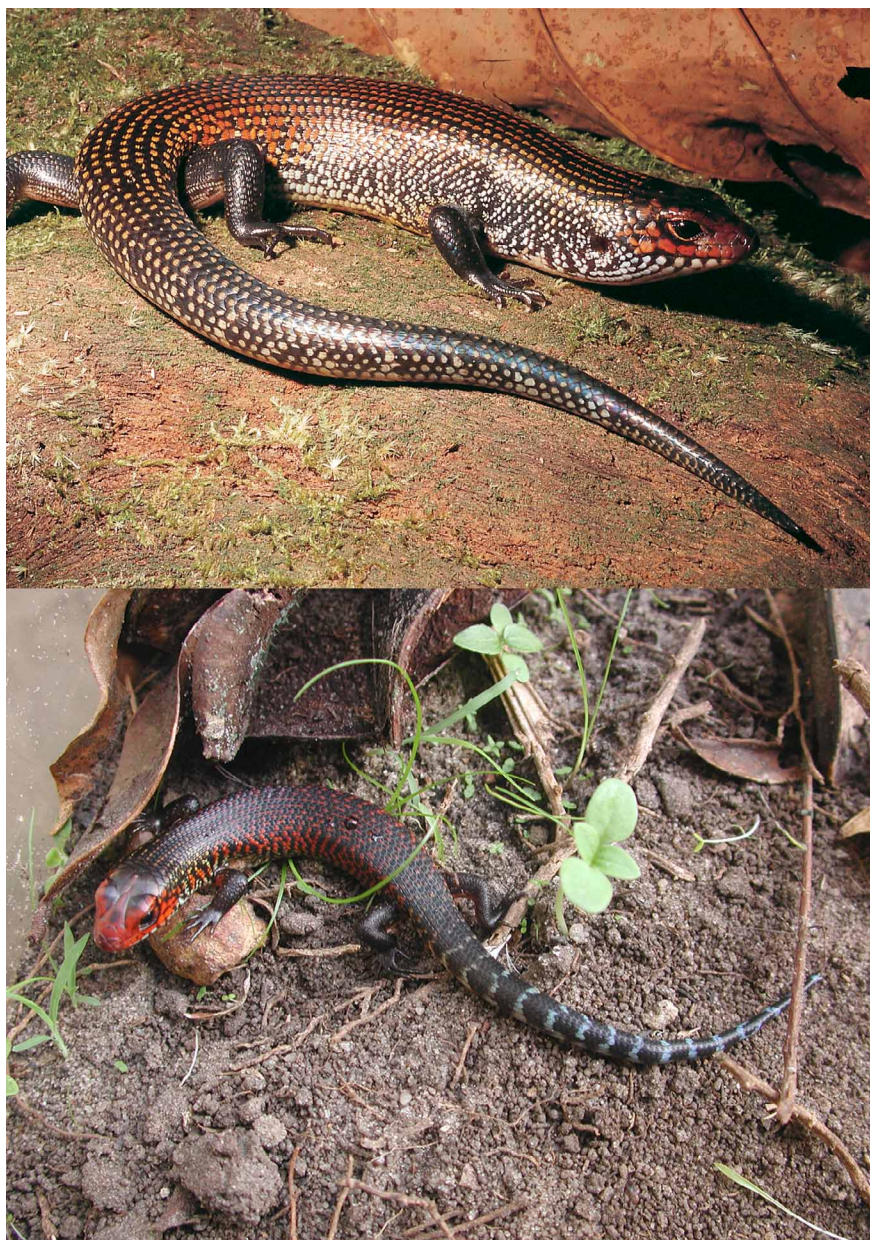


FIGURE 11. *Lepidothyris striatus*, above an adult specimen from Gamba region, Gabon, Photo by W. Branch; below a juvenile specimen from Gamba, Ogooué–Maritime Province, southwestern Gabon, Photo by E. Tobi.

L. striatus has the following combination of characters: body long and bulky; head short but high and bulky, not well set off against the body, scales on head smooth; nostrils positioned laterally; ear opening with two lobule scales; dorsal scales with three strong keels, lateral scales weaker keeled with three keels, ventral scales smooth; limbs are short but strong; tail strong and not compressed, tail scales with three keels.

Colouration in life: dorsal and lateral parts of the body speckled red, black and white, front part of the body and lateral sides of the head predominantly red, lateral parts of the body and tail predominantly black in colour; upper side of the extremities dark red to black, underside white to cream; belly ground coloured white to cream with chestnut brown to dark red pale stripes on the throat.

Size. In average *L. striatus* reaches a SVL of 155.6 with a maximum of 166.5 and a minimum of 137.0 mm.

Key to the species and subspecies:

- 1 Throat and belly white; sublabial scales white with a black dot in each scale 2
- Throat dark, belly white or with darker lines; sublabial scales black with a white dot in each scale. 3
- 2 Blackish to dark red above, with stripes; lateral body stripes framed with white dots; sublabial scales ground coloured reddish to white, black on the upper parts *L. hinkeli hinkeli*
- Brownish-yellowish above, without stripes on the back; sublabial scales reddish to white without black dots, lateral body stripes not surrounded with white dots *L. hinkeli joei*
- 3 With lateral stripes; no ear lobules..... 4
- Without lateral stripes; ear lobules present *L. striatus*
- 4 Black, brownish-yellowish above; 31 to 34 scales around midbody, throat darker than in *L. f. harlani*..... *L. fernandi fernandi*
- Brownish-yellowish above; 34 scales around midbody, throat and belly lighter as in nominate form; between ear opening and forelimb black without brighter blotches *L. fernandi harlani*

TABLE 2. Comparison of the pholidosis of the species of the genus *Lepidothyris*. For details see Material & Methods

