

**The dentitions of recent and fossil scincomorphan lizards
(Lacertilia, Squamata) – Systematics, Functional Morphology,
Palecology**

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Dipl.-Geol. Ralf Kosma

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Abstract: Lizard remains are common in numerous Mesozoic and Cenozoic excavation sites. The taxonomy of fossil lizards depends greatly on morphological features of the dentaries, since the mandibles are the most resistant bones and most fossil lizard assemblages are dominated by dentaries.

The Upper Jurassic limnic lignites of Guimarota (Leiria, Portugal) contained well preserved disarticulated bones of the well known paramacellodids *Becklesius hoffstetteri* and *Paramacellodus oweni*, and a new lizard tentatively referred to the Scincidae; the assemblage is dominated by a diversity of burrowing *Saurillodon* species, which are tentatively referred to the Scincidae.

The various localities in the Tertiary deposits of the South German Freshwater Molasse contained, apart from remains of Lacertidae and Anguimorpha, rare fragmentary dentaries of *Bavariascincus mabuyaformis* gen. et sp. nov. (tentatively referred to the Scincidae) and *Bavaricordylus ornatus* gen. et sp. nov. (tentatively referred to the Cordylidae).

The separation of the new fossil taxa is based on the investigation of 270 extant scincomorphan species, which revealed new character features that allow a more exact differentiation of species on an osteological basis. Especially the patterns of striation in combination with the general tooth crown morphology in many extant species show characteristic features.

Many scincomorphan lizards are opportunistic insectivorous feeders, but some species are dietary specialized to various degrees. The trophic structures of the extant lizards often revealed a strong influence of adaptive alterations which disguise the taxonomic useful characteristics.

During the Kimmeridgian and Oxfordian of the Iberian Peninsula *Saurillodon* represented an ecomorph which is probably comparable to the extant acontine skinks of Southern Africa.

A distinct method of casting lizard mandibles was used to acquire an extensive collection of scincomorphan dentitions which enabled the comparison between extant and fossil material.

Zusammenfassung: Echsen sind ein häufiger Bestandteil der Wirbeltierfaunen in zahlreichen mesozoischen und känozoischen Ausgrabungsstätten. Die Taxonomie fossiler

Echsen hängt überwiegend von morphologischen Merkmalen der Dentalia ab, da die Unterkiefer als verwitterungs-resistenteste Knochen des Skeletts in fossilen Echsen-Gemeinschaften überrepräsentativ vertreten sind.

Die oberjurassischen limnischen Lignite von Guimarota (Leiria, Portugal) beinhalteten gut erhaltene disartikulierte Knochen der Paramacellodiden *Becklesius hoffstetteri* und *Paramacellodus oweni* und des möglichen Scinciden *Chalcidosaurus guimarotensis* gen. et sp. nov.; dominiert wird diese Fauna allerdings von mehreren Arten der wühlenden Gattung *Saurillodon*, die vorläufig zu den Scincidae gestellt wird.

Verschiedene Lokalitäten innerhalb der tertiären Ablagerungen der Süddeutschen Süßwassermolasse enthielten neben Überresten von Echten Eidechsen (Lacertidae) und Anguimorpha auch seltene fragmentarische Dentalia von *Bavariascincus mabuyaformis* gen. et sp. nov. (vorläufig zu den Scincidae gestellt) und *Bavaricordylus ornatus* gen. et sp. nov. (vorläufig zu den Cordylidae gestellt).

Die Abtrennung der neu beschriebenen fossilen Taxa ergibt sich aus der Untersuchung von 270 rezenten Arten der Scincomorpha, die neue Merkmale erbrachten, welche eine exaktere Unterteilung von Arten auf osteologischer Basis erlauben. Insbesondere die Striationsmuster und die generelle Zahnkronenmorphologie vieler rezenter Arten zeigen charakteristische Merkmale.

Viele Scincomorpha sind opportunistische Insektenfresser, doch einige Arten haben sich in unterschiedlichem Maße nahrungstechnisch spezialisiert. Die Ernährungsstrukturen rezenter Echsen offenbaren oft einen großen Einfluss adaptiver Überprägungen, welche die taxonomisch verwertbaren Merkmale verschleiern oder überdecken.

Während des Kimmeridgium und des Oxfordium repräsentierte *Saurillodon* auf der Iberischen Halbinsel einen Ökotyp, dessen rezentes Pendant die acontinen Skinke des südlichen Afrikas darstellen.

Ein besonderes Abgussverfahren, welches die Duplizierung von Echsen-Unterkiefern ermöglicht, wurde angewandt, um eine umfangreiche Sammlung scincomorpher Bezahnungen anzulegen, die anatomische Vergleiche zwischen Rezentmaterial und Fossilmaterial erlaubt.

1. Introduction

The dentitions of scincomorphans show a high variability concerning the development of complex patterns of striations, tooth crown morphology, and the dental morphology in general. For the determination of the systematic position of a fossil lizard the use of dental characters as taxonomic features is most important. The question is whether a character is of taxonomic value, or an adaptation to a special diet. This problem is best solved by a comparison of the dentitions of a large number of recent scincomorphan species; a comparably detailed investigation is still outstanding. Accordingly, the dentitions of 270 extant scincomorphan species (of 95 genera) were investigated for this study to apply the results to fossil lizards from the Jurassic of Portugal and the Tertiary of Southern Germany (see chapters “Geological setting of the Guimarota mine” and “Geological settings and fossil contents of the Scincomorpha-bearing localities in the Bavarian Freshwater Molasse” for detailed information). In contrast to fossil lizard remains, the specific affiliation of an extant mandible is exactly known since the significant characters were investigated before the specimen was skeletonized. Therefore a representative number of mandibles from recent species were casted at American and European osteological collections, belonging to the six scincomorphan families Cordylidae, Gerrhosauridae, Lacertidae, Scincidae, Teiidae (after HARRIS et al. (2001) excluded from the Scincomorpha), and Xantusiidae. Among these extant taxa the continuance of certain characters (e.g., the presence or absence of a cuspis lingualis; the presence or absence of striae dominantes; the form, lengths, and arrangement of the cutting edges) was investigated. Many characters seem to be unstable since they are largely influenced by adaptations to a certain diet. Specifically, the patterns of striations depend on adaptive forces and are often the result of functional morphology. According to RENSBERGER (1995) the presence of striae in mammalian teeth indicate power strokes and are therefore regarded as being adaptative. Since the functional morphology of teeth is greatly scale dependent, a different reason for the presence of striae in the teeth of small lizards can be expected than in the teeth of large mammals. Interestingly the development of some character combinations is restricted to a single

taxon (e.g., long, conical, and recurved teeth with faint longitudinal striations in *Sphenomorphus muelleri*; perfectly parallel striae with a pronounced relief in *Mochlus fernandi*), whereas other features are wide spread within a species group (e.g., the development of a cuspis lingualis in the Cordylidae; tricuspidity in the Lacertidae and Teiidae; bulbeous tooth bases and almost unwrinkled enamel surfaces in Gallotiinae).

Historically most examinations of Mesozoic vertebrates concentrated on forms with large body sizes like crocodiles and dinosaurs. Since the small sized squamates represent a large percentage in younger Mesozoic faunal assemblages, they are assumed to play an important role in terrestrial ecosystems of this epoch. The squamate record begins in the Middle Jurassic (Bathonian) of Britain, and the Jurassic and Early Cretaceous assemblages of Laurasia are dominated by scincomorphans, particularly Paramacellodidae (EVANS & CHURE 1997).

The saurofauna of the Upper Jurassic locality Guimarota contrasts with the Lower Cretaceous lizard assemblages from Galve (Spain), and Anoual (Morocco), which were initially described by RICHTER (1994), in the dominance of burrowing lizards of the genus *Saurillodon* instead of a paramacellodid dominance (*Becklesius*, *Paramacellodus*).

The Caenozoic *Bavariascincus mabuyiformis* gen. et sp. nov. (tentatively referred to the Scincidae) and *Bavaricordylus ornatus* gen. et sp. nov. (tentatively referred to the Cordylidae) from the South German Freshwater Molasse immigrated to Europe as parts of a new squamate fauna after the return of tropical climatic conditions and the collision of Eurasia with Africa at the beginning of the Miocene.

Several pathological abnormalities were observed in the recent lizard material. The abnormal tooth replacement mode in an individual of *Sphenomorphus variegatus* resulted in the development of a “multiple tooththrow”. This unusual phenomenon is first described in this thesis.

The dentitions of many of the extant scincomorphan species documented in this thesis have never before been investigated in detail. Recently, fossil lizard workers repeatedly pointed out the importance of a detailed lizard tooth crown analysis (EVANS & SEARLE 2002).

The classification of disarticulated lizard remains has always been very problematical, a fact that was already noticed by other authors: "... lizard dentaries have limited value at this taxonomic level because there are relatively few parameters that can vary. It would be difficult to separate many living species on dentary structure alone..." (WALDMAN & EVANS 1994). Hopefully this issue will prove as a help in the determination and classification of prospective fossil lizard material.

Institutional abbreviations – A M N H, American Museum of Natural History, New York; **BMNH**, British Museum of Natural History, London; **IFSZ**, Internationales Forschungszentrum für systematische Zoologie der Humboldt-Universität, Berlin; **Priv. Coll. Evans**, private collection of Dr. Susan EVANS, University College, London; **SDS**, San Diego Natural History Museum; **SRK**, collection of Ralf KOSMA (these specimens will be housed at the Niedersächsisches Landesmuseum Hannover (NLMH/osteol. coll.) from winter 2003 on), Universität Hannover; **USNM**, United States National Museum (Smithsonian Institution), Washington D.C.; **ZFMK**, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn.

2. Material and Methods

2.1 Material

The majority of the extant material investigated for this thesis (Scincomorpha *sensu* ESTES 1983) is housed within the osteological collections of European and American natural history museums. Silicon moulds of scincomorphan lower jaws were taken at the following collections: Internationales Forschungszentrum für systematische Zoologie der Humboldt-Universität, Berlin; Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; British Museum of Natural History, London; the private collection of Dr. S. EVANS, University College, London; American Museum of Natural History, New York; United States National Museum (Smithsonian Institution), Washington D.C.; and the San Diego Natural History Museum, collection Dr. ETHERIDGE. Casts of the

forementioned moulds were then made at the geological laboratories of the universities of Hannover and Braunschweig. The museum numbers and taxonomic position of the moulded scincomorphan lower jaws are listed in the appendix.

Additionally, an extensive collection of original skeletal material was acquired during the research phase of this thesis; more than 300 specimens of different squamate taxa were collected, most belonging to the Scincomorpha. This material was collected by placing advertisements in herpetological magazines and in the Internet. Many private keepers and importers of lizards placed deceased captive specimens at my disposal. Prof. Dr. W. BÖHME, Bonn, left many specimens from the practica-collection of the ZFMK, while Dr. G. KÖHLER, Frankfurt a.M., made many scincomorphans from the old MERTENS-Collection (Senckenberg) available. Dr. A. BROSCINSKI and S. BROSCINSKI made several deceased cordylids, gerrhosaurids, and scincids available for research. Several Australian burrowing skinks were loaned or exchanged against various Chamaeleonidae from Dr. M. HUTCHINSON of the South Australian Museum. Additionally, Dr. M. WUTKE, Mainz, made diverse individuals of his private collection available for study. The maceration of the frozen specimens, as well as those preserved in alcohol, was carried out at the Staatliches Naturhistorisches Museum Braunschweig.

The fossil material originates from two deposits distinctly separated from each other both temporally and spatially:

The first group of fossil mandibles originates from the Upper Jurassic coal mine of Guimarota, Portugal (Lower Kimmeridgian). This material is deposited in the collection of Dr. A. BROSCINSKI, Niedersächsisches Landesmuseum Hannover at the moment, but the specimens belong to the Freie Universität Berlin and will finally go back to Lisboa, Portugal. It consists of several thousand disarticulated paramacellodid pieces, out of which only the dentaries and fragments of dentaries were used for this thesis. Most of these specimens are excellently preserved.

The second group of fossil mandibles originates from diverse localities of the Upper Tertiary of the Bavarian Freshwater-Molasse (Older and middle series of the OSM (MN5-MN6; Karpatian to middle Badenian). These

specimens are located in the collection of the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich. The peculiarity of these mandibles was first noticed by Dr. M. BÖHME, Munich, during her studies of the lower vertebrate assemblages of the Bavarian Freshwater-Molasse. The lizard remains were imbedded in clastic (often non solid) sediments like conglomerates, feldspar-enriched sandstones, and sandy marls.

2.2 Methods

All moulds were made with Elastosil M 4500 silicone-latex (Drawin Vertriebs-GmbH) and its accessory hardener, T 12. Each jaw was bedded ventrally into an underlayer made of plastillin. In preparing the mandible in this manner, it was important that no air pockets be allowed to form between the bone and the plastillin where silicone could seep in. Afterwards, the embedded mandible was framed with a strip of foil. The mandible was then brushed carefully with a thin layer of silicone to prevent bubbles. After a short period, the silicone started to vulcanize and the entire mould was slowly poured. The mould was separated from the jaw after becoming completely hardened, which usually took two or three days. During demoulding, several drops of alcohol were placed between the surface of the bone and the mould to facilitate in the separation. The casts were made of the epoxyd-resin Rütapox® 0166/S 20 (Bakelite AG) and its accessory hardener H 105 B. First, the negative of the jaw in the mould was brushed with a thin layer of resin. The entire negative was then filled with resin. Next, the moulds were placed into an exsiccator (vacuum) to draw out any bubbles under pressure from the cast that may have been produced during filling. The finished, hardened casts were sawed in order to take scanning electron microscope images of them, which would not have been advisable with original bones. The sawed jaw fragments and teeth were washed one after the other in acetone with the help of a brush to remove sawdust. The sawed, cleaned, and dried casts were adhered to sample plates from scanning electron microscopy. Afterwards, the casts were coated with gold and the photographic documentation occurred at the Göttinger Zentrum für Geowissenschaften, Abt. Geobiologie, Göttingen. The scanning electron microscope

used for this thesis was a "Rasterelektronenmikroskop-Tischgerät Hitachi S 2300".

The maceration of frozen and alcohol preserved lizards (SRK-collection) was made by carcass beetles (*Dermestes lardarius*) and supervised by M. FORTHUBER, Staatliches Naturhistorisches Museum Braunschweig. In return for M. FORTHUBER's commitment, numerous new specimens were added to the collection of the Staatliches Naturhistorisches Museum Braunschweig. For maceration, alcohol-preserved lizards were skinned manually and placed in water for several days before being skeletonized by the dermestids. The lizard skulls were then degreased with acetone and bleached with hydrogen peroxide. The illustrations of extant originals and the fossils of Guimarota were produced at the Institut für Geowissenschaften der Technischen Universität Braunschweig with a WILD-stereo microscope and an accessory camera lucida drawing mirror (Flachbild-Zeichenspiegel).