| | <i>L. striatus</i> | <i>L.f. fernandi</i> | <i>L. f. harlani</i> | <i>L. h. hinkeli</i> | <i>L. h. joei</i> |
|------|-----------------------------|-------------------------------|-------------------------------|-----------------------------|-------------------------------|
| SVL | 155.57 (137.0/166.51) (8) | 141.07 (102.51/ 161.2) (31) | 122.83 (96.34/ 153.95) (27) | 115.26 (95.74/ 145.0) (25) | 115.52 (76.0/ 146.0) (19) |
| TAL | 179.88 (175.03/184.73) (2) | 172.95 (223.0/133.2) (10) | 139.8 (111.31/ 184.97) (7) | 126.72 (110.0/ 160.0) (10) | 136.82 (112.0/ 155.0) (5) |
| RTAL | 1.13 (1.05/1.20) (2) | 1.24 (1.11/ 1.45) (10) | 1.19 (1.06/ 1.30) (7) | 1.15 (0.89/ 1.35) (10) | 1.26 (1.14/ 1.48) (5) |
| HL | 28.77 (32.63/20.85) (8) | 27.53 (20.43/ 33.49) (31) | 23.13 (17.55/ 28.64) (27) | 23.35 (18.51/ 30.16) (25) | 23.31 (19.09/ 28.2) (19) |
| HB | 22.73 (20.20/26.48) (8) | 22.27 (17.59/ 26.52) (30) | 16.81 (12.58/ 24.01) (27) | 19.43 (14.15/ 27.43) (25) | 17.47 (14.3/ 25.91) (19) |
| HH | 18.3 (15.43/20.3) (8) | 17.04 (10.6/ 20.73) (31) | 12.3 (8.97/ 16.26) (27) | 14.59 (10.3/ 18.5) (25) | 12.94 (10.5/ 26.24) (19) |
| EMB | 33.22 (32/35) (9) | 30.9 (30/ 34) (29) | 33.77 (33/ 34) (26) | 35.56 (34/ 37) (25) | 36 (34/ 38) (18) |
| VE | 61.33 (57/67) (9) | 57.37 (56/ 67) (30) | 60.36 (57/ 65) (25) | 68.92 (63/ 75) (25) | 66.3 (61/ 77) (17) |
| SL | 7.7–7.6 (8–8/7–7) (9) | 8.4–8.2 (7–7/ 9–8) (26) | 8–8 (8–8/ 8–8) (9) | 8–7.9 (7–7/ 9–8) (25) | 7.9–8.1 (7–8/ 8–9) (18) |
| IL | 7.5–7.3 (6–6/9–8) | 7.8–7.7 (6–7/ 8–8) (25) | 7.8–7.8 (7–7/ 8–8) (9) | 7.6–7.5 (7–7/ 8–9) (25) | 7.6–7.7 (7–7/ 8–9) (18) |
| ED | 2–2 (2–2/2–2) (9) | No | No | 2–2 (2–2/ 2–2) (25) | 2–2 (2–2/ 2–2) (19) |
| LFF | 12.0–12.3 (11–11/14–15) (9) | 11.6–11.6 (10–10/ 13–13) (27) | 10.6–10.6 (9–9/ 14–13) (27) | 10.4–10.3 (9–9/ 13–13) (25) | 10–9.5 (9–9/ 11–11) (15) |
| LFT | 15.9–16.3 (15–16/17–17) (9) | 14.7–14.7 (13–12/ 17–16) (27) | 13.6–14.0 (11–13/ 16–17) (25) | 12.4–12.9 (9–9/ 16–17) (23) | 13.2–13.2 (11–12/ 15–16) (15) |

Molecular comparison. Regarding the molecular data inbetween the different taxa of *Lepidothyris*, the uncorrected 16S pairwise sequence divergences between the different taxa were calculated as follows: *L. h. hinkeli* **sp. n.** Eastern DR Congo – *L. h. hinkeli* **sp. n.** Rwanda= 0.8%; *L. f. fernandi* Cameroon – *L. f. harlani* Ghana= 3.1%; *L. f. fernandi* Cameroon – *L. striatus* PR Congo= 2.4%; *L. f. harlani* Ghana – *L. striatus* PR Congo= 2.2%; *L. h. hinkeli* **sp. n.** Rwanda – *L. striatus* PR Congo= 3.3%; *L. h. hinkeli* **sp. n.** Rwanda – *L. f. harlani* Ghana= 4.1%; *L. h. hinkeli* **sp. n.** Rwanda – *L. f. fernandi* Cameroon= 3.3%; *L. h. hinkeli* **sp. n.** eastern DR Congo – *L. f. fernandi* Cameroon= 3.5%; *L. h. hinkeli* **sp. n.** eastern DR Congo – *L. f. harlani* Ghana= 4.1%; *L. h. hinkeli* **sp. n.** eastern DR Congo – *L. striatus* PR Congo= 3.3%.

The molecular analyses therefore distinctly corroborate our morphological results as they clearly support the distinctiveness of the two new taxa as well as of the two resurrected taxa. The genetic differences within this species group may indicate that the whole genus *Lepidothyris* is a comparatively young radiation, where species development is still ongoing. This is consistent with our zoogeographical interpretation of the phylogenetic history of the different taxa.