For completing the final illustrations, technical ink pens (Rapidographs, ROTRING) with 0.18 to 0.70 mm tip diameters in combination with black charcoal grease pencils for shading were used. The paper used was coquille board, "Runzelkornpapier" in German, of the category "PRÄGNANT Bilddruck-Papier". The technique used for the illustrations can be found in "Naturwissenschaftliches Zeichnen und Illustrieren" (FISCHER 1999).

3. Terminology of scincomorphan teeth

Historically, most authors working on lizard dentitions are confined to describing the general shape of the tooth (pointed, blunt, etc.), the number of cusps (unicuspid/unicuspate, bicuspid/bicuspate, tricuspid/tricuspate, multicuspid/multicuspate), or to noticing if striations are present or absent. Precise descriptions of the patterns of striations (e.g. number, length, and orientation of striations) were scarcely found in the literature. The most complete attempt to describe the numerous morphological structures (specifically the microstructures of the enamel surfaces in the tooth crowns) of lacertilian teeth was initiated by RICHTER (1994). Most of the descriptive terms named by RICHTER were also used in this

thesis, but since RICHTER applied her new terminology for a low number of basal Mesozoic taxa, this already existing terminology had to be improved in order to be used to describe the highly diverse tooth morphologies found in recent scincomorphan taxa.

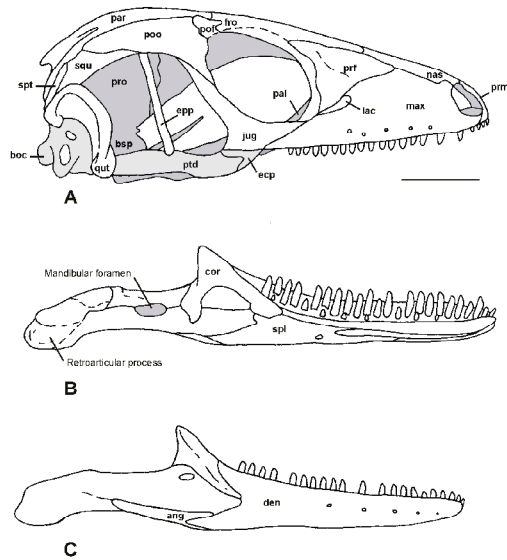


Fig. 1: Terminology of the skull bones and the mandibles in a characteristic scincomorphan (*Zonosaurus madagascariensis*) (after LANG 1991). A: skull in right lateral view; B: left mandible in lingual view; C: right mandible in labial view. Abbreviations: ang = angular; bsp = basisphenoid; boc = basioccipital; cor = coronoid; den = dentary; ecp = ectopterygoid; epp = epipterygoid; fro = frontal; jug = jugal; lac = lacrimal; max = maxilla; nas = nasal; pal = palatine; par = parietal; pof = postfrontal; poo = postorbital; prf = prefrontal; prm = premaxilla; ptd = pterygoid; qut = quadrate; spl = splenial; squ = squamosal. Scale bar: 5 mm

Three sections of the scincomorphan tooth can be recognized: The tooth crown forms the apical section of the tooth; the tooth neck (or shaft, referred to as the cervix dentis by SMITH & DODSON 2003) forms the intermediate section of the tooth; the tooth basis forms the basal section of the tooth, which is connected to the bone of the jaw ramus. The tooth bases of all scincomorphan taxa are attached to the labial parapet of the dentary (pleurodont condition). The cross-sections of these three sections are highly variable, especially the tooth neck can be transversally or mesially expanded. The lingual

surfaces of the tooth crowns are flattened or concave in most scincomorphans.

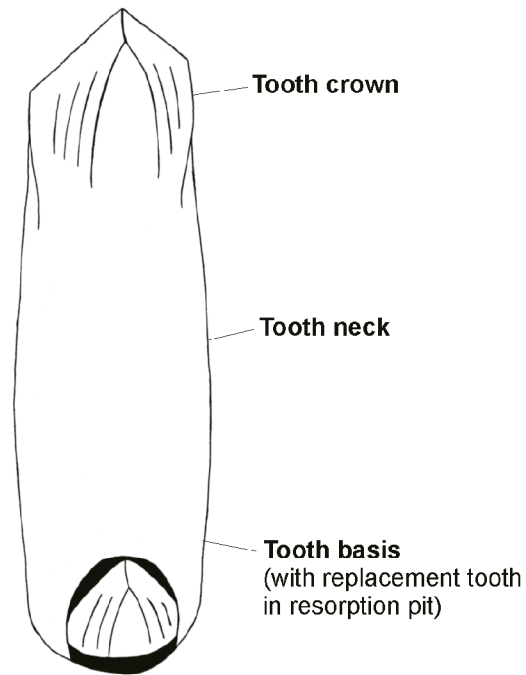


Fig. 2: Tooth terminology of a complete paramacellodid tooth.

The typical scincomorphan tooth crown is dominated by two cutting edges, the anteriorly situated crista mesialis *sensu* RICHTER (1994) and the posteriorly situated crista distalis *sensu* RICHTER (1994). The crista mesialis is longer than the crista distalis in the majority of the investigated teeth; both cristae converge apically and form an outer tip at their point of intersection; this is the cuspis labialis *sensu* RICHTER (1994). The cuspis labialis is usually the main cusp of the tooth.

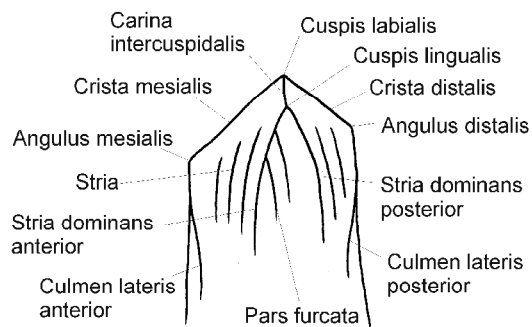


Fig. 3: Terminology of a schematic paramacellodid tooth crown (after RICHTER 1994).

Additionally, a subordinate lingual cusp, the *cuspis lingualis sensu RICHTER (1994)*, is developed in many taxa. The *cuspis lingualis* is situated in a less elevated position than is the *cuspis labialis*; it is formed by two apically converging main striae at their point of intersection. These main striae, the *stria dominans anterior sensu RICHTER (1994)* and the *stria dominans posterior sensu RICHTER (1994)*, run across the concave lingual surface of the tooth crown and are distinctly pronounced. This is the typical situation in most taxa of the Mesozoic Paramacellodidae as well as in most taxa of the recent Gerrhosauridae and Cordylidae.

However, among the Scincidae (and, to a lower extent, among the Lacertidae) the tooth crown morphology often differs from this pattern. Here, the *cuspis lingualis* is not formed by the striae dominantes but instead by a second system of apically converging cutting edges, the *crista lingualis anterior* and the *crista lingualis posterior*. These lingually situated cutting edges run parallel to the *cristae mesialis et distalis*, and are separated from them by the sulcus of the *antrum intercristatum* which is sometimes rather deep. This condition was found in numerous recent scincomorphan taxa; it is particularly abundant among the Scincidae.

A straight or concave ridge is often found running from the *cuspis labialis* to the *cuspis lingualis*. This ridge is the *carina intercuspidalis sensu RICHTER (1994)*. In many taxa with a well developed *antrum intercristatum*, the *carina intercuspidalis* crosses the sulcus transversally and divides the *antrum intercristatum* into an anterior and a posterior portion.

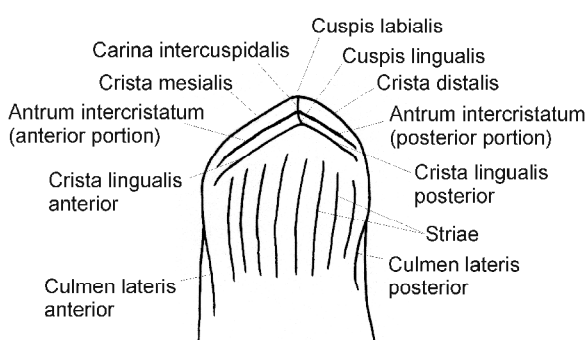


Fig. 4: Terminology of a schematic scincid tooth crown.

Laterally, the *crista mesialis* transforms into the angular, more or less prominent *angulus mesialis sensu RICHTER (1994)*, which represents the transition zone between the apical cutting edge and a downward running sinus-shaped ridge, the *culmen lateris anterior sensu RICHTER (1994)*. A comparable condition is found at the posterior section of the tooth crown, where the *crista distalis* transforms laterally into the rather acute *angulus distalis sensu RICHTER (1994)*; from here, the prominent ridge of the *culmen lateris posterior sensu RICHTER (1994)* runs downward in a sinus-shaped bow. Both *culmines lateres* decrease and finally vanish at the lingual surface of the transition zone between the tooth crown and the tooth neck.

The lingual surface of the tooth crown between the *culmines lateres* is concave or flattened in most scincomorphans; here, the characteristic striations are developed. The striae are often arranged in two bundles, an anterior and a posterior one, which converge apically without intersecting (in Paramacellodidae, several Gerrhosauridae, Cordylidae, and Scincidae). These systems of striations are often dominated by the aforementioned prominent striae dominantes. The striae dominantes are the only striae which meet apically. However, in numerous taxa, especially among the Scincidae, all striae are uniform in shape and length, and arranged in parallel orientation.

RICHTER (1994) described bifurcations of the striae dominantes; these are called the *partes furcatae sensu RICHTER (1994)*, which run across the otherwise not ornamented surface between the striae dominantes. The *partes furcatae* are developed either in the *stria dominans anterior* or in the *stria dominans posterior*, but never at both striae dominantes in a single tooth (RICHTER 1994). However, this restriction has to be broadened, since various stages of bifurcation exist in recent scincomorphans. In many taxa, the surface between the striae dominantes is heavily striated, and bifurcations were also found in subordinate striae as well as in the striae dominantes.

An extremely faint longitudinal wrinklage of the tooth enamel surfaces, the *lineae finae sensu RICHTER (1994)*, is sometimes developed in the spaces between the ordinary striae. The *lineae finae* are arranged parallel to the surrounding striations.

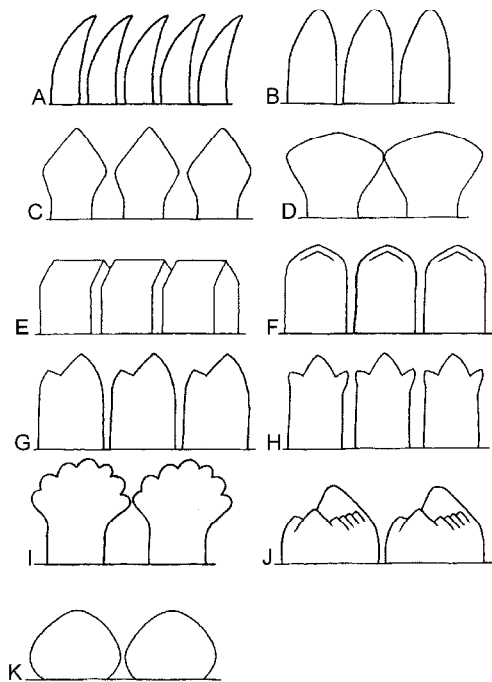


Fig. 5: Morphotypes of scincomorphan teeth:

A: unicuspid, recurved (these fang-like teeth are often found in burrowing skinks and in the sympysical region of many lacertids and teiids); B: unicuspid, simple conical (e.g., in some small insectivorous scincids and xantusiids); C: lanceolate or leaf-shaped (e.g., in the arboreal herbivorous skink *Corucia zebrata*); D: mesially expanded (in some partly herbivorous species of the scincid genus *Egernia*), here the occlusal cutting edges of all teeth together form a single cutting edge of the entire tooth row; E: chisel-shaped (e.g., in the semiaquatic scincid genus *Tribolonotus*), here the occlusal cutting edges of all teeth together form a single cutting edge of the entire tooth row; F: bicuspid condition with a cuspis labialis and a cuspis lingualis (in many cordylids, gerrhosaurids, and scincids, sometimes in lacertids, rarely in teiids and xantusiids); G: bicuspid condition with a central main cusp and a mesially situated lateral cusp (predominantly in lacertids and teiids); H: tricuspid condition with a central main cusp and a mesially and a distally situated lateral cusp respectively; I: multicuspid (e.g., in the gerrhosaurid *Angolosaurus skoogi*, the lacertid *Gallotia stehlini*, and the scincid *Macrosцинсус coctei*; all are herbivores), here the occlusal cutting edges of all teeth together form a single serrated cutting edge of the entire tooth row; J: molariform (e.g., in the predominantly herbivorous teiid genera *Dicrodon* and *Teius*); K: globular (e.g., in durophagous taxa of the Teiidae (*Ameiva fuscata*, *Ameiva plei*, *Tupinambis merianae*) and the Scincidae (*Cyclodomorphus melanops*, *Hemisphaeriodon gerrardi*, *Tiliqua gigas*, *Tiliqua occipitalis*, *Tiliqua scincoides*, *Tiliqua rugosa*, *Novoeumeces schneideri*)).

4. Descriptions of the dental morphologies of recent Scincomorpha

Class **Reptilia** LAURENTI, 1768

Subclass **Diapsida** OSBORN, 1903

Infraclass **Lepidosauria** HAECKEL, 1869

(Diagnosis: see BENTON 1985)

Superorder **Squamata** MERREM, 1820

(Diagnosis: see PORTER 1972, and BENTON 1985)

This superorder, which includes the lizards and snakes, is the most successful and diversified living group of reptiles. Except for Antarctica and extreme altitudes and latitudes, the suborder is presently cosmopolitan.

Order **Sauria** MCCARTNEY, 1802

(Diagnosis: see ESTES 1983)

Suborder **Lacertilia** OWEN, 1842

(Diagnosis: see ESTES 1983)

Infraorder **Scincomorpha** CAMP, 1923

(Diagnosis : see ESTES 1983, ESTES, DE QUEIROZ & GAUTHIER 1988, and RICHTER)

Superfamily **Scincoidea** OPPEL, 1811

(Diagnosis: see ESTES 1983, ESTES, DE QUEIROZ & GAUTHIER 1988, LANG 1991, and RICHTER 1994)

The Scincoidea (*sensu* ESTES et al. 1988) consist of the extant Scincidae and Cordyliformes *sensu* LANG (Gerrhosauridae and Cordylidae, LANG 1991) and, additionally, of the fossil Paramacellodidae from the Upper Jurassic and Lower Cretaceous.