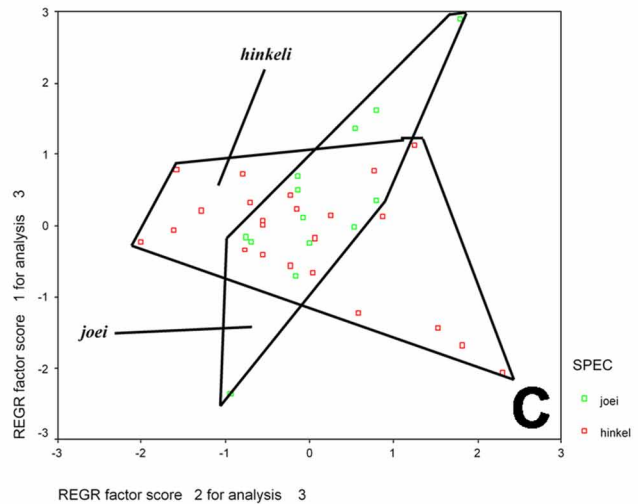
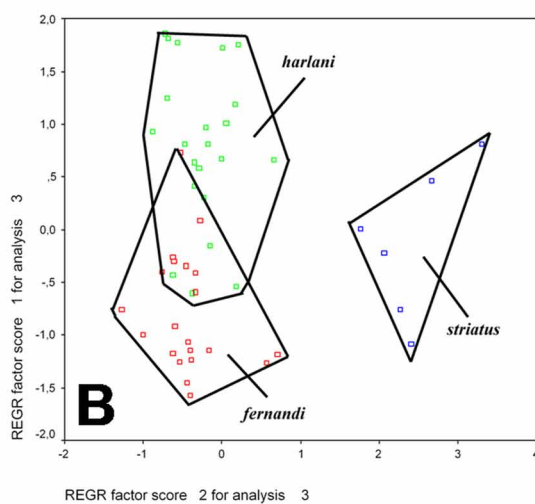
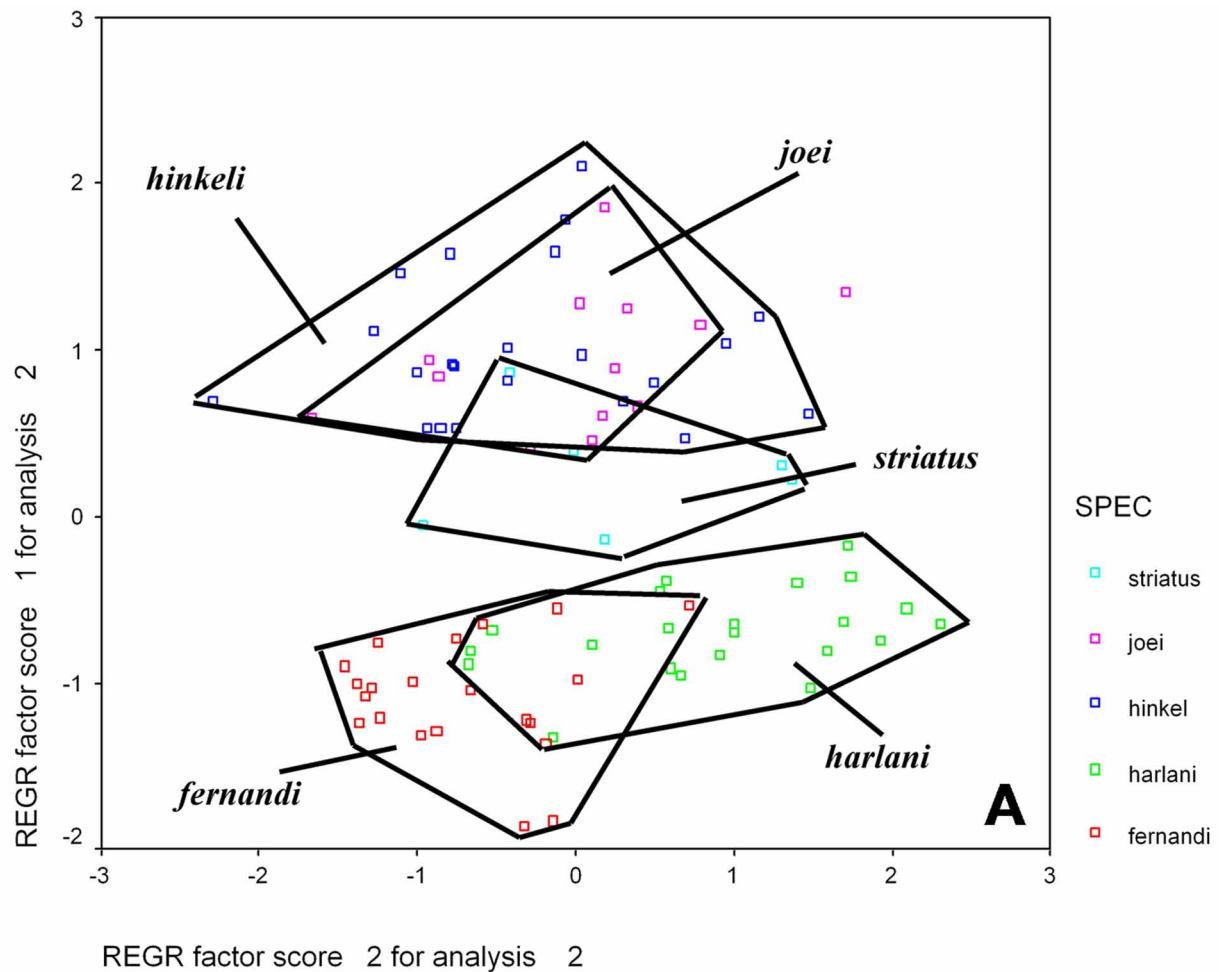


FIGURE 12. Principal Component Analysis of the *L. fernandi* s. l. complex. **A**= all species of the genus included. **B**= only western and central African taxa included (*L. fernandi* s. str. species group). **C**= only individuals of *L. hinkeli* included.

Principal component analysis

The PCA of the pholidosis results in two distinct groups (see fig. 12, a) and separates the East African taxa from the West and Central African ones. A split within the Central and West African group, between

L. striatus and *L. fernandi*/*L. harlani* becomes firstly obvious if the PCA is done separately (see fig. 12, b). This split separates the southern central *L. striatus* from the Central and West African taxa. In the East African group a split in distinct groups is not possible (see fig. 12, c), because in these analyses only characteristics from pholidosis and morphometrics are used, whereas the colouration as the main character to distinguish the different geographic populations was not used. Therefore, regarding only pholidosis and morphometrics a subspecific classification is not possible and only three populations are distinct to each other.