4.1 Systematics and descriptions of the recent Scincomorpha

4.1.1 Family Cordylidae GRAY, 1837

Consists of two subfamilies (Chamaesaurinae, Cordylinae).

(Diagnosis: see ESTES 1983, MCDOWELL & BOGERT 1954; OLMO & ODIERNA 1980; RIEPPEL 1980)

Cordylids are usually robust-bodied lizards with strongly keeled or very spiny tails. Osteoderms are well developed dorsally from head to tail. Their chests and bellies bear a lighter osteoderm shield and often abutting, smooth scales. Scales are arranged in circles around the body. *Chamaesaura* has extremely reduced limbs and a snakelike body.

4.1.1.1 Subfamily Chamaesaurinae

(Diagnosis: see KUHN 1940)

Chamaesaura Schneider, 1801

Chamaesaura macrolepis (COPE, 1862)

(Pl. I, Figs. 1-3)

Number of examined specimens: 3 adults

Distribution:

Zimbabwe, Swaziland, Republic of South Africa, Tanzania, Zambia, and Angola.

Dental morphology:

The dentaries of the ophiomorph *Chamaesaura macrolepis* bear 24 to 25 tooth positions. The dentition is homodont. The teeth of specimen SDS 59535 are cylindrical and slender. The tooth crowns are lingually flattened. All teeth are unicuspid. The cross-sections of tooth bases are identical with cross-sections of the tooth necks. The tooth crowns are rounded since they lack anguli. The culmen lateris anterior and the culmen lateris posterior are the same length. The pronounced stria dominans anterior converges with the shorter stria dominans posterior. The two striae dominantes form the cuspis lingualis at their point of intersection. The carina intercuspidalis runs as a transversal ridge from the cuspis lingualis to the centrally positioned cuspis labialis. The resorption pits are horizontally expanded. The teeth appear to be bend in posterior direction as a result of the oblique

longitudinal axes. The ratio toothlength:diameter of tooth neck is 4.2:1.0.

In specimen ZFMK 7822, the teeth are short and stout. Here the ratio toothlength:diameter of tooth neck amounts to 2.0:1.0. Striations are not developed; the culmines lateres anterior et posterior alone are visible.

Diet:

The diet of *C. macrolepis* consists of small orthopterans and spiders (LOVERIDGE 1944). This author mentions flies, moths, grasshoppers, caterpillars, crickets, and beetle larvae as food sources for other species of the genus *Chamaesaura*.

Remarks:

A progressive reduction of limbs occurs within the genus *Chamaesaura*. The limb reduction is most evolved in *Chamaesaura macrolepis*, where only vestiges of hind limbs are present. *C. aena* still shows four limbs which are slightly reduced, but have five claws. *C. anguina* also has four limbs, but those are styliiform and show only two claws (DUERDEN 1922).

Chamaesaura is the most "primitive" genus of the Cordylidae (BROSCHINSKI & SIGOGNEAU-RUSSELL 1996, LANG 1991).

4.1.1.2 Subfamily Cordylinae

(Diagnosis: see KUHN 1940)

Cordylus LAURENTI, 1768

Cordylus cataphractus BOIE, 1828

(Pl. I, Figs. 4-6)

Number of examined specimens: 4 adults

Distribution:

Southwestern Africa (western Cape Province).

Dental morphology:

The dentaries of *Cordylus cataphractus* bear 16 to 18 tooth positions. The cross-sections of the tooth bases are circular. The tooth necks are shaft-like in shape. The lingual surfaces of the tooth crowns are distinctly flattened. The tooth sockets are very narrow whereas the teeth become more broadened apically. The maximum widths are reached in the tooth crowns, which distinctly contrast with the tooth necks. The angle between the crista mesialis and the crista distalis encloses 140 degrees. As a result of this large apical angle,

the occlusal cutting edges run almost horizontally and, together with the prominent angulus mesialis and angulus distalis, give rise to the subquadratic appearance of the tooth crown. The labial surfaces of the tooth crowns are slightly convex and smooth. A pronounced pattern of striations is developed on the lingual surface of the tooth crown between the culmen lateris anterior and the culmen lateris posterior. Apically, the prominent stria dominans anterior and an equally prominent stria dominans posterior together form the acute angle of the elevated cuspis lingualis. In many teeth of *C. cataphractus*, one or more partes furcatae are developed between the two striae dominantes. The point of intersection between the pars furcata and the stria dominans posterior is mostly situated in the immediate vicinity of the cuspis lingualis. The transversally running carina intercuspidalis is very short and straight. Additional striae are often developed between either the stria dominans anterior and the culmen lateris anterior or between the stria dominans posterior and the culmen lateris posterior. The number of these striae can vary between none and three in several teeth of an individual. Mostly there is one stria developed in this area. In older teeth the striations often become unrecognizable.

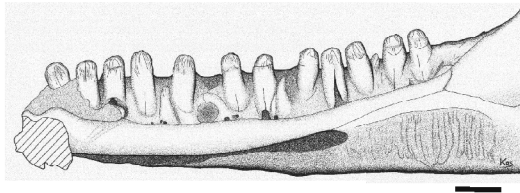


Fig. 6: *Cordylus cataphractus*
(specimen SRK 00.147)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

Stomach contents analyses on *C. cataphractus* showed a diet dominated by termites (MOUTON 1999). Captive specimens of this species consumed larvae of the beetle *Zophobas morio*, caterpillars of the moth *Galleria mellonella*, and mediterranean crickets (*Grillus bimaculatus*). Captive juveniles of *C. cataphractus* consume almost exclusively moth-larvae and regularly refused crickets (WESIACK & VOGEL 1993). *Tenebrio*-larvae (mealworms) were often regurgitated while earthworms were refused. However, *C. cataphractus* was observed eating other lizards (Lacertidae) and eggs (LOVERIDGE 1944).

Remarks:

These viviparous lizards roll themselves up like a ball as a defensive behavior, grasp their tail with their jaws and offer their spiny back to the predator.

Cordylus cordylus (LINNAEUS, 1758)

Number of examined specimens: 3 adults

Distribution:

Southern Cape Province, southeast Orange Free State to Natal.

Dental morphology:

Cordylus cordylus bears approximately 20 tooth positions in each jaw ramus. The tooth bases are slender and the tooth necks are of cylindrical shape. The tooth crowns are mesially widened. This expansion of the tooth crowns is most striking in the posterior section of the tooth row, which leads to a distinct subheterodonty. The tooth crowns rise above the labial parapet of the dentary. The labial surfaces of the teeth are slightly convex and perfectly smooth. In contrast to this, the lingual surfaces of the tooth crowns are flattened or concave and show prominent striations (especially in the teeth of the central portion of the tooth row). The culmines lateres anterior et posterior are the same length. The cuspis labialis and the cuspis lingualis are not separated in most teeth; they are situated in a slightly posterior position. Therefore, the crista mesialis is longer than the crista distalis. The angulus distalis of a tooth occasionally contacts the angulus mesialis of the following tooth; accordingly the tooth crowns are in line, whereas the tooth bases are in a more widely spaced arrangement.

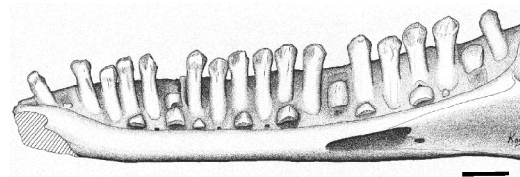


Fig. 7: *Cordylus cordylus*
(specimen SRK 00.047)
Right dentary; lingual view
Scale bar: 1.0 mm

The striations of the investigated specimens of *C. cordylus* are not arranged in complex patterns. In some teeth, the stria dominans anterior and the stria dominans posterior are well developed; other teeth even lack these

main stations. Especially the posteriormost teeth are almost always smooth. Bundles of prominent vertical striac are present on the anterior lingual surfaces of the tooth crowns in the central portion of the tooth row. The resorption pits are circular.

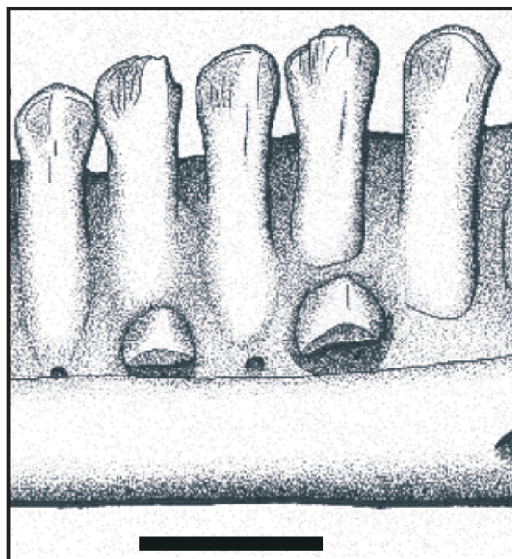


Fig. 8: *Cordylus cordylus* (specimen SRK 00.047)
Close up view of the central portion of the right dentary (tooth positions 10-14); lingual view
Scale bar: 1.0 mm

Diet:

The prey of *C. c. cordylus* consists of beetles, cockroaches, crickets, and locusts. Additionally, juvenile skins of the genus *Mabuya* are consumed. Wild living *C. c. cordylus* accept offered meat, pieces of oranges, and consume lichens from rocks (LOVERIDGE 1944). Captive juveniles of the dwarf girdled lizard consumed earthworms, locusts, cockroaches, caterpillars, flies, moths, *Tenebrio molitor*-larvae, and pieces of meat.

***Cordylus giganteus* SMITH, 1844**

Number of examined specimens: 4 adults

Distribution:

Republic of South Africa, northeast Orange Free State, western Natal, and southeastern Transvaal.

Dental morphology :

The tooth morphology of *Cordylus giganteus* differs fundamentally from the dental morphology of other Cordylidae. The dentaries bear 22 to 25 tooth positions. The tooth bases

are strongly broadened transversally, which results in a chisel-shaped appearance of the teeth. The cross-sections of the tooth bases resemble the outlines of the number 8 since the surfaces of the tooth flanks (*Lata sensu* RICHTER 1994) are concave shaped. The teeth appear very symmetrical since the cusp is situated in a central position, and the culmines lateres are the same length. The enamel surface between the culmen lateris anterior and the culmen lateris posterior is almost flat, whereas the surfaces are concave in the immediate vicinity of the culmines. The labial surfaces of the teeth are smooth. The lingual surfaces of the extraordinary compressed tooth crowns are also smooth in the majority of the investigated specimens. If striations are developed in this area at all, they are very weak and are not arranged in complex patterns. A striking character of *C. giganteus* is the morphology of the tooth crowns, which are very slim compared to other Cordylidae. The sinus-shaped anguli mesialis et distalis are distinctly pronounced. The angle between the crista mesialis and the crista distalis encloses 120 degrees. The resorption pits are of circular shape.

Numerous foramina are developed in the bony material of the interdentary spaces; these foramina are arranged in lines and strongly resemble similar structures in the anguimorph *Ophisaurus apodus*.

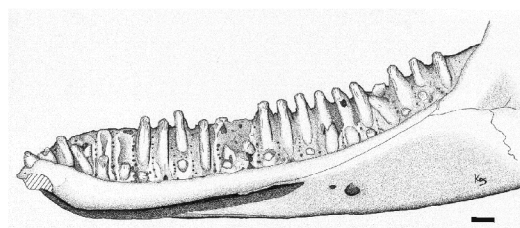


Fig. 9: *Cordylus giganteus* (specimen SRK 00.150)
Right dentary; lingual view
Scale bar: 1.0 mm



Fig. 10: *Cordylus giganteus* (specimen SRK 00.150)
Right dentary; occlusal view
Scale bar: 1.0 mm

Diet:

C. giganteus preys on various invertebrates, such as beetles, grasshoppers, millipeds, termites, and spiders. Vertebrates and plant matter are also assumed to form parts of the diet (ADOLPHS 1987). Captive specimens of *C. giganteus* accepted cockroaches, *Tenebrio*-larvae, small frogs, pinky mice, and raw meat (LOVERIDGE 1944). *C. giganteus* consumed locusts, crickets, house crickets, and fresh fruits in the vivarium of another author (ROGNER 1994).

Cordylus johnstoni

Number of examined specimens: 1 adult

Remark:

Cordylus johnstoni is not a valid species, but since several striking characters were found in the dentition of specimen SDS 63039, and because of the uncertainty in grouping this specimen with another taxon, the name is retained in this thesis.

Dental morphology:

The teeth of specimen SDS 63039 are short and thickset. The tooth crowns hardly rise above the labial parapet of the dentary. The teeth reach their largest diameters in the middle section of the tooth necks. The cross-sections of the teeth are circular. The culmen lateris anterior and the culmen lateris posterior are the same length. The labial surfaces of the teeth are smooth whereas prominent striations are developed on the lingual surfaces of the tooth crowns. The stria dominans anterior and the stria dominans posterior converge at a 90° angle and form the cuspis lingualis. The cuspis lingualis is connected with the cuspis labialis by an extremely short carina intercuspidalis. The crista mesialis and the crista distalis encompass an angle of 160 degrees; this large apical angle results in a rounded shape of the tooth crown. One or seldom two pares furcatae are developed in several teeth. Maximally two prominent striae are situated between the stria dominans anterior and the culmen lateris anterior. Exceptionally, additional striae are found between the stria dominans posterior and the culmen lateris posterior. The ratio toothlength:diameter of tooth neck is 2.2:1.0. The resorption pits are horizontally expanded. Some small foramina are developed in the lingual bony matrix of the dentary; these foramina are restricted to areas in the immediate vicinity of the tooth bases. The total

number of these foramina is smaller than in *Cordylus giganteus*. The teeth of *C. johnstoni* are distinctly narrowly spaced.

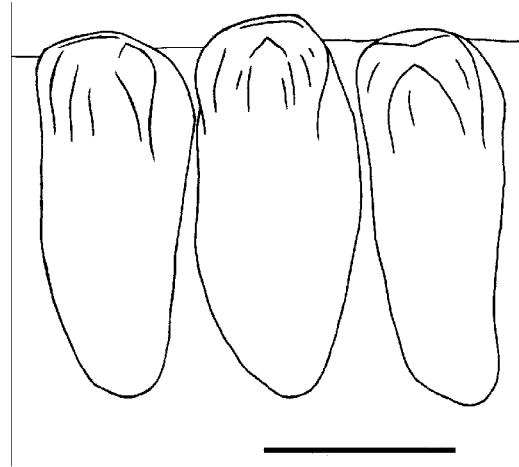


Fig. 11: *Cordylus johnstoni* nomen dubium (specimen SDS 63039)
Schematic drawing of the central portion of the right dentary, illustrating the complex pattern of striations of the tooth crowns; lingual view
Scale bar: 0.5 mm

Diet:

No data concerning the dietary spectrum of *C. johnstoni* are available.