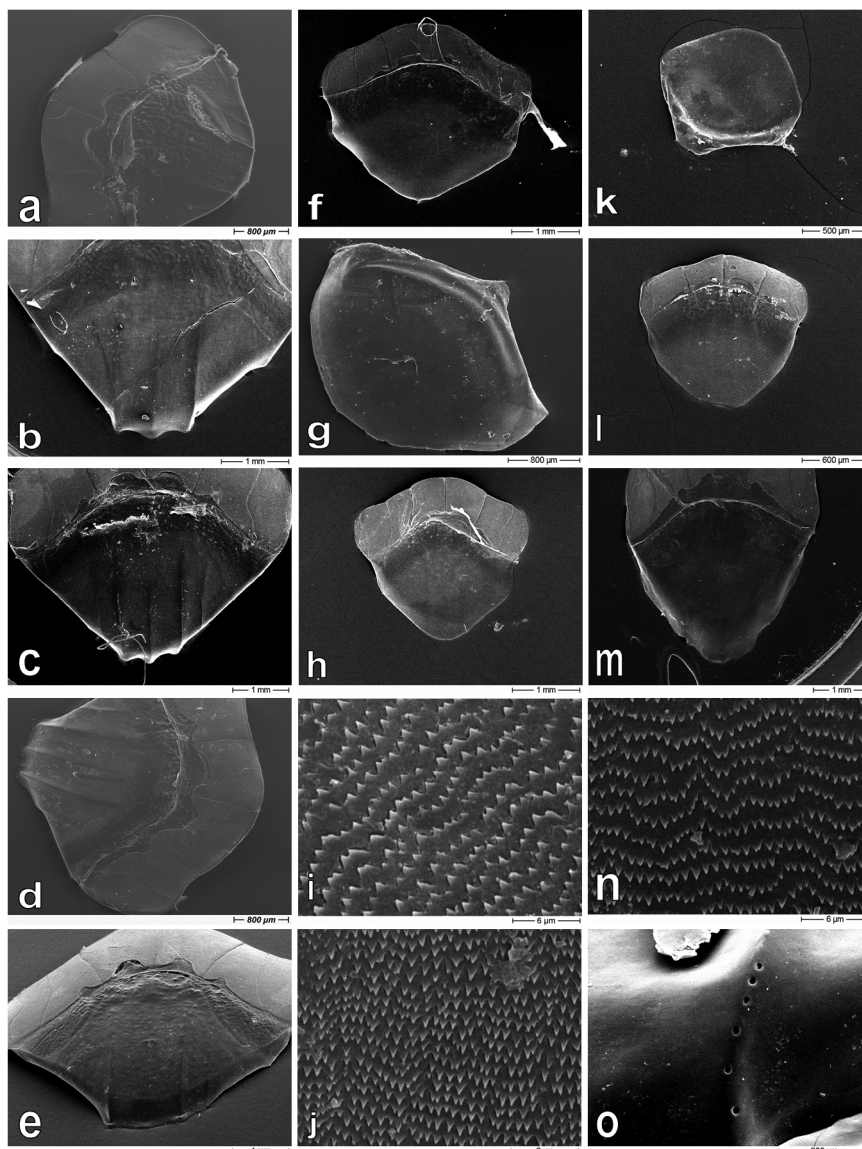


FIGURE 13. SEM images of dorsal midbody scales. **a=** *Lepidothyris fernandi fernandi*; **b=** *Lepidothyris fernandi harlani*; **c=** *Lepidothyris hinkeli hinkeli*; **d=** *Lepidothyris fernandi joei*; **e=** *Lepidothyris striatus*; **f=** *Mochlus afer*; **g=** *Mochlus sundevalli*; **h=** *Mochlus guineensis*; **i=** *Lepidothyris fernandi harlani* (detail of the fine structure of the scale surface); **j=** *Lygosoma bowringi* (detail of the fine structure of the scale surface); **k=** *Lygosoma quadrupes*; **l=** *Lygosoma bowringi*; **m=** *Lygosoma koratense*; **n=** *Mochlus afer* (detail of the fine structure of the scale surface); **o=** *Lepidothyris f. harlani* (sensible pores on the scale surface).

Scale morphology of the genus. Details of the morphology of the scales are shown in fig. 12 by SEM images. The comparison of the scales clearly shows some similarities between the taxa of the genus *Lepidothyris*. But comparisons with other related taxa of the genera *Mochlus*, *Lygosoma* and *Riopa* show clear differences in shape and structure, especially in the keels. This is a further proof that *Lepidothyris* is a monophyletic clade which deserves full genus rank. As also mentioned by Perret & Wuest (1983) the cuticular

fine structure of the scales of closely related taxa within the genus *Lygosoma* (fide Greer 1977), even though somewhat similar, shares also typical characteristics (e.g. the position of the pores) with members of the genus *Trachylepis* (e.g. *T. planifrons* from Kenya; see Perret & Wuest 1983). But the rows of spiky lobes in the fine structure is also present in genera like *Lepidothyris*, *Lygosoma*, *Afroablepharus*, *Trachylepis* and *Chalcides*, and is therefore probably a characteristic of the subfamily ‘Scincinae’ (see Schmitz et al 2005a, Brantley et al. 2005).

Known distribution of the species of the genus *Lepidothyris*. The genus *Lepidothyris* with its now known five taxa has a known distribution from Sierra Leone in north–west Africa across the continent through the Central African Republic to Kenya in the East and the northern Zambian border in the South. Records from Togo and Benin are lacking so far.

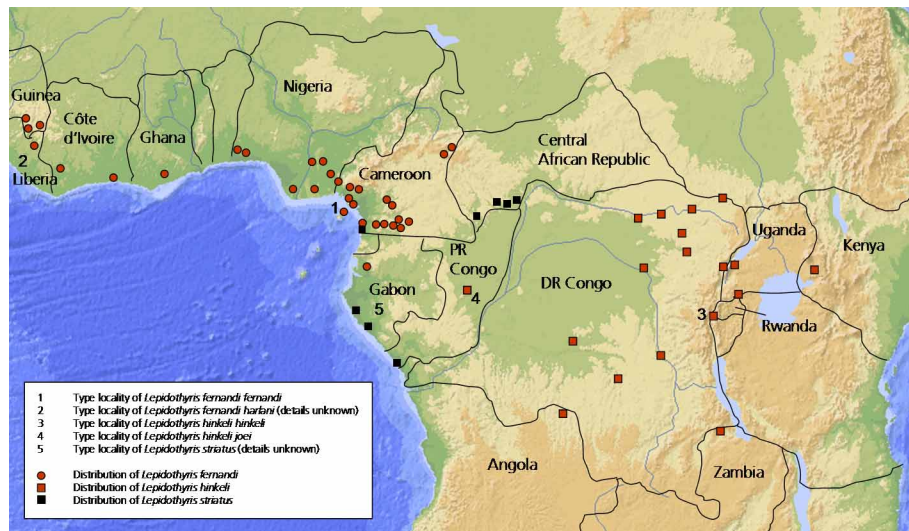


FIGURE 14: Distribution of the genus *Lepidothyris* (for references of localities see fig. 15 and 16).

Lepidothyris fernandi harlani is restricted to western Africa and is known from Sierra Leone (Zug 1983), Guinea (Angel *et al.* 1954), Liberia (Grandison 1956), Ivory Coast (ZFMK 76711; MNHG 1228.005–015) and Ghana (ZFMK 83614–628). Nigeria is probably a transition area and also Togo and Benin if the species occurs there.

Lepidothyris fernandi fernandi is restricted to western Central Africa and is known from Equatorial Guinea (here only known from its type locality Bioko Island), Cameroon (e.g. Böhme 1975; Lawson 1993), Nigeria (Dunger 1973) and Gabon (ZFMK 26925)].

Lepidothyris hinkeli hinkeli is restricted to middle and eastern Africa and is known from the DR Congo (Schmidt 1919), Rwanda (Fischer & Hinkel 1992), Uganda (Vonesh 2001), Kenya (Spawls *et al.* 2002; Wagner & Böhme 2007) and Zambia (IRSNB 4713).

Lepidothyris hinkeli joei is restricted to central-southern Africa and is known from the PR Congo (ZFMK 64410), DR Congo (MNHG 2539.071) and Angola (Laurent 1964).

Lepidothyris striatus is known from Gabon (corrected type locality fide Hallowell 1860; IRSNB 16897; USNM 561500; Pauwels *et al.* 2002a), Cameroon (ZMH R08219), PR Congo (RM 4671, 4672), Central African Republic (Chirio & Ineich 2006; MNHN 1997.3100, 1997.3101) and probably the DR Congo. The type specimens of *Euprepes leoninus* Fischer, 1884 (a synonym of *L. striatus*) are supposedly from Sierra Leone (Fischer 1883, 1884) but it is highly doubtful that the species occurs there (figs. 13, 14). The specimen of *L. striatus* from Bipindihof near Kribi in Cameroon is of special interest because in the same series also *L. fernandi* (ZMH R08220) was collected at the same time by the same collector. This documents a sympatric occurrence of the two species in southern Cameroon.