Cordylus peersi (HEWITT, 1932)
(Pl. I, Figs. 7-8)

Number of examined specimens: 2 adults

Distribution:

Little Namaqualand.

Dental morphology:

The dentaries of *Cordylus peersi* bear 21 tooth positions on average. A weak subheterodonty is developed in this species. The teeth of the symphyseal region as well as teeth of the central portion of the tooth row are cylindrical whereas the posterior teeth are conical in lingual view. The cross-sections of the tooth necks are circular. The labial surfaces of the teeth are convex and smooth. The lingual surfaces of the tooth crowns are heavily striated in specimen SRK 00.060. The teeth of the anterior half of the tooth row are bicuspid. The cuspis labialis is connected with the lower situated cuspis lingualis by the transversal oriented carina intercuspidalis which forms a concave sulcus, whose deepest point is situated near the cuspis labialis. Similar conditions were

described for various species of the Gekkonidae (SUMIDA & MURPHY 1987). Lingual of the crista mesialis, a parallel ridge runs from the cuspis lingualis to the culmen lateris anterior. Therefore, the apical cutting edge, which is formed by the cristae mesialis et distalis appears to be two-staged. Both cusps form sharp, pyramidally formed, and slightly mesolingually bent tips. The striations are dominated by the striae dominantes anterior et posterior. A maximum of three additional striae are developed in the spaces between these two main striae and the culmines lateres. In the posterior parts of the tooth row, the patterns of striations are less complex. The complete pattern of striations is best preserved at the replacement tooth in tooth position 7 of specimen SRK 00.060. This embryonal tooth was not in function and wear facets are therefore absent. In specimen ZFMK 29406, only two striae are found which are the striae dominantes anterior et posterior. The ratio toothlength:diameter of tooth neck is 1.8:1.0. The resorption pits of *C. peersi* are dorsally expanded.

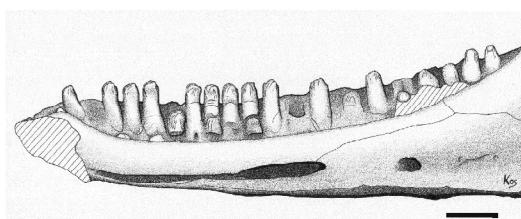


Fig. 12: *Cordylus peersi*
(specimen SRK 00.060)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

C. peersi predominantly consumes arthropods. Large insects (including caterpillars) are preferred.

***Cordylus polyzonus* SMITH, 1838**

Number of examined specimens: 8 adults

Distribution:

Central and western Cape Province, western Orange Free State, and southern Namibia.

Dental morphology:

The dentaries of *Cordylus polyzonus* bear 22 tooth positions on average. In lingual view, the outer shapes of the teeth vary from short and thickset (specimen SRK 00.048) to

slender (specimen ZFMK 7805). As in *Cordylus giganteus*, several teeth of *C. polyzonus* show transversally expanded bases. All labial enamel surfaces are smooth. Prominent culmines lateres anterior et posterior are developed at the lingual surface of the tooth crown. Some distinct striae dominantes anterior et posterior are developed on the enamel surfaces between the culmines lateres in most teeth. The two main striae converge at the cuspis lingualis, which coincides with the cuspis labialis (specimen ZFMK 7805) or is separated from the cuspis labialis by a short carina intercuspidalis (specimen BMNH 63.2.21.28). The angle between the stria dominans anterior and the stria dominans posterior varies in different teeth. In several teeth, up to seven striae are found between the two main striae. One or two additional striae are often situated either between the stria dominans anterior and the culmen lateris anterior or between the stria dominans posterior and the culmen lateris posterior. The crista mesialis is often longer than the crista distalis. The cuspis labialis is recurved in the posterolingual direction. The resorption pits are shaped circularly.

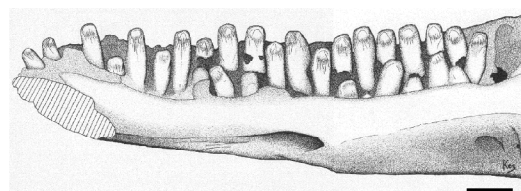


Fig. 13: *Cordylus polyzonus*
(specimen SRK 00.048)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

C. polyzonus consumes beetles and grasshoppers in its natural habitat (ROGNER 1994). In addition, stomach contents analyses showed colorful grasshoppers of the species *Zonocercus elegans* (known to induce nausea when eaten) as well as grass stems (LOVERIDGE 1944).

***Cordylus tropidosternum* (COPE, 1869)**

Number of examined specimens: 10 adults

Distribution:

Eastern and southern Africa.

Dental morphology :

The dentaries of the investigated *Cordylus tropidosternum* specimens bear 21 tooth positions on average. The teeth are slender and show transversally elongated oval cross-sections. The apical thirds of the teeth rise above the labial parapet of the dentary. The labial surfaces of the teeth are convex and smooth. The lingual surfaces of the tooth crowns are inwardly curved. In this area, striations are developed which form complex patterns in several teeth. The culmines lateres anterior et posterior are distinctly pronounced. The crista mesialis is longer than the crista distalis, which makes the cuspis labialis shift from a central position into a slightly posterior position. The majority of the teeth show a well developed stria dominans anterior and a prominent stria dominans posterior as well. The angle between these two main striae encompasses 70 degrees. In specimens SRK 00.001 and ZFMK 7810 the cuspis labialis is connected with the pointed and pronounced cuspis lingualis by a concave carina intercuspidalis, whereas the carina intercuspidalis is absent in specimen ZFMK 14849. The development of additional striations underlies intraspecific variation. Additional striations can be absent in one specimen or form complex patterns in another specimen. The formation of complex patterns leads to the development of several partes furcatae and maximally two striae which are situated either between the culmen lateris anterior and the stria dominans anterior or between the culmen lateris posterior and the stria dominans posterior. The cuspis labialis is often more mesolingually recurved than the cuspis lingualis. The ratio toothlength:diameter of tooth neck is 4.8:1.0. The resorption pits are circular or slightly expanded in the ventral direction.

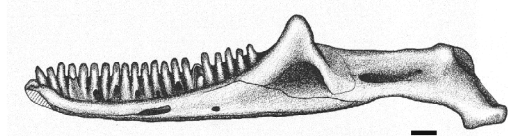


Fig. 14: *Cordylus t. tropidosternum*
(specimen SRK 00.001)
Right mandible; lingual view
Scale bar: 1.0 mm

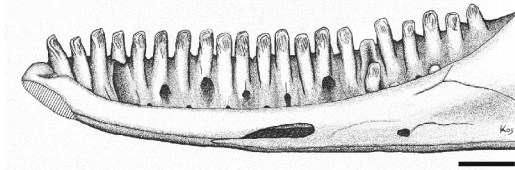


Fig. 15: *Cordylus t. tropidosternum*
(specimen SRK 00.001)
Right dentary; lingual view
Scale bar: 1.0 mm

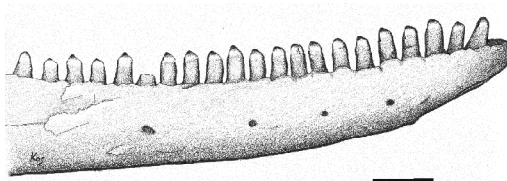


Fig. 16: *Cordylus t. tropidosternum*
(specimen SRK 00.001)
Right mandible; labial view
Scale bar: 1.0 mm

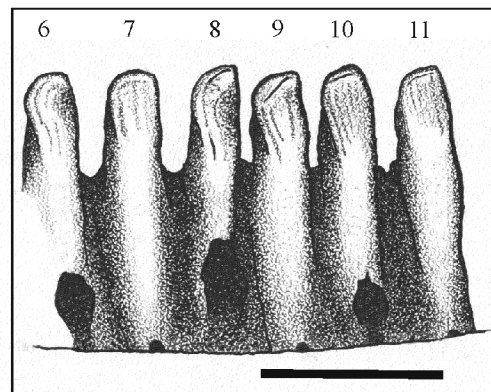


Fig. 17: *Cordylus t. tropidosternum*
(specimen SRK 00.001)
Central portion of the right tooth row, demonstrating
the patterns of striations; lingual view
Scale bar: 1.0 mm

Diet:

LOVERIDGE treated this species as a subspecies of *Cordylus cordylus* (LOVERIDGE 1944). On the basis of stomach contents analyses, this author recorded termites, glow worms, and small grasshoppers as prey items. Insect larvae are also consumed (AUERBACH 1985). Captive specimens of *C. tropidosternum* in the vivarium of BROSCINSKI consume larvae of *Tenebrio molitor*, occasionally spiders, and small house crickets *Acheta domestica* (pers. observation). These captive specimens consumed large amounts of the

soft-bodied larvae from the moth *Galleria mellonella* (BROSCHINSKI, pers. comm.). At least two of BROSCHINSKI's older individuals showed difficulties in either locating or chewing the prey items. After maceration, these specimens showed a massive loss of teeth in their lower as well as in their upper jaws.

Cordylus ukingensis (LOVERIDGE, 1932)

Number of examined specimens: 1 adult

Distribution:

Southern highlands of Tanzania.

Dental morphology:

The only available specimen of *Cordylus ukingensis*, SRK 00.022, is a female. The jaw rami bear 21 tooth positions each. A distinct subheterodonty is developed within the tooth row. Accordingly, the anterior teeth are cylindrical and slender whereas the posterior teeth appear robust and stocky. The tooth crowns scarcely contrast with the tooth necks.

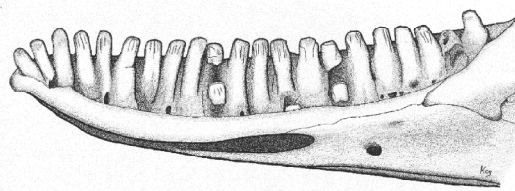


Fig. 18: *Cordylus ukingensis*
(specimen SRK 00.022)
Right dentary; lingual view
Scale bar: 1.0 mm

The culmines lateres anterior et posterior are more pronounced in the posterior teeth than they are in the anterior teeth. The labial enamel surfaces are smooth whereas the lingual surfaces of the tooth crowns are slightly concave or flattened and show irregular bundles of weakly developed striae. These striations are not arranged in complex patterns. The transition zones between the anterior flank and the crista mesialis, as well as between the posterior flank and the crista distalis, are each shaped as a sinus and not as a sharp angulus, leading to the blunt shape of the tooth crown. The longitudinal axes of the anterior teeth bend caudally (except tooth positions 1 to 5), while the longitudinal axes of the posterior teeth bend in rostral direction. The resorption pits are circular in the initial phase of the replacement process and become ventrally elongated during progressing replacement. Tooth replacement

takes place synchronously in about each third tooth.

Diet:

No data on the prey spectrum of *C. ukingensis* are available.

Cordylus warreni (BOULENGER, 1908)

Number of examined specimens: 7 adults

Distribution:

Southern Africa (several subspecies).

Dental morphology:

The dentaries of *Cordylus warreni* bear 19 to 20 tooth positions on average. The teeth are robust and relatively narrowly spaced. The tooth necks and tooth bases are bulbous. The narrow tooth crowns contrast with the tooth necks. On the lingual enamel surface, a depression runs from the tooth basis to the tooth crown in several teeth. This structure is not present in all investigated specimens. The cross-sections of the teeth are slightly expanded in transversal direction. The labial enamel surfaces are smooth. The crista mesialis is longer than the crista distalis in the anterior teeth whereas these two cutting edges form a straight line in the posterior teeth. The sinus-shaped culmines lateres frame a concave area. On this concave surface, characteristic patterns of striations are found. The prominent striae dominantes anterior et posterior converge to an angle of 45° to 60° and form the elevated cuspis lingualis. Bundles of two or three additional striae are situated between the main striae and the culmines lateres. These striations run parallel to the striae dominantes but they end apically before intersecting. Numerous faint striae are developed in the transition zone between the tooth neck and the tooth crown on the lingual surface of the 11th tooth of the right dentary in specimen SRK 00.066. The ratio toothlength:diameter of tooth neck is 2.4:1.0. The resorption pits are expanded in the apical direction.

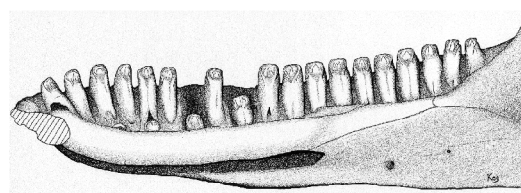


Fig. 19: *Cordylus warreni*
(specimen SRK 00.066)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The stomach of a specimen of *C. w. warreni* contained 32 *Eristalis*-maggots and shell fragments of a large snail. The stomach of another specimen contained millipedes and ants, and a large grasshopper was found in the stomach of a third specimen (LOVERIDGE 1944). These compounds suggest a generalized diet for this species. Captive *C. warreni* consumed arthropods, frogs, lizards, and terrestrial snails (ROGNER 1994).

Platysaurus SMITH, 1844

Platysaurus capensis SMITH, 1844
(Pl. I, Fig. 9)

Number of examined specimens: 4 adults

Distribution:

Southern Namibia and adjacent Cape Province.

Dental morphology:

The dentaries of *Platysaurus capensis* bear 22 to 24 homodont teeth. The slender and cylindrical teeth are shaped in a peg-like fashion. The interdentary spaces correspond to the half of a tooth diameter. The convex labial surfaces of the teeth are unwrinkled. The lingual surfaces of the tooth crowns are slightly flattened and the framing culmines lateres anterior et posterior are only weakly developed. The crista mesialis is always longer than the crista distalis. This condition leads to a posterolingual recurvature of the tooth tips. The anterior teeth are slightly more pointed than the posterior teeth and show a tendency for bicuspidity. The subordinate cusp (the cuspis lingualis) is situated directly underneath the cuspis labialis. Both cusps are connected by the steep ridge of the concave carina intercuspidalis.

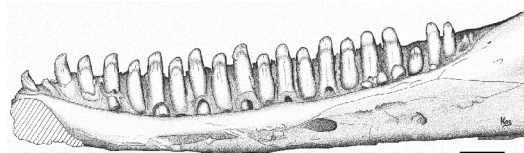


Fig. 20: *Platysaurus capensis*
(specimen SRK 00.188)
Right dentary; lingual view
Scale bar: 1.0 mm

The tooth crowns of the posterior teeth are perfectly blunt. Striations are restricted to the lingual surfaces of the tooth crowns. However,

complex patterns of striations were not found. The tooth crowns rise above the labial parapet of the dentary. The ratio toothlength:diameter of tooth neck is 3.8:1.0. The resorption pits are circular in shape.

Diet:

P. capensis consumes small insects.

Remarks:

The members of the genus *Platysaurus* inhabit crevices and fissures of vertical rock walls in Southern Africa, where these agile hunters prey on minute insects. The flattened shape of the body is an adaptation to the narrow rock crevices the lizards use to hide in the case of danger.

Platysaurus intermedius MATSCHIE, 1891

Number of examined specimens: 1 adult

Distribution:

Southern Africa (several subspecies).

Dental morphology:

The only available specimen of this species belongs to the subspecies *Platysaurus intermedius rhodesianus* FITZSIMONS, 1941. The right dentary bears 24 tooth positions. The teeth are homodont, short and poor in characteristic features. The interdentary spaces correspond to the radius of the tooth cross-sections. The lingual surfaces of the tooth crowns are flattened whereas the labial surfaces are convex. The cusps of most teeth are lost or worn. If present, the cusp is distinctly pointed and slightly recurved in the lingual direction. The culmines lateres anterior et posterior run across the lata and do not turn to the lingual surfaces of the teeth. All teeth lack anguli, which results in perfectly conical outlines of the teeth. Striations are absent. In several teeth of specimen BMNH 1908.5.20.3, the cusps are broken so that the boundary plane between dentine and tooth enamel (the EDJ) is visible. The thickness of the enamel layers is identical at all sides of the teeth. The resorption pits are covered by mucosa and therefore cannot be described here.

Diet:

Stomach contents analyses in 285 specimens of *P. intermedius rhodesianus* proved the following dietary composition: 8 % Blattidae, 1 % Mantidae, 15 % Locustidae, 4 % Isoptera, 1 % Neuroptera, 5 % Hemiptera, 10 % Lepidoptera-larvac, 33 % Coleoptera (adults), 4 % Coleoptera-larvae, 2 % Diptera, 35 % Hymenoptera (ants), 10 % Hymenoptera

(bees, wasps), 4 % Arachnida, 3 % Diplopoda, 1 % vertebrates (juvenile *Typhlosaurus* sp.), and 17 % plant matter (BROADLEY 1978).

Pseudocordylus SMITH, 1838

Pseudocordylus microlepidotus (CUVIER, 1829)

(Pl. I, Fig. 10)

The status of this genus is unclear at the moment.

Number of examined specimens: 3 adults

Distribution:

Cape Province and Little Namaqualand.

Dental morphology :

The mandibles of *Pseudocordylus microlepidotus* bear 18 to 21 tooth positions. The teeth are slender and the tooth crowns contrast distinctly with the tooth necks. The cross-sections of the teeth show a conspicuous transversal expansion. The flanks are flattened. The labial surfaces of the teeth are convex and unwrinkled. The lingual surfaces of the tooth crowns are inwardly curved. The crista mesialis is a little longer than the crista distalis. These two cutting edges form the cuspis lingualis, which is directed posterolingually. The angle between the two cutting edges appears very large (160°) in lingual view. Accordingly, the outer shape of the tooth crown is blunt. The culmen lateris anterior and the culmen lateris posterior are the same length; together, the culmines frame the concave inner surface of the tooth crown. The anguli mesialis et distalis are only weakly pronounced. The pattern of striations varies individually. Many teeth of specimen BMNH 64.2.21.27 e.g. completely lack striations, while other teeth of this specimen show at least weakly developed striae dominantes anterior et posterior. Contrastly, the system of striations is well developed in specimen ZFMK 7820. Here, the predominantly shorter striae dominantes anterior and the longer striae dominantes posterior form the prominent cuspis lingualis at their point of intersection, which is situated underneath the cuspis labialis. Both cusps are connected by the ridge of the relatively long carina intercuspidalis. The angle encompassed by the two converging striae dominantes amounts to 80°. A rather prominent isolated stria is developed in most teeth between the stria dominans anterior and the culmen lateris

anterior, and between the stria dominans posterior and the culmen lateris posterior as well. A maximum of five additional striae are found in the concave area between the two main striae. These additional striae run parallel in the basal portion of the tooth crown and they almost converge underneath the cuspis lingualis. The distances between these striae are very uniform. The ratio toothlength:diameter of tooth neck is 3.1:1.0.

Diet:

P. microlepidotus microlepidotus consumes wingless locusts and lichens (LOVERIDGE 1944). The dietary spectrum of *P. microlepidotus fasciatus* includes beetles, crickets, grasshoppers, isopods, snails, and even small lizards (LOVERIDGE 1944). In contrast to the related *Pseudocordylus capensis*, which in nature preys predominantly on bees and wasps, *P. microlepidotus* is less specialized. In captivity, these lizards consume insects, pinky mice, dog food, and occasionally fruits and vegetables. The members of this species often developed an individual taste in captivity (ROGNER 1994).

Remarks:

Under a functional morphologically point of view, the individual preference for certain food items is reflected by the wide variety of tooth crown morphologies within this species.

4.1.2 Family Gerrhosauridae
BOULENGER, 1884

Consists of two subfamilies (Gerrhosaurinae, Zonosaurinae).

Diagnosis:

Scales are arranged in transverse rows and are underlain by osteoderms but no spines to the extent seen in cordylids. Prominent lateral fold along the body. Some taxa with reduced limbs (genus *Tetradactylus*).

4.1.2.1 Subfamily Gerrhosaurinae

Angolosaurus FITZSIMONS, 1953

Angolosaurus skoogi (ANDERSSON, 1916)

(Pl. I, Figs. 11-12)

Number of examined specimens: 1 adult

Distribution:

Northern Namib desert of Namibia and southern Angola.

Dental morphology:

Angolosaurus skoogi is the only member of the Gerrhosauridae characterized by a multicuspid dentition. The right dentary of ZFMK 7819 bears 14 tooth positions. The anterior teeth are unicuspid; the number of additional cusps increases in the caudal direction. The posteriormost teeth show a maximum of 7 cusps. The replacement teeth already have the complete count of lateral cusps which is characteristic for the particular tooth position. The tooth bases are cylindrical and have almost circular cross-sections. The tooth crowns are expanded mesially. The flattened apical half of the tooth fans out hand-like and transforms into several cusps. These cusps form a mesial row in which the central cusp indicates the highest and most prominent elevation. The lateral cusps themselves are blunt and have a sagittal cutting edge. The side cusps decrease in size from the central cusp in the anterior as well as in the posterior direction. All enamel surfaces are smooth. Striations are absent. The mode of tooth replacement is iguanid. The resorption pits are ventrally elongated.

Diet:

The diet of *A. skoogi* is rather unusual since this species is the only member of the Gerrhosauridae which is predominately herbivore (BÖHME, W., pers. comm.). These plated lizards feed almost exclusively on seeds in some parts of their desert-like habitat in the northern Namib (GREENE 1982).

Remarks:

The monospecific genus *Angolosaurus* forms the stem Angolosaurini of the subfamily Gerrhosaurinae.

The mesially widened multicuspid teeth are interpreted as an adaptation to a vegetarian diet. *Angolosaurus* is regarded as the earliest diverging taxon of the Gerrhosauridae (LANG 1991).

***Gerrhosaurus* WIEGMANN, 1828**

***Gerrhosaurus flavigularis* WIEGMANN, 1828**
(Pl. I, Figs. 13-15)

Number of examined specimens: 4 adults

Distribution:

Ethiopia, Kenya, Somalia, Sudan, Tanzania, Malawi, Zambia, Mozambique, eastern Republic of South Africa, Swaziland, Botswana, Namibia, and Zimbabwe.

Dental morphology:

Each jaw ramus of *Gerrhosaurus flavigularis* bears 19 to 20 unicuspid teeth. In the posterior teeth of one specimen (the left mandible of specimen USNM KdQ 134), a distinct tendency for bicuspidity was observed. Hence, a lateral cusp is situated anterolaterally of the main apex in this individual. This lateral cusp originates from the angulus mesialis. Here, the crista mesialis runs in a V-shaped manner. However, the teeth are usually slender and cylindrical; the tooth necks show circular cross-sections. The cross-sections of the tooth bases are transversally expanded. The collar-shaped culmines lateres anterior et posterior are distinctly pronounced. Both culmines converge apically. In most teeth, the culmen lateris anterior extends further in basal direction than does the shorter culmen lateris posterior. Prominent striations are found on the lingual enamel surfaces. These striations underlie great intraspecific variability. These various patterns of striations include individuals with a short stria dominans posterior and weak lineae finae (e.g., specimen AMNH 73607) as well as individuals with a complex tooth crown morphology (e.g., specimen USNM KdQ 134). In *G. flavigularis*, this complex tooth crown morphology consists mainly of the apically converging striae dominantes anterior et posterior; these form the prominent cuspis lingualis at their point of intersection and are connected with the elevated cuspis labialis by the transversally running carina intercuspidalis. The cuspis labialis represents the highest altitude of the tooth. The stria dominans anterior shows a bifurcation basally so that a well developed pars furcata branches off the main stria. Another prominent stria runs parallel to the culmen lateris anterior and crosses the lingual surface of the mesially situated side cusp; this stria almost reaches the angulus mesialis. Some less prominent additional striae run between the stria dominans posterior and the rounded sinus-shaped angulus distalis. The entire lingual surfaces of the tooth crowns are slightly concave, whereas the labial surfaces are somehow more curved outward. The resorption pits are ventrally expanded. One individual, belonging to the subspecies *G. f. fitzsimonsi* (specimen ZFMK 7813), shows a dental morphology that strongly resembles the

dental morphology of specimen USNM KdQ 134; however, it lacks the complex patterns of striations found in the later.

Diet:

G. flavigularis is predominantly insectivorous. The diet consists of grasshoppers, locusts, crickets, cockroaches, mantids, ants, millipedes, bananas, and watermelon (LOVERIDGE 1942). Another less specified quotation mentions arthropods and plant matter as parts of the diet of *G. flavigularis* (AUERBACH 1985). In captivity, these plated lizards consume pinky mice, juvenile birds, reptiles, moths, and sweet fruits (NIETZKE 1998).

***Gerrhosaurus major* DUMÉRIL, 1851**

Number of examined specimens: 4 adults

Distribution:

Eastern and southeastern Africa.

Dental morphology:

Gerrhosaurus major bears 16 to 18 homodont teeth in each mandible. All teeth are unicuspid. The tooth necks show circular cross-sections whereas the tooth bases are slightly widened transversally. The tooth crowns are slightly concave lingually and they are convex labially. The concave inner surfaces of the tooth crowns are framed by the culmines lateres. Both culmines are approximately equal in length and stretch across 20 % of the total tooth length. The angle which is encompassed by the crista mesialis and the crista distalis is 160° to 170°. As a result of this extended apical angle, the sagittal cutting edge runs almost horizontal.

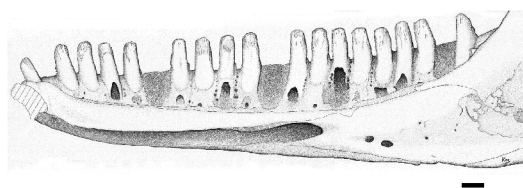


Fig. 21: *Gerrhosaurus major*
(specimen SRK 00.156)
Right dentary; lingual view
Scale bar: 1.0 mm

Striations are hardly visible. Some specimens with weak reliefs on the lingual enamel surfaces show striae dominantes anterior and striae dominantes posterior, which are slightly silhouetted against the tooth surfaces. *G. major* lacks complex patterns of striations. All labial

enamel surfaces are smooth. The resorption pits are ventrally elongated.

Diet:

The captive *G. major* specimens of BROSCINSKI showed a predominantly insectivore diet (BROSCINSKI, pers. comm.), consisting of *Tenebrio molitor* and *Zophobas morio* larvae, crickets, and locusts. Occasionally, pinky mice and bananas dipped in honey were offered to the lizards and eaten voraciously. In nature, *G. major* preys on additional carabids and polydesmids (LOVERIDGE 1942). In addition to the former items, these plated lizards also consume smaller lizards, bananas, diverse meat-pieces, mice, fish, spiders, and larger insects. Large prey items are killed by being shaken and crushed against rocks. Fecal pellets of *G. major*-specimens from Kenya suggested a preference for large snails (*Achatina* sp.). The soft parts of the snails are torn off by quick bites, since *G. major* is not capable of crushing the shells of the snails. Stomach contents of *G. m. major* showed the leg of a beetle together with small beans and grass (LOVERIDGE 1942). Grass is often consumed involuntary during foraging. Stomach contents of 23 specimens of *G. m. bottegoi* included winged termites (LOVERIDGE 1942).

***Gerrhosaurus validus* SMITH, 1849**

Number of examined specimens: 3 adults

Distribution:

Transvaal, southern Mozambique, Zululand, Malawi, Zambia, Swaziland, Zimbabwe, Namibia, and Angola.

Dental morphology:

The dentaries of *Gerrhosaurus validus* bear 25 to 26 tooth positions. The tooth necks are cylindrical and rather slender. The cross-sections of the teeth are circular and increase apically. The tooth crowns are convex and smooth labially whereas the lingual surfaces are concave and striated. The culmen lateris anterior is longer than the culmen lateris posterior. The anguli are both distinctly pronounced. The cuspis labialis and the deeper situated cuspis lingualis are close to each other; both cusps are lingually recurved, so that the tip of the tooth consists of two lip-shaped bulges. In lingual view, the tooth crowns are of blunt shape. The lingual striations consist of two or three prominent ridges which run in apical direction across the concave surfaces of

the tooth crowns. Striations are not represented in all teeth, and they are not found in all investigated individuals. The anteriormost teeth never show prominent striae. The resorption pits are ventrally expanded.

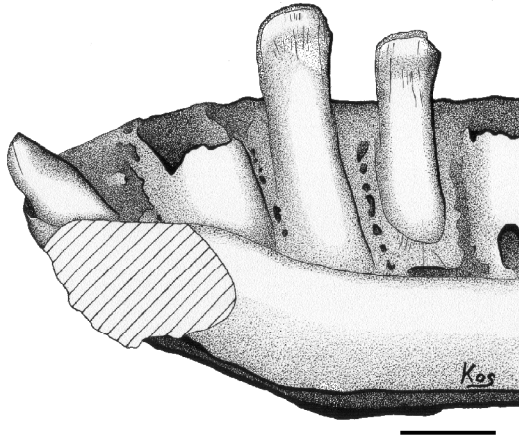


Fig. 22: *Gerrhosaurus validus* (specimen SRK 00.154) Anterior portion of a right dentary (tooth positions 1-4 from 24); lingual view
Scale bar: 1.0 mm

Diet:

The diet of *G. validus* consists of orthoptera and other insects (LOVERIDGE 1942). Additionally, some millipedes, scorpions, berries, and fruits are consumed (PATTERSON 1997).