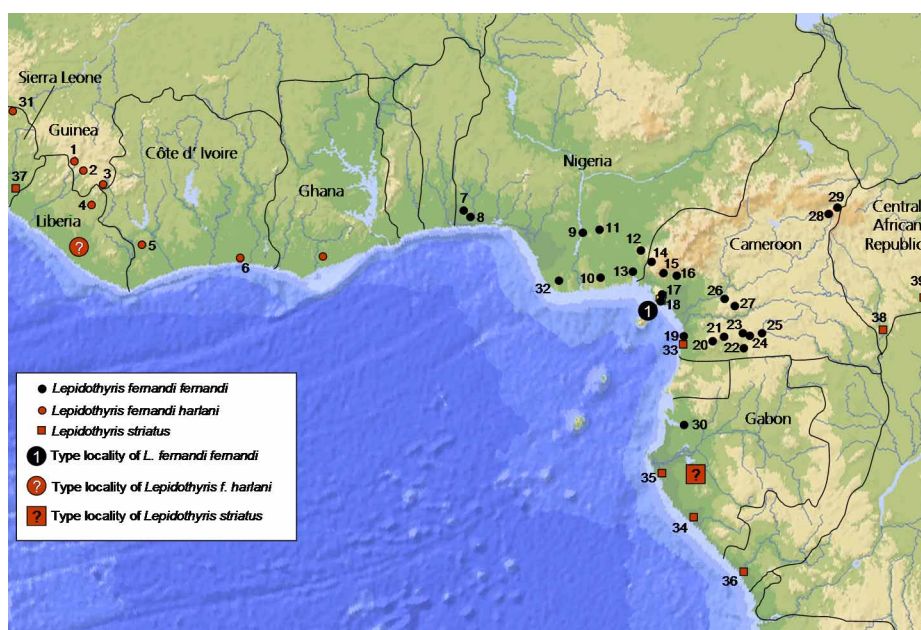


FIGURE 15. Distribution of *L. fernandi*: 1= Guinea: Ziama Forest (Böhme 1993), 2= Guinea: N'Zebela (Chabanaud 1921), 3= Guinea: Mount Nimba (Grandison 1956, Angel et al. 1954); 4= Liberia: Boah (=Boa) (Grandison 1956); 5= Côte d'Ivoire: Tai National Park (ZFMK 76711), 6= Côte d'Ivoire: Abidjan (MHNG 1228.005–015); 7= Nigeria: Ilaro near Lagos (Dunger 1973, BM 19001261), 8= Nigeria: Songo Otta (Dunger 1973), 9= Nigeria: Asaba (Dunger 1973, BM 955316), 10= Nigeria: Okoloma (Dunger 1973), 11= Nigeria: Oil River (= Oji River) (Dunger 1973, BM 888291–92), 12= Nigeria: Oban Hills (Dunger 1973, BM 19085121), 13= Nigeria: Calabar (Dunger 1973, BM 64452, 745282); 14= Cameroon: Korup National Park (Lawson 1993, ZFMK 61250), 15= Cameroon: Dikume (ZFMK 5816), 16= Cameroon: Nyasoso (ZFMK 56015), 17= Cameroon: Buea (ZFMK 15586), 18= Cameroon: Limbe (=Victoria) (NHM 10035), 19= Cameroon: Kribi (ZFMK 8846), 20= Cameroon: Foulassi (MHNG 1013.092–098), 21= Cameroon= Ebolowa (MHNG 1228.017.018), 22= Cameroon: Assok (MHNG 2094.006), 23= Cameroon: Moueko (MHNG 917.098), 24= Cameroon: Sangmélina (NHM 10032), 25= Cameroon: Bitye (NHM 10028), 26= Cameroon: Eyodoula (NHM 10030), 27= Cameroon: Campus (MHNG 1228.016), 28= Cameroon: Ngam (MHNG 917.096–097), 29= Cameroon: Batouri (MHNG 1013.099); 30= Gabon: Kama River (ZFMK 26925); 31= Sierra Leone: Outamba–Kilimi National Park (Zug 1983); 32= Nigeria: Eket (Akani et al. 2002). Distribution of *L. striatus*: 33= Cameroon: Zenkerfarm, Bipindihof near Kribi (ZMH R08219); 34= Gabon: Gamba, Cette Cama, 2°42'17''S 9°59'35''E (IRSNB 16897); 35= Gabon: Loango National Park (USNM 561500); 36= PR Congo: near Point Noire, 4° 41' 17.52"S, 11° 58'18.264"O (RM 4671,4672); 37= Sierra Leone: without exact locality and very questionable (ZMB 10479, 10480); 38= Central African Republic: Bayanga (Chirio & Ineich 2006; MNHN 1997.3100–102); 39= Central African Republic: Barrière entrée Ecofac (Chirio & Ineich 2006; MNHN 1997.3106); 40= Gabon: Franceville (identification from images); 41= Cameroon: Kongo (NMW 8230); 42= Cameroon: Bitye (NMW 10028).

Ecology and ethnozoology of the lizards of the genus *Lepidothyris*. Up to now, only rather few field data are available regarding the ecology of the different taxa. All taxa are found in rainforest areas or nearby, but it is possible that they are able to adapt themselves to changed conditions if the continuous forest is disturbed (Schmidt 1919). Knoepfler (1974) found several individuals in secondary forest and plantations in Gabon, and similar observations were made by Schmitz *et al.* (2000) in western Cameroon.

Most old references described the taxa as being a nocturnal (Hauschild & Gaßner 1995; Laurent 1964) or partly nocturnal (Schmidt 1919) species, but it is in fact a diurnal species in breeding situations (Veltum 2005). Also Böhme (1975) collected one specimen at Kribi (Cameroon) which was active during midday. All observed specimens were ground-dwelling and resting near or fleeing into self-burrowed earth holes. Taylor & Weyer (1958) reported *L. fernandi harlani* from Liberia as 'somewhat aquatic' and mentioned specimens which enter shallow water bodies in the rivers.