4.1.2.2 Subfamily Zonosaurinae

(Diagnosis: see MEIER 1988)

Tracheloptychus PETERS, 1854

Tracheloptychus madagascariensis PETERS, 1854

Number of examined specimens: 1 adult

Distribution:

Southern Madagascar.

Dental morphology:

The mandibles of *Tracheloptychus madagascariensis* bear 16 to 17 tooth positions. The tooth necks are slender and cylindrical. The cross-sections of the teeth are transversally expanded. The anterior teeth are unicuspid and transform into bicuspid teeth in the central section of the tooth row. Tricuspid teeth are found in the posterior portion of the dentary.

The shapes of the tricuspid teeth resemble the generalized bauplan of lacertid teeth. The mesial side cusps as well as the distal side cusps are shorter than the main apex. The angle between the apex and the side cusps encompasses 100°. In occlusal view, all three cusps are situated in a line running parallel to the jaw margin. The labial surfaces of the teeth are smooth whereas faint parallel striations are found on the lingual surfaces of the tooth crowns.

Diet:

T. madagascariensis inhabits the dunes of Southern and Southeastern Madagascar and competes with *T. petersi* in this area. The prey items of *T. madagascariensis* are arthropods (ROGNER 1994).

Tracheloptychus petersi GRANDIDIER, 1869 (Pl. I, Fig. 17)

Number of examined specimens: 1 adult

Distribution:

Southwestern Madagascar.

Dental morphology:

The tooth count as well as the morphology of the teeth of *Tracheloptychus petersi* is similar to the dentition of *T. madagascariensis*. The posteriormost tooth positions 16 and 17 are occupied by tricuspid teeth. The last tooth of the tooth row shows faint striations on its lingual surface. The enamel surfaces of all other teeth are smooth. The ratio toothlength:diameter of tooth neck is 2.4:1.0.

Diet:

Opposing the common assumption that *T. petersi* is strictly vegetarian, some authors proved a consumption of crickets in this species (HENKEL und SCHMIDT 1995). Captive specimens of *T. petersi* also consumed mediterranean crickets (*Grillus bimaculatus*) and *Tenebrio molitor* larvae (mealworms) in my vivarium. However, ripe fruits (leeches, sharon-fruits, pears, grapes, berries etc.) and fruit-puddings are preferred by these agile plated lizards. Soft fruits and pudding are licked up with the tongue. This preference of sweet fruits suggests an at least partly vegetarian diet in the natural habitat. The tendency for a herbivore diet often observed in lizards living in arid climates, is in accord with the former observations.

Remarks:

T. petersi is hiding in the sandy ground for long periods and is, like *Scincus scincus*, able to “swim” in the sand over short distances. In contrast to some burrowing skinks, feeding takes place above the ground surface without exception.

Zonosaurus BOULENGER, 1887

Zonosaurus haraldmeieri BRYGOO & BÖHME, 1985

Number of examined specimens: 1 adult

Distribution:

Northern Madagascar.

Dental morphology:

The dentaries of *Zonosaurus haraldmeieri* bear 24 tooth positions. The dental morphology of *Z. haraldmeieri* is similar to the dental morphology of *Zonosaurus laticaudatus*.

Diet:

Z. haraldmeieri preys on insects and snails which are actively crushed. Even after a long fasting period, fruits are not accepted (ROGNER 1994).

Zonosaurus laticaudatus (GRANDIDIER, 1869) (Pl. I, Fig. 18)

Number of examined specimens: 2 adults

Distribution:

Western areas of Madagascar.

Dental morphology :

The mandibles of *Zonosaurus laticaudatus* bear 18 tooth positions on average. As a result of the bulbous curvature of the tooth bases, the habitus of the teeth is almost conical. The labial surfaces of the teeth are slightly convex and they lack striations. The lingual surfaces of the tooth crowns are flattened or concave. The culmen lateris anterior and the culmen lateris posterior are the same length and reach the central area of the tooth neck. The angulus mesialis is more pronounced than the angulus distalis and almost reaches the habitus of a lateral cusp. Some three striae are developed in most teeth, with the central stria being the most pronounced. The striae converge apically. In specimen ZFMK 57148, the striations are rather indistinct and only the central stria is well developed; it forms a ridge running in

basal direction. The angle between the crista mesialis and the crista distalis encompasses 110° to 130°. In specimen ZFMK 7256, the enamel is flaked off from several tooth necks. In these areas, striations of the dentine surfaces became visible. These parallel arranged striations stretch to the tooth bases. Up to 60 of these “dentine striae” are found per tooth. The striae are situated around the entire tooth. The dentine striations do not correspond with the enamel striations. The resorption pits are ventrally expanded.

Diet:

Z. laticaudatus dwells in primary and secondary forests. The species is spread in humid as well as in arid areas. Therefore, *Z. laticaudatus* is obviously not adapted to a special diet and the lizards are considered to be generalized insectivores. In its natural habitat, MEIER (1988) observed this species joining *Zonosaurus madagascariensis* during a meal of banana peels and rotting mangos.

Remarks:

The wrinkles observed at the exposed dentine surfaces in an individual of *Zonosaurus laticaudatus* (specimen ZFMK 7256) strongly resemble the ornamentations observed by SANDER (1999) on the etched tooth surface of an indeterminate rauisuchid: “However, in the rauisuchid tooth, flaked-off enamel exposes the underlying dentine which shows a similar kind of striation brought about by the linear arrangement of the dentine tubules. This suggests that the striations are somehow linked with the arrangement of the dentine tubules. As dentinal influence on enamel deposition can generally not be detected during amelogenesis in tetrapods, it is surprising to find such a link at cessation of enamel deposition. The parallel arrangement of dentine tubules and surface striations suggests that the striations may somehow reflect the arrangement of the ameloblasts in the epithelium.” (SANDER 1999). Accordingly the EDJ is not always represented as a smooth plane.

Zonosaurus madagascariensis (GRAY, 1831) (Pl. I, Fig. 19)

Number of examined specimens: 1 adult

Distribution:

Eastern coast of Madagascar between Maroansetra and Tamatave as well as Nossi Bé and the opposing coast. Isolated specimens were found in western Madagascar.

Dental morphology:

The dentary of the investigated *Zonosaurus madagascariensis* specimen bears 19 slender and cylindrical teeth. The anterior teeth show pronounced culmines lateres anterior et posterior and distinct striations; these striations consist of bundles of maximally six parallel running striae per tooth. The striae are situated on the lingual surface between the two culmines lateres. All labial surfaces are smooth. The tooth crowns of the anterior teeth are convex lingually, and the tips are slightly recurved in the lingual direction. The cross-sections of the anterior teeth are subtriangular with the acute angle being lingually directed. The posterior teeth of *Z. madagascariensis* are bicuspid with a low socket-shaped lateral cusp being situated in a position mesially of the main apex. The culmines lateres anterior et posterior are only weakly pronounced in the posterior teeth. Striations are absent in this section of the tooth row. The replacement teeth are distinctly pointed. The angle between the crista mesialis and the crista distalis is 55° to 60°. The pointed cusps of the replacement teeth represent a strong contrast to the apical angle of 110° found in the teeth which are already in function. The ratio toothlength:diameter of tooth neck is 3.0:1.0. The resorption pits of *Z. madagascariensis* are ventrally expanded or drop-shaped so that the apical margins of several resorption pits taper to a point.

Diet:

Z. madagascariensis often dwells in human settlements. This plated lizard is a skilful hunter of small insects. Additionally, sweet fruits are accepted (HENKEL & SCHMIDT 1995). I have kept individuals of this species in a vivarium for several years now, but they always refused plant matter. Despite the repeated offering of sweet fruits, these items were intensively investigated by the lizards, but were not eaten. However, the lizards voraciously consume semiadult mediterranean crickets (*Grillus bimaculatus*), house crickets (*Acheta domestica*), and larvae of the mealbeetle (*Tenebrio molitor*) instead. The prey animals are quickly grasped and then rotated between the upper and lower jaws with the tongue, so that the chitinous cuticulae are crushed in several places. Afterwards, the prey items are swallowed. A similar feeding behavior was observed in captive specimens of *Zonosaurus ornatus* in my vivarium.

Zonosaurus maximus BOULENGER, 1896
(Pl. I, Fig. 20; Pl. II, Figs. 1-2)

Number of examined specimens: 2 adults

Distribution:

Middle east of Madagascar along the rivers Faraony, Matitana, Mananara, and Tolongoina.

Dental morphology :

The right mandible of specimen ZFMK 7802 bears 24 tooth positions. The teeth are of slender and cylindrical habitus and unicuspid throughout the tooth row. In *Zonosaurus maximus*, the crista mesialis is distinctly longer than the crista distalis. The culmen lateris anterior stretches across the entire apical third of the tooth, whereas the culmen lateris posterior is substantially shorter. The convex labial surfaces of the teeth are smooth. A single central stria is situated on the lingual surface of the tooth crown (like in *Zonosaurus laticaudatus* (specimen ZFMK 57148)) which forms a vertical ridge that rises above the concave area between the culmines lateres. Complex patterns of striations were not found. In specimen ZFMK 7825, the central vertical stria is rather pronounced, but in contrast to specimen ZFMK 7802, two additional striae are developed here. These striae are situated anteriorly and posteriorly of the main stria. The three striae converge apically. The ratio toothlength:diameter of tooth neck is 3.5:1.0. The resorption pits are circular.

Diet:

In captivity, *Z. maximus* accepts dog food and catfood, bananas and other fruits as well as crickets, locusts, and various large prey animals (ROGNER 1994). No data concerning dietary preferences of wild populations are available. Since the ecosystem inhabited by *Z. maximus* as well as its behavior resembles the habitats and the behavior of several semiaquatic and at least partially ichthyophageous skinks, a certain percentage of fish and tadpoles can be assumed for the diet of this species.

Remarks:

Z. maximus is the only semiaquatic species of the genus. The lizards are less quick moving on solid ground than other *Zonosaurus* species, but *Z. maximus* is a good swimmer with a laterally compressed tail. The lizards are able to dive for several minutes. In the wild, these lizards inhabit the banks of rivers, always prepared for escaping to the water in the case

of danger. *Z. maximus* represents the largest species of the genus.

Zonosaurus quadrilineatus (GRANDIDIER, 1867)

(Pl. II, Fig. 3)

Number of examined specimens: 1 adult

Distribution:

Southwestern Madagascar.

Dental morphology:

The teeth of *Zonosaurus quadrilineatus* appear more stout than the teeth of its congenetics. The number of tooth positions is strongly reduced so that only 15 tooth positions are present in specimen ZFMK 7804. The cross-sections of the teeth are circular. The labial enamel surfaces are smooth whereas the flattened lingual surfaces of the tooth crowns are heavily striated. The culmen lateris posterior is one third longer than the culmen lateris anterior. The crista distalis is shorter than the crista mesialis which leads to a cuspis labialis situated far posteriorly. The teeth lack the carinae intercuspidales since the cuspis lingualis is not separated from the cuspis labialis. The stria dominans anterior and the stria dominans posterior are well developed in all intact teeth. An additional prominent stria is situated between the stria dominans anterior and the culmen lateris anterior in many teeth. The 11th tooth in the left dentary of specimen ZFMK 7804 shows a bifurcation of the stria dominans posterior. The labial surface of the 13th tooth shows a wide-spaced wrinkling of the enamel in this specimen. The outer shape of this tooth appears angular in lingual view since the angulus distalis and the angulus mesialis are both pronounced. The angle between the crista mesialis and the crista distalis encloses 130°. The ratio toothlength:diameter of tooth neck is 2.1:1.0.

Diet:

This species is rather common in areas inhabited by humans. In addition to a predominantly insectivorous diet, *Z. quadrilineatus* consumes berries and other small fruits under natural conditions. In captivity, these plated lizards accept house crickets, crickets, *Zophobas* larvae, caterpillars, other insects, and fruits.

4.1.3 Family Lacertidae BONAPARTE, 1831

Consists of two subfamilies (Gallotiinae, Lacertinae).

(Diagnosis: see ESTES 1983)

4.1.3.1 Subfamily Gallotiinae MAYER & BENYR, 1994

(Diagnosis: see BISCHOFF 1998)

The more basal Gallotiinae split from the Lacertinae approximately 35 million years ago and originate from the Iberian Peninsula (BISCHOFF 1998).

Gallotia BOULENGER, 1916

Gallotia atlantica (PETERS & DORIA, 1882)

(Pl. II, Fig. 4)

Number of examined specimens: 3 adults

Distribution:

Canary Islands (Lanzarote, Fuerteventura, Lobos, La Graciosa, Montaña Clara, Roque del Este).

Dental morphology:

The right dentary of specimen BMNH 1967.1496 bears 18 tooth positions. The teeth of *Gallotia atlantica* are cylindrical and transform from the unicuspid anterior teeth over several bicuspid central teeth to the tricuspid posterior teeth. The pointed central cusp is longer than the anterior and posterior side cusps. The tooth bases are broadened. While the tooth surfaces of specimen ZFMK 7834 are unwrinkled, the teeth of the specimens BMNH 1967.1496 and ZFMK 34964 are heavily striated. The striations are restricted to the lingual surfaces of the tooth crowns. Approximately ten striae are found between the culmines lateres. The striae converge apically in the immediate vicinity of the tip of the main cusp. The striae are running straight. Often two or three pronounced striae dominate the other weaker striae. Bifurcations of the striae are common. Isolated striae can be found on the lingual surfaces of the lateral cusps. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 2.2:1.0. The resorption pits are circularly shaped.

Diet:

Like other lizards from the Canary Islands, *G. atlantica* is an omnivorous species, with a predominantly vegetative diet. The

flowers of *Launaea arborescens* represent an important food item of this species (BISCHOFF 1998). The animal part of the diet is made up predominantly by the larvae of flies of the genus *Lucilia* and maggots. Stomach contents of *G. atlantica* additionally showed tenebrionids, elaterid larvae, noctuid caterpillars, small butterflies, termites, Aphodiinae (dung beetles), Coccinellidae (ladybugs), Carabidae, Coelopidae, Cochinille lice (*Dactylopius coccus*; the consumption of the Conchinille lice leads to a red coloration of the lizards bones), ripe fruits of *Opuntia ficus-barbarica*, and berries of *Zygophyllum fontanesii*. Lizards inhabiting the vegetationless Roque del Este consume parts of songbirds which are killed by falcons and are often fed to the juveniles of these birds of prey. Altogether, *G. atlantica* consumes a wide variety of food items (BISCHOFF 1998).

Gallotia caesaris (LEHRS, 1914)
(Pl. II, Figs. 5-8)

Number of examined specimens: 8 adults

Remark:

Two specimens of *Gallotia caesaris gomerae* are cataloged under the synonym *Gallotia galloti gomerae* (ZFMK 4108 and ZFMK 4110), and one specimen of *Gallotia caesaris caesaris* is cataloged under the synonym *Gallotia galloti caesaris* (ZFMK 4114).

Distribution:

Canary Islands (El Hierro, La Gomera).

Dental morphology:

The right dentary of specimen SRK 00.113 bears 17 tooth positions. The teeth are cylindrical with the anterior teeth being slender and the posterior teeth are barrel-shaped and enlarged. The anterior teeth are unicuspid while the 5th tooth is already bicuspid; all teeth between tooth position 5 and 17 are tricuspid. The lateral cusps are dominated by a central main cusp which shows a pointed tip with an inner angle of 80° enclosed by the crista mesialis and the crista distalis. The cutting edges of the central cusp are rather sharp. The lingual surfaces of the tooth crowns are flattened or concave in the immediate vicinity of the well developed culmines lateres. The teeth of all investigated specimens of *G. caesaris* are almost free of striations. Extremely fine striae are found on the lingual surfaces of the tooth crowns in the specimens

ZFMK 4108, ZFMK 4110, ZFMK 4114, and on the anteriormost teeth of specimen SRK 00.113. These striae are numerous, short, and converge apically. The labial enamel surfaces of the teeth are always unwrinkled. The ratio toothlength:diameter of tooth neck amounts to 3.6:1.0 in anterior teeth and is 2.2:1.0 in the posterior teeth. The resorption pits are circular; resorption pits are present at the bases of the majority of the teeth within a tooth row. Most of the resorption pits contain fully developed tooth crowns of the replacement teeth.

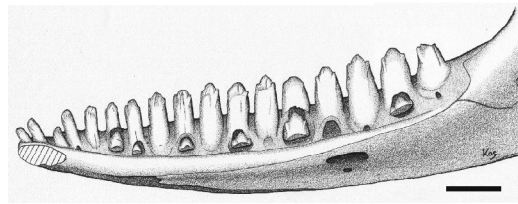


Fig. 23: *Gallotia caesaris*
(specimen SRK 00.113)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

G. caesaris is an omnivorous species. Fecal pellets proved a consumption of orthopterans (*Sphingonotus* sp., undetermined Locustidae, *Guanchia* sp.), hemipterans (*Nezara viridula*, Anthocoridae), dipterans (Cecydomidae, Tripedidae), hymenopterans (undetermined Chalcidae, undetermined Sphecidae, *Halictus* sp., Formicidae, undetermined hymenopterans), coleopterans (undetermined Staphylinidae, undetermined Melyridae, *Thanasimus paivae*, *Dapsa* sp., *Coccinella algerica*, *Chilocorus renipustulatus*, *Hegeter occator*, *Apion radiolus*, *Laparocerus* sp.), marine isopods, and spiders (BISCHOFF 1998). The plants eaten by *G. caesaris* are *Rubia fruticososa*, *Psoralea bituminosa*, and *Artemisia thuscula*. Additionally, the lizards consume ripe fruits of *Opuntia dillenii* and *Opuntia ficus-barbarica* as well as the yellow flowers of *Schizogyne sericea* bushes and the nectar of *Euphorbia obtusifolia*. In the neighborhood of waste deposits on El Hierro (the so-called "Concheros"), the lizards were observed eating the remains of various marine fishes, mussels, marine snails (*Patella* sp.), goats, rabbits, and chicken as well as the flies drawn to the Concheros.

Gallotia galloti (OUDART, 1839)
(Pl. II, Fig. 9)

Number of examined specimens: 8 adults

Distribution:

Canary Islands (La Palma, Tenerife, Roque de Garachico, Roque Dentro de Anaga, Roque Fuera de Anaga).

Dental morphology:

The morphology of the teeth of *Gallotia galloti* is identical to the morphology of the teeth of the above described and closely related *Gallotia caesaris*. The dentaries of the investigated specimens of *G. galloti* bear 17 to 20 tooth positions.

Diet:

The omnivorous diet of *G. galloti* consists of a minor animal and a major vegetarian percentage, at least in adult specimens. Juveniles often prefer animal food items. The lizards consume flowers and fruits of *Opuntia dillenii*, leaves and flowers of *Euphorbia balsamifera*, leaves of *Kleinia neriifolia*, *Argyranthemum frutescens*, *Lycium intricatum*, *Micromeria* f. *varia*, *Rumex lunaria*, flowers of *Launaea arborescens*, *Lavendula* sp., *Convolvulus scoparius*, *Schizogyne sericea*, fruits of *Plocama pendula*, *Rubia fruticosa*, *Ficus carica*, fresh twigs and berries of the endemic *Plocama pendula*, seeds of *Neochamaelea pulverulenta*, *Withania aristata*, *Lycium intricatum*, *Atriplex semibaccata*, *Scilla* cf. *haemorrhoidalis*, tomatoes, grapes, bananas, insects, spiders, isopods, ants (*Camponotus rufoglaucus*), and Cochinille lice (*Dactylopius coccus*). *G. galloti* shows a strong preference for beetles of the genus *Atlantis*. Locusts, even if they are common, are not accepted for unknown reasons. The lizards show cannibalistic tendencies, so parasites (*Sarcocystis* sp.) are transferred from one individual to another by the swallowing of autotomized tails. Road-killed *G. galloti* are often eaten by their conspecifics. In contrast to other lizards, *G. galloti* uses its forelimbs to handle large prey items, and not the hindlimbs (BISCHOFF 1998). The partly frugivorous *G. galloti* plays an important role in the dispersal of seeds (VALIDO & NOGALES 1994). The diet underlies great seasonal changes. BROSCHINSKI (pers. comm.) offered bird food to wild lizards on La Palma; the lizards skilfully separated the grains from their capsules with chewing movements of the jaws.

Gallotia stehlini (SCHENKEL, 1901)
(Pl. II, Figs. 10-11)

Number of examined specimens: 4 adults

Distribution:

Canary Islands (Gran Canaria).

Dental morphology:

The right dentary of specimen BMNH 19671.1738-57 bears 24 tooth positions. The teeth are unusual in being multicuspid; they therefore strongly contrast the teeth of other investigated *Gallotia* species which are at best tricuspid. The tooth bases and tooth necks are cylindrical and slender. The lingually and labially compressed and mesially expanded tooth crowns rise above the labial parapet of the dentary. A single main cusp dominates over three or even four lateral cusps in most teeth throughout the tooth row. The arrangement of the lateral cusps is often asymmetrical so that only one lateral cusp is found mesially of the main cusp and two lateral cusps are situated distally of the main cusp (specimen BMNH 19671.1738-57) whereas three mesial and one distal lateral cusps are found in another individual (specimen ZFMK 7876). All cusps form a straight mesial row. The cutting edges are rather sharp. The culmines lateres are short and weakly developed. The lateral cusps decrease in size the further they are remote from the central main cusp. The lingual surfaces of the cusps are more distinctly outwardly curved than their labial surfaces. All enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.6:1.0. The resorption pits are circular in shape. However, the tooth morphology of *Gallotia stehlini* strongly resembles the tooth morphology of the gerrhosaurid *Angolosaurus skoogi*.

Diet:

The dietary spectrum of this omnivorous giant lizard is dominated by vegetable food items. Behavior observations showed that the diet of *G. stehlini* consists of fruits of *Plocama pendula*, buds of *Euphorbia o. obtusifolia*, dry leaves of *Ricinus communis*, flowers and leaves of *Salvia canariensis*, fruits of *Opuntia dillenii*, and dragonflies (MOLINA BORJA 1986). In addition to the above mentioned food items, *G. stehlini* was observed grazing the minute yellow flowers of *Launaea arborescens* and fruits and seeds of *Rubia fruticosa* and *Teline rosmarinifolia* were found in fecal pellets (BARQUÍN DIEZ et al. 1986, BISCHOFF 1998). Additionally, the lizards

occasionally prey on small mammals, birds, lacertids, *Tarentola b. boettgeri*, *Chalcides sexlineatus*, smaller individuals of their own species, and carrion (BISCHOFF 1998).

Remarks:

The change of habitats from mainland to islands often went with dietary changes from insectivore to herbivore, and lizards that already have plants in their diet when living on the mainland seem to be more successful in colonizing islands (VAN DAMME 1999). Herbivory in lizards is often associated with a larger body size and insularity as this is the case in *G. stehlini*. On islands where predation pressure is a less limiting factor than it is on the mainland, lizards can safely bask for long periods of time and thus are enabled to digest plant matter (VAN DAMME 1999).

Psammodromus FITZINGER, 1826

Psammodromus algirus (LINNAEUS, 1758)
(Pl. II, Figs. 12-14)

Number of examined specimens: 3 adults

Distribution:

Italy, Portugal, Spain, France, Tunisia, Algeria, Morocco.

Dental morphology:

The right dentary of specimen USNM 199210 bears 21 tooth positions. The teeth are relatively robust and cylindrical with lingually flattened or concave tooth crowns. The teeth of the anterior portion of the tooth row are unicuspid whereas the teeth of the central and posterior sections of the tooth row are bicuspid. The minute lateral cusps are situated in a mesial position and are clearly separated from the main cusps. The cristae mesialis et distalis of the main cusps are quite sharp. The development of striations distinctly varies within the investigated individuals. In the specimens USNM 199210 and ZFMK 4086, one or two long and apically converging striae are found at the lingual surfaces of the apices. In specimen ZFMK 7864, up to nine prominent striae are situated at the concave lingual surfaces of the tooth crowns. The expansions of these striae are irregular this individual. The striae converge in the immediate vicinity of the main apex. The labial tooth surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.3:1.0. The resorption pits of *Psammodromus algirus* are of circular shape

and the pattern of striations is already found in embryonal replacement teeth.

Diet:

P. algirus is the largest species of the genus and it consumes locusts, dragonflies, small butterflies, flies and their larvae, earthworms, spiders (Lycosidae and Thomisidae), insect larvae (Geometridae, Diptera, Tenebrionidae), Thysanurae, bugs, Orthoptera (*Ephippigera* sp., young crickets), Hymenoptera (Apidae, Formicidae, and Sphecidae), Lepidoptera (Pyralidae, Noctuidae), Diptera (Tipulidae, Culicidae, Muscidae), and various Coleoptera (BÖHME 1981). The prey items are actively selected by the lizards (Diaz & Carrascal 1990).

Psammodromus hispanicus FITZINGER, 1826
(Pl. II, Fig. 15)

Number of examined specimens: 1 adult

Distribution:

Portugal, Spain, France.

Dental morphology:

The teeth of *Psammodromus hispanicus* strongly resemble the teeth of *Psammodromus algirus*. In comparison to *P. algirus*, the bicuspid posterior teeth of the only available specimen of *P. hispanicus* show larger lateral cusps, and the surfaces of the teeth of *P. hispanicus* are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.3:1.0. The resorption pits are of circular shape.

Diet:

P. hispanicus consumes small beetles, spiders, and ants (Formicidae) (MELLADO et al. 1975).

4.1.3.2 Subfamily Lacertinae MAYER & BENYR, 1994

Acanthodactylus WIEGMANN, 1834

Acanthodactylus boskianus (DAUDIN, 1802)

Number of examined specimens: 5 adults

Distribution:

Morocco, Algeria, Tunisia, Libya, Egypt, Mauritania, Mali, Niger, Nigeria, Sudan, Ethiopia, Eritrea, Saudi Arabia, United Arab Emirates, Oman, Israel, Syria, Iraq, Turkey.

Dental morphology:

The right dentary of specimen SRK 00.118 bears 25 tooth positions. The teeth in the tooth positions 1 to 5 are unicuspid whereas all following teeth are bicuspid. The lateral cusps are situated mesially of the main cusps. The teeth are of slender and cylindrical habitus with slightly lingually flattened tooth crowns. The cutting edges appear rather sharp. The culmines lateres are short and weakly developed. Several teeth show wear facets; apart from this, the enamel surfaces are smooth. The ratio toothlength:diameter of tooth neck is 4.5:1.0. The resorption pits of *Acanthodactylus boskianus* are circular or slightly elongated in the dorsal direction. Replacement processes take place at the bases of almost all teeth throughout the entire tooth row.

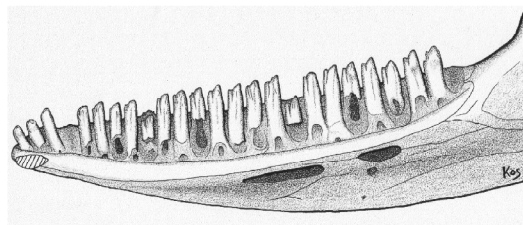


Fig. 24: *Acanthodactylus boskianus* (specimen SRK 00.118)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

In captivity, *A. boskianus* preys on insects, spiders, and pieces of meat (ROGNER 1994). At least one wild population is partly herbivorous (VAN DAMME 1999).

Acanthodactylus erythrurus (SCHINZ, 1833)

Number of examined specimens: 3 adults

Distribution:

Portugal, Spain, Morocco, Algeria.

Dental morphology:

The right dentary of specimen SDS 65156 bears 22 tooth positions. The teeth appear slender in lingual view, whereas a transversal expansion of the tooth bases becomes visible in occlusal view. The anterior teeth are unicuspid; the teeth occupying the central and posterior portions of the tooth row are bicuspid with the small lateral cusp being situated mesially of the main cusp. The cutting edges of the lingually flattened tooth crowns

are sharp. Usually the enamel surfaces are unwrinkled. The tooth crown morphology of specimen ZFMK 7873 differs from the other investigated specimens: In the posterior teeth of ZFMK 7873, each main cusp is divided into a prominent and pointed cuspis labialis and a deeper situated cuspis lingualis which is formed by the pronounced striae dominantes anterior et posterior. The labial tooth surfaces are always unwrinkled. The ratio toothlength:diameter of tooth neck is 5.0:1.0. The resorption pits are of circular shape.

Diet:

The diet of *Acanthodactylus erythrurus* consists of beetles, Hymenoptera, locusts, caterpillars, ants, and even a juvenile *Psammodromus algirus* was found in the stomach of an *A. erythrurus* individual (SALVADOR 1981; in: BÖHME 1981).

Acanthodactylus pardalis (LICHTENSTEIN, 1823)

(= *Acanthodactylus maculatus* (LICHTENSTEIN, 1823)

(Pl. II, Fig. 16)

Number of examined specimens: 2 adults

Distribution:

Algeria, Libya, Egypt, Israel, Jordan.