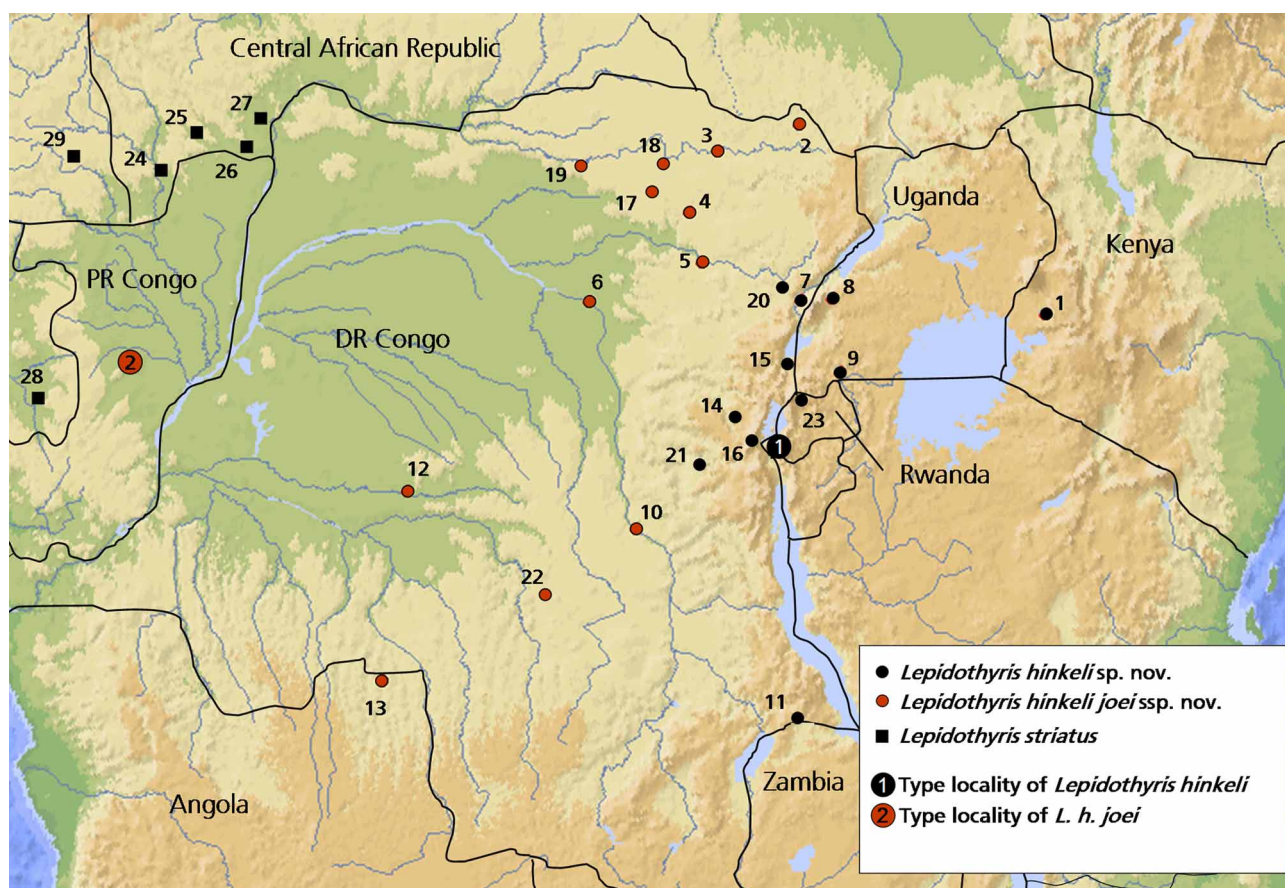


FIGURE 16. Distribution of *L. hinkeli*: 1= Kenya: Kakamega Forest (NMK L/2147); 2= DR Congo: Garamba National Park (DeWitte 1966), 3= DR Congo: Niangara (Schmidt & Noble 1919), 4= DR Congo: Medje (Schmidt & Noble 1919), 5= DR Congo: Avakubi (Schmidt & Noble 1919), 6= DR Congo: Kisangani (=Stanleyville) (Schmidt & Noble 1919), 7= DR Congo: Virunga National Park (IRSNB 12898); 8= Uganda: Kibale National Park (Vonesh 2001), 9= Uganda: Bwindi Impenetrable Forest (Drews & Vindum 1997); 10= DR Congo: Nyangwe (Boulenger 1897); 11= DR Congo: Musosa (IRSNB 2643); 12= DR Congo: Dekese (MHNG 2539.071); 13= Angola: Dundo (Laurent 1964); 14= DR Congo: Irangi (MHNG 2699.51, ZFMK 58674), 15= DR Congo: Kagera National Park (IRSNB 12894), 16= DR Congo: Albert National Park (IRSNB 6653), 17= DR Congo: Yangambi (IRSNB 4562), 18= DR Congo: Zobia (IRSNB 4481–83), 19= DR Congo: Ibembo (IRSNB 4485), 20= DR Congo: Teturi (IRSNB 4486), 21= DR Congo: Mulungu (IRSNB 4523), 22= DR Congo: Tshibati (IRSNB 9944); 23= Rwanda: Kagera National Park (IRSNB 12897). Distribution of *L. striatus*: 24= Central African Republik: Bayanga (Chirio & Ineich 2006; MNHN 1997.3100-102); 25= Central African Republik: Barrière entrée Ecofac (Chirio & Ineich 2006; MNHN 1997.3106); 26= Central African Republik: S.C.A.D. (Chirio & Ineich 2006; MNHN 1997.3103); 27= Central African Republik: Zimba (Chirio & Ineich 2006; MNHN 1997.3104-106); 28= Gabon: Franceville (identification from images); 29= Cameroon: Kongo (NMW 8230).

One specimen in Ituri Forest (eastern DR Congo) was found inside a termite hill and also in a self-burrowed lode leading from the outside of the hill to the inside (pers. comm. Reto Kuster). The diet of the *Lepidothyris* taxa comprises a variety of arthropods and includes also some hard-shelled beetles, gathered from the ground among the leaves (Schmidt 1919). In captivity the individuals are highly aggressive against each other which may indicate a strong territoriality, and the breeding of the species is difficult (Veltum 2005). But single specimens quickly become tame in captivity and they even accept juvenile frogs, geckos and agamas as food. All taxa are oviparous with clutches up to 12 eggs (Veltum 2005). In all species the tail is very easy to autotomize but regenerates well (Schmidt 1919). Hughes (1988) supposed a longevity of *L. fernandi* of one and a half years, whereas Mudrack (1976) mentioned five years. Moss (2007) gave proof of a longevity of more than ten years. A similar longevity in the related taxa of the genus is expected.

While being similar in its biology to *L. fernandi* and *L. hinkeli*, the revalidated species *L. striatus* seems not quite such a rain forest depending species as the other taxa of the genus. Pauwels *et al.* (2004) collected specimens in swamp forests and one specimen near to a temporary pond at Loango National Park, Gabon. Thus it is possible that this species has a slightly different habitat preference than other members of the genus, who mostly occur in primary forests of the Guineo–Congolian rain forest block and its fragments. All known localities in Estuaire and Ogooué–Maritime, both Gabon, are situated at altitudes very close to sea level, and in Loango National Park it was found just a few hundred meters from the sea. The biotopes where *L. striatus* was found in Gabon include coastal forest, inland swamp forest, inland primary dense forest, secondary forest gallery forest in savanna–forest mosaic, and gardens in urbanized areas (latter observation based on one single case in Libreville) as well as secondary forest and abandoned plantations mentioned in Knoepffler (1974).

L. striatus is extremely secretive – in six years of field work in Gabon (2001–2006), the third author has never observed a specimen outside of pitfall or funnel traps. Of more than three dozens of specimens collected in pitfalls in Ogooué–Maritime Province, most attempted to bite when first handled, frenetically twisting their body though none had recourse to caudal autotomy. In 2005–2006, the third author kept a locally–collected adult specimen for four months in Gamba, Gabon. It quickly became tame and accepted the whole variety of locally–collected live preys offered to it: earthworms, insects (beetle larvae, mealworms, cockroaches, flies, crickets, grasshoppers), ground spiders, juvenile hemisotid frogs (*Hemisus perreti* Laurent, 1972), juvenile geckos [*Hemidactylus mabouia* (Moreau de Jonnès, 1818)], and juvenile agamas *Agama agama* (Linnaeus, 1758).

In the DR Congo some tribes e.g. Medje and Mangbetu are horrified to touch or just to see an individual (Schmidt 1919). Knoepffler (1974) mentioned from Gabon that the local *Lepidothyris* species was very feared by locals from Ogooué–Ivindo Province who believe it be extremely venomous. Similar local prejudices regarding the local specimens were reported from western Cameroon (Schmitz *et al.* 2000). In Libreville and in Ogooué–Maritime Province where specimens of *L. striatus* were shown alive to local Gabonese persons, they unanimously told that this lizard is extremely venomous. A large number of separately and independently interviewed persons from the same localities agreed on the only way to survive if a man is bitten by this skink: “have sexual intercourse with his sister on the roof of the family house”. Nobody could answer the question about what to do in case a bitten man has no siblings or only brothers, and nobody knew remedies for bitten women.

Zoogeographical discussion. An accepted paradigm for speciation is the so called ‘refuge theory’. The concept was first postulated for South America by Haffer (1974) and later applied to Africa by Diamond & Hamilton (1980), Mayr & O’Hara (1986) and Fjeldså & Lovett (1997). The theory requires periodic habitat fragmentation driven by global fluctuations to provide the conditions for speciation by isolation. Africa’s flora and fauna were only moderately affected by tectonic changes and the most important determinants of the zoogeographic patterns of species was periodic aridity alternating with moist periods in the Pleistocene (Livingstone 1975, 1993; Hamilton 1976, 1982; DeMenocal 1995) and Holocene (Nicholson 1994). New species have evolved in forest fragments (=refugia) which remained stable during the climatic changes. These refugia were postulated in Sierra Leone–Liberia, Ivory Coast–Ghana, Cameroon–Gabon, East DR Congo and East Tanzania. Fjeldså & Lovett (1997) pointed out that this distribution pattern is a result of post–speciation redistribution during the Pleistocene. The fact that the taxa of the genus *Lepidothyris* and other members of the African herpetofaunal forest community e.g. *Adolfus africanus* (Köhler *et al.* 2003), *Feylinia currori* (Wagner & Schmitz 2006) and *Amietophrynus superciliaris* (Köhler *et al.* 2003) are not known from the lower Congo Basin supports the hypothesis that the species survived the dry periods in rainforest refugia in mountainous areas. The taxa of the genus *Lepidothyris* show this typical distribution pattern of rainforest reptile communities (Wagner *et al.* 2008), but not in all postulated refugia.

The recent disjunct distribution of the *Lepidothyris* taxa is therefore likely the result of a separation during the Pleistocene, so that there are now three distinct lineages in West, South–Central and East Africa. In the West African lineage (*L. fernandi*) also a second more recent separation is postulated in the extreme western part of the distribution area. It is quite likely that the populations were initially separated during the very dry

African past by the Dahomey Gap, which resulted in the two now recognisable different subspecies. The Dahomey Gap is a broad savannah corridor in Benin (the formerly Dahomey), separating the rain forest blocks, which underwent by several vegetation changes during the last 150.000 years, whereas the rain forest vegetation appeared during the last interglacial and the early- and mid-Holocene (Dupont & Weinelt 1996; Salzmann & Hoelzmann 2005).

But looking more closely on the current distribution of the East African lineage (*L. hinkeli*) it is obvious that there also must have been a separation in the near past. The isolated refuge of *L. hinkeli hinkeli* is must be postulated at the northern part of the Albertine Rift. From there the taxon expanded southwards along the Rift to Zambia and eastwards to the Kakamega Forest in western Kenya (see fig. 15). This distribution pattern correlates well with the relationship pattern in the chameleon genus *Rhampholeon*. Mathee *et al.* (2004) have found a close relationship between *R. boulengeri* from the northern part of the Rift and taxa from the southern ARC Mountains. Another species of the genus, *R. spectrum*, is distributed from Cameroon to the northern parts of the DR Congo and likewise in the northern part of the Albertine Rift and has its closest allies in the northern ARC Mountains. This pattern resembles the postulated the close pan-African forest block during 40 to 19 million years before present (Burgess *et al.* 1998). The forest refuge of the second east African taxa, *L. hinkeli joei*, is not as clear as in the nominate form. It is probable that the two taxa were separated by a savannah corridor and the refuge of *L. h. joei* was likely lowland to submontane forest somewhere in the northern part of the Congo basin and the taxon is now distributed in lower elevation around the Congo basin and along the western border of the Rift Mountains.

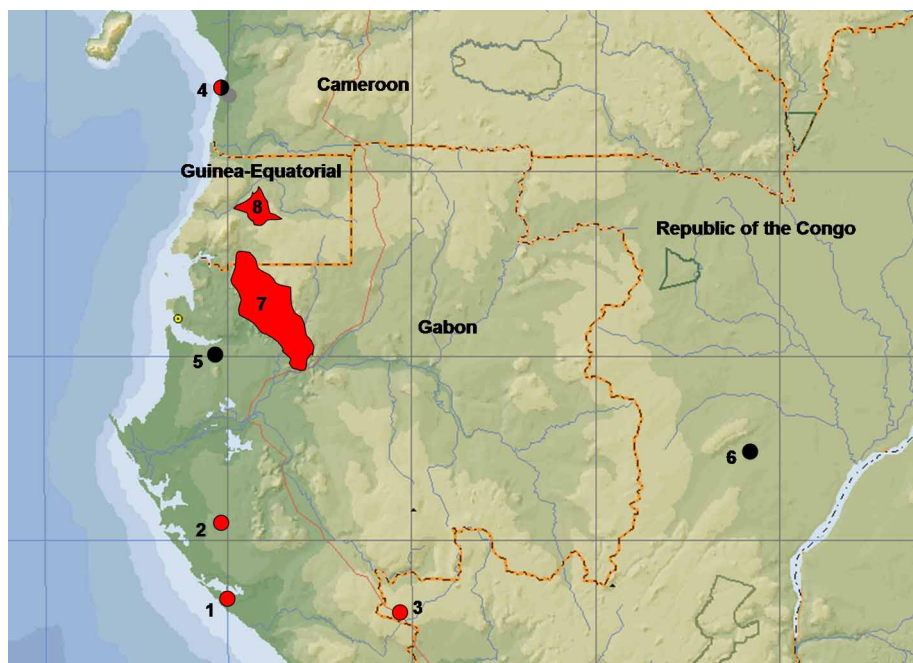


FIGURE 17. Distribution of the genus *Lepidothyris* in Gabon and surrounding countries. 1= *L. striatus*: Gabon, Gamba region, Sette Gama route (ISBN 16897); 2= *L. striatus*: Gabon, Gamba region (fig. 4); 3= *L. striatus*: PR Congo, Kouilou region (fig. 3); 4= *L. striatus* & *L. f. fernandi*: sympatric record: Cameroon, Bipindihof near Kribi (ZMH R08219–20); 5= *L. f. fernandi*: Gabon: Kama River (ZFMK 26925); 6= *L. hinkeli*: PR Congo, Oyo, Bokouélé (ZFMK 64410); 7= Gabon: Monts de Cristal; 8= Guinea-Equatorial, Monte Alén.

The distribution of *L. striatus* indicates a third refuge in Gabon. Despite the fact that the type locality of its junior synonym *E. leoninus* (described as *E. elegans*) is Sierra Leone, (which is likely as much in error as the one mentioned in the original description of *L. striatus* already corrected by Hallowell 1860) the distribution centre seems to be in Gabon. Like the other taxa of the genus, this resurrected taxon is also found in rain forest areas. For this reason it is to be expected that there was a forest refuge, a “core-area” during Pleistocene. This postulated refuge is probably located at the Monts de Crystal in Gabon and the Monte Alén in Equatorial-Guinea.

This region is known for its diversity of plants (Sosef 1994; Barthlott *et al.* 1996; Cribb *et al.* 1989; Wilks 1990) and for its diversity and endemism of vertebrates, especially amphibians and reptiles (De la Riva 1994; Gossmann *et al.* 2002; Lötters *et al.* 2001, 2005; Pauwels *et al.* 2002b). It seems clear that *L. striatus* was restricted to this refuge and is now under extension northwards to the CAR, southwards along the coastal forests to Gabon and eastwards to the PR Congo. In the isolation of the refuge also the biology of the species changed and presently also occurs in swamp and coastal forests (Pauwels *et al.* 2004). Until this day the species has not yet been collected directly in the postulated refuge area, but this can be explained the secretive biology of this species.

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Appendix

Additional specimens of *Lepidothyris* examined for this work. The following acronyms and abbreviations are used: IRSNB= Institut Royal des Sciences naturelles de Belgique, Brussels; MHNG= Muséum d'Histoire Naturelle, Genève, Switzerland; MNHN= Muséum National d'Histoire Naturelle, Paris, France; NMK= National Museums of Kenya, Nairobi, Kenya; RM= Redpath Museum, Montreal, Canada; USNM= United States National Museum, Washington, USA; ZFMK= Zoologisches Forschungsmuseum A. Koenig, Bonn, Germany; ZMB= Zoologisches Museum Berlin, Germany; ZMH= Zoologisches Museum Hamburg, Germany. Specimens in alphabetical order of the country records, collection numbers in parenthesis.

Lepidothyris fernandi fernandi. Cameroon: Assok (MHNG 2094.006); Batouri (MHNG 1013.99); Kribi: Bipindihof (ZMH R08220); Edib (ZFMK 67574–75, 68304); Korup (ZFMK 61248, 61250); Mekeng: Ossoebemwa (MHNG 2161.68); Mt. Kupe (ZFMK 68303); Mt. Nlonako (ZFMK 68959, 78814), Nguengué (ZFMK 78026–27); Nbuako (ZFMK 73497); Sangmelima: Foulassi (MHNG 1013.97– 98, 963.042), Ngam (MHNG 917.097); without exact locality (ZFMK 5815–16, ZFMK 8846, ZFMK 18111, ZFMK 15586, ZFMK 69018). Equatorial Guinea: Bioko Island (ZMH R08222–23, NMW 10040). Gabon: Coma River: Rhembo (ZFMK 26925).

Lepidothyris fernandi harlani. Côte d'Ivoire: Abidjan (MHNG 1228.5– 12), without locality (NMW 20077); Tai National Park (ZFMK 76711). Ghana: without exact locality (ZFMK 83614–28). Guinea: Mount Nimba (MNHN 1993.0455–0457, MNHN 1943.0068). Liberia: without exact locality (ZMH R03143, R08225). Nigeria: without exact locality (ZMH R08224).

Lepidothyris hinkeli hinkeli. DR Congo: Albert National Park: Butahu, Semliki (IRSNB 14140), Kiavikere, Kabambeu (IRSNB 14139), Kibengi (IRSNB 6653), Ngokoi (IRSNB 14141), Rutshuru (IRSNB 14133), Station Mutsora (IRSNB 13911, 14124, 14126, 14128, 14129 a + b, 14130, 14135, 14138); Kivu: Irangi (ZFMK 58674, MHNG 2699.51), Mulungu (IRSNB 4525, 4528), Teturi, Butembo (IRSNB 4486); Virunga: Rutshuru Mvambi (IRSNB 12895). Kenya: Kakamega Forest (NMK L/2147). Rwanda: Kagera National Park (IRSNB 12897), without exact locality (ZFMK 66701–02). Zambia: Musosa (IRSNB 4713).

Lepidothyris hinkeli joei. DR Congo: Gamora: E Lwiru (IRSNB 12804); Ibembo (IRSNB 4485 a+b); Kasai/Occidental: Dekese (MHNG 2539.71); Kivu: Busanganya, Mulungu (IRSNB 4523), Kagera National Park, Chutes Rutshuru (IRSNB 12894); South Kivu: Mushofi (IRSNB 9140), Tschibati (IRSNB 9944); Stanleyville, Yangambi (IRSNB 4487, 4562); Uele: Ibembo (IRSNB 4484), Zobia (IRSNB 4481–83); Virunga: Rutshuru (IRSNB 12896); Virunga

National Park: Ibatama (IRSNB 12898 a–c). PR Congo: Oyo, Bokouélé (ZFMK 64410).

Lepidothyris striatus. Cameroon: Bitye (NMW 10028, 10029); Kongo (NMW 8230), Zenkerfarm, Bipindihof near Kribi (ZMH R08219); Central African Republik: Bayanga (MNHN 1997.3100-102), Barrière entrée Ecofac (MNHN 1997.3106), S.C.A.D. (MNHN 1997.3103), Zimba (MNHN 1994.8698, MNHN 1995.5625, MNHN 1997.3104-106); DR Congo: without exact locality (IRSNB 1106 a+b). Gabon: Gamba, Cette Cama, 2°42'17''S 9°59'35''E (IRSNB 16897), Loango National Park (USNM 561500); without exact locality (MNHN 1973.1545, MNHN 1968.0070–0071, MNHN 1968.0073–0076). PR Congo: near Point Noire, 4° 41' 17.52"S, 11° 58'18.264"O (RM 4671,4672); Sierra Leone: without exact locality and questionable (ZMB 10479, 10480).