Dental morphology:

The teeth of *Acanthodactylus pardalis* are robust and slightly transversally expanded at their bases. Like in its congenetics, the anterior teeth are unicuspid whereas the teeth in the central and posterior portions of the tooth row are bicuspid. The lateral cusp is situated in a mesial position and is rather small. The cutting edges between the two cusps are only slightly concave in form. All enamel surfaces are perfectly smooth. Compared to other investigated *Acanthodactylus* species, the cusps are relatively blunt. The ratio toothlength:diameter of tooth neck amounts to 3.4:1.0. The resorption pits are circular in shape.

Diet:

A. pardalis is an insectivorous species (VAN DAMME 1999).

Acanthodactylus scutellatus (AUDOUIN, 1809)

Number of examined specimens: 2 adults

Distribution:

Algeria, Tunisia, Libya, Egypt, Israel, Mali, Niger, Chad, Sudan, Iraq, Saudi Arabia, Kuwait.

Dental morphology:

The right dentary of specimen SRK 00.117 bears 27 tooth positions. The anterior teeth (tooth positions 1 to 8) are unicuspid whereas the teeth in tooth positions 9 to 27 are predominantly bicuspid with the exception of two central teeth, which lack the lateral cusps as a result of intensive wear. The teeth are slender and transversally slightly expanded at their bases. The lateral cusp is always smaller in size than the main cusp and is situated in a mesial position. The crista mesialis of the main cusp is longer than the crista distalis. The lateral cusp is distinctly separated from the main cusp by an inward curvature of the mesial cutting edge. The tooth tips are relatively pointed. All enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.4:1.0 in *Acanthodactylus scutellatus*. The resorption pits are dorsally elongated.

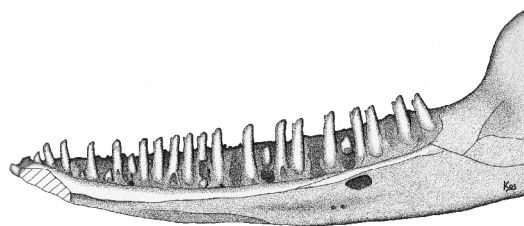


Fig. 25: *Acanthodactylus scutellatus* (specimen SRK 00.117)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

A. scutellatus is an insectivorous species (VAN DAMME 1999).

Algyroides BIBRON & BORY, 1833

Algyroides marchi (VALVERDE, 1958)

Number of examined specimens: 1 juvenile, 3 adults

Distribution:

Spain.

Dental morphology:

The right dentary of specimen SRK 00.038 bears 21 tooth positions. The tooth

positions 1 to 6 bear unicuspid teeth; the teeth in tooth positions 7 to 21 are bicuspid with a small mesial side cusp and a prominent main cusp. The posteriormost teeth show a tendency for tricuspidity since the angulus distalis is prominent and almost cusp-like. The teeth of *Algyroides marchi* are cylindrical and robust with mesially expanded tooth crowns. The enamel surfaces of the juvenile specimen A 25 Priv. Coll. EVANS are perfectly smooth whereas there are several scratches and wear facets on the tooth enamel surfaces of specimen SRK 00.038 which is a fully grown adult of a higher individual age. An extraordinary robust tooth is found in tooth position 17 in the specimen SRK 00.038. The ratio toothlength:diameter of tooth neck is 2.8:1.0. The resorption pits are circularly or irregularly shaped.

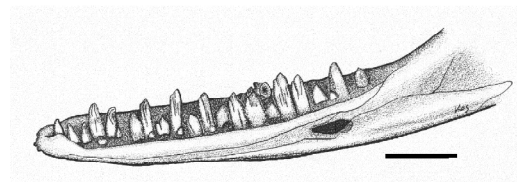


Fig. 26: *Algyroides marchi* (specimen SRK 00.038)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

A. marchi consumes various arthropods (ROGNER 1994). The preferred prey items are Arachnidae (IN DEN BOSCH 1986).

Algyroides nigropunctatus (DUMÉRIL & BIBRON, 1839)

Number of examined specimens: 1 adult

Distribution:

Italy, Istria, Croatia, some adriatic islands, Montenegro, Albania, Greece, Ionian islands.

Dental morphology:

The left mandible of the solely available specimen SRK 00.031 bears 24 tooth positions. The teeth of *Algyroides nigropunctatus* are moderately slender and cylindrical with lingually flattened tooth crowns. All teeth posterior of tooth position 8 are bicuspid with a small mesially situated lateral cusp and a larger main cusp whereas the anterior teeth are unicuspid. The crista mesialis is always longer than the crista distalis. A

maximum of six faint striae are found at the lingual surfaces of the tooth crowns of the anterior teeth. The striae converge apically. The enamel surfaces of the central and posterior teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.3:1.0. The resorption pits are of oval shape with a minor dorsal elongation.

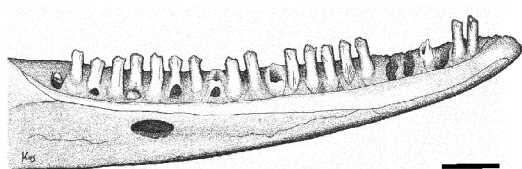


Fig. 27: *Algyroides nigropunctatus* (specimen SRK 00.031)
Left dentary; lingual view
Scale bar: 1 mm

Diet:

The prey items of *A. nigropunctatus* are larger on average compared to the prey items of the smaller sized *Algyroides marchi*. However, even bees are consumed by *A. nigropunctatus* (IN DEN BOSCH 1986).

Archaeolacerta MERTENS, 1921

Archaeolacerta bedriagae (CAMERANO, 1885)

Number of examined specimens: 1 adult

Distribution:

France (Corsica), Italy (Sardinia).

Dental morphology:

The tooth morphology of *Archaeolacerta bedriagae* strongly resembles the tooth morphology of *Darevskia chlorogaster*.

Diet:

A. bedriagae consumes locusts, crickets, beetles, spiders, isopods, *Lithobius* sp., and small fruits (DIESENER & REICHHOLF 1985).

Darevskia ARRIABAS, 1997

Darevskia chlorogaster (BOULENGER, 1908)
(Pl. II, Fig. 17)

Number of examined specimens: 2 adults

Remark:

The specimen housed at the British Museum (it lacks a museum catalog number) is cataloged as *Lacerta chlorogaster*.

Distribution:

Azerbaijan, Iran.

Dental morphology:

The right dentaries of the examined *Darevskia chlorogaster* specimens bear 21 tooth positions each. The teeth are slender and cylindrical and show lingually flattened tooth crowns. The anterior teeth are unicuspid whereas the central and posterior teeth are bicuspid with a distally situated and very pointed main cusp and a mesially situated lateral cusp which is blunt and smaller than the main cusp. The tip of the main cusp is divided into a cuspis labialis and a lower cuspis lingualis. Both cusps are connected by the straight ridge of the carina intercuspidalis. The cuspis lingualis is formed by the prominent striae dominantes anterior et posterior. These main striae run parallel to the cristae mesialis et distalis and they run parallel to the culmines lateres in their basal portions. Apically, the striae dominantes meet at a 70 degree angle. Additional fine striae are found between the striae dominantes as well as on the lingual surfaces of the mesial lateral cusps. The ratio toothlength:diameter of tooth neck amounts to 2.4:1.0. The resorption pits of *D. chlorogaster* are of circular shape.

Diet:

The diet of *D. chlorogaster* consists probably of various arthropods.

Darevskia rudis (BEDRIAGA, 1886)

Number of examined specimens: 4 adults

Remark:

The investigated museum specimens, all of which belong to the subspecies *Darevskia rudis bischoffi* (BÖHME & BUDAK, 1977), are cataloged under the synonym *Lacerta rudis bischoffi*.

Distribution:

Turkey, Georgia, Russia, Azerbaijan.

Dental morphology:

The right dentary of specimen SRK 00.171 bears 21 tooth positions. The teeth are slender and cylindrical in the anterior portion of the tooth row, but become gradually more robust in the posterior portion of the tooth row. In the caudal direction, the teeth transform from an unicuspid over a bicuspid (main cusp and mesial side cusp) to a tricuspid (central

main cusp with a small mesial side cusp and a minute distal side cusp) habitus. The lingual surfaces of the tooth crowns are slightly concave. The main cusps are usually divided into a prominent *cuspis labialis* and a lower *cuspis lingualis*; the later is formed by the *striae dominantes anterior et posterior*. Some five to seven additional *striae* are found on the lingual surfaces of the tooth crowns. These *striae* are very fine and are situated between the *striae dominantes* as well as on the lingual surfaces of the mesial side cusps. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.2:1.0. The resorption pits are circular.

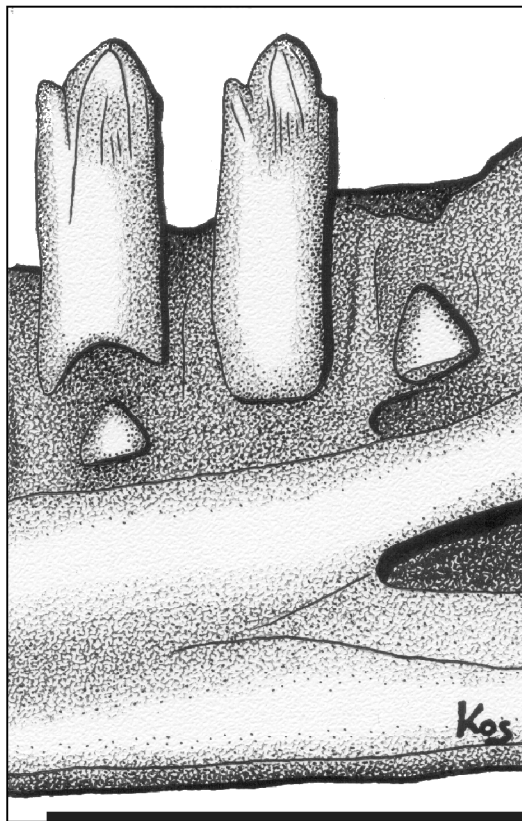


Fig. 28: *Darevskia rudis* (specimen SRK 00.171) Posterior portion of a right dentary (tooth positions 15-17 from 21); lingual view
Scale bar: 1 mm

Diet:

Darevskia rudis is the largest member of the *Darevskia saxicola* group and is therefore enabled to swallow relatively large prey items. In distinct contrast to most other lacertids, *D. rudis* consumes even plant matter, e.g. elderberries (*Sambucus nigra*) and berries of *Phytolacca americana* (ROGNER 1994) in

addition to arthropods. The lizards also consume snails (*Cepaea* sp.) whose shells are crushed between the jaws. The diet composition is completed by beetles, orthopterans, lepidopterans, spiders, earthworms, and conspecific juvenile lizards (BÖHME 1984).

Eremias WIEGMANN, 1834

Eremias arguta (PALLAS, 1773)

Number of examined specimens: 2 adults

Distribution:

Turkey, Romania, Iran, Russia, Azerbaidzhan, Kazakhstan, Armenia, Uzbekistan, Kyrgyzstan, Moldova, Ukraina, Georgia, Tajikistan, Mongolia, China.

Dental morphology:

The right dentary of specimen SRK 00.094 bears 23 tooth positions. The teeth are bulbous and extremely narrowly spaced. The cross-sections of the teeth are circular at the tooth bases and at the tooth necks whereas the tooth crowns are lingually flattened. The four anteriormost teeth are unicuspid; all following teeth are bicuspid with a distally situated main cusp and a mesially situated lateral cusp. The *culmines lateres* are pronounced in *Eremias arguta*. The apical cutting edges are sharp and the *cristae mesiales* are longer than the *cristae distales*. *Striae* are restricted to the lingual surfaces of the tooth crowns. The *striae* are rather irregular, but they show a tendency to a parallel arrangement; most *striae* converge apically. A maximum of eight *striae* are found per tooth. In addition, several teeth show intensive wear facets. The ratio toothlength:diameter of tooth neck is 4.4:1.0.

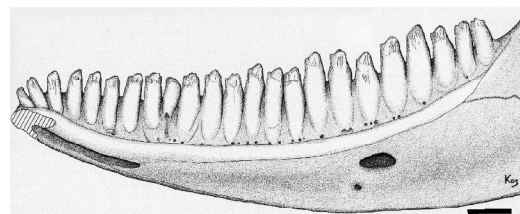


Fig. 29: *Eremias arguta* (specimen SRK 00.094) Right dentary; lingual view
Scale bar: 1 mm

The resorption pits are minute and of perfectly circular shape. At the bases of several teeth, two or even three resorption pits are developed.

These cavelets are arranged parallel to the dental shelf and they unite during further replacement to a single large resorption pit, like it is visible in tooth position 9 of specimen SRK 00.094.

Diet:

The diet of *E. arguta* is probably comparable to the diet of *Eremias pleskei* which consumes various arthropods (ROGNER 1994).

***Eremias scripta* (STRAUCH, 1867)**

Number of examined specimens: 2 adults

Distribution:

Kazakhstan, Turkmenistan, Iran, Afghanistan, Pakistan, Uzbekistan, Tajikistan.

Dental morphology:

The right dentary of specimen SRK 00.208 bears 23 tooth positions. The central and posterior teeth show a tendency for bicuspidity, but the lateral cusps are less prominent as they are in the investigated *Eremias arguta* specimens. The main cusps are pointed and are formed by two lingual ridges which converge apically. Apart from these ridges and the surfaces between them, the lingual surfaces of the tooth crowns are flattened. Some rather faint and apically converging striations are found in the posteriormost tooth. The ratio toothlength:diameter of tooth neck is 3.3:1.0. The resorption pits are shaped circularly.

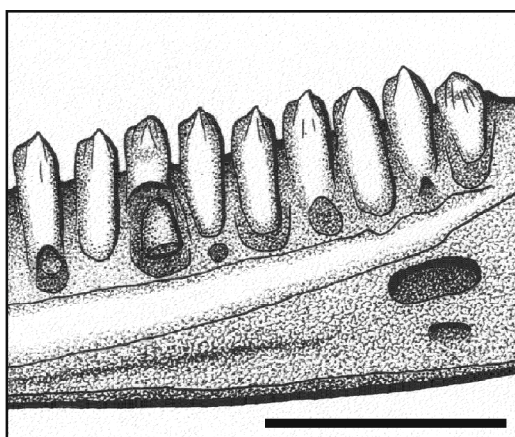


Fig. 30: *Eremias scripta* (specimen SRK 00.208)
Posterior portion of a right dentary (tooth positions 15-23 from 23); lingual view
Scale bar: 1 mm

Diet:

The diet of *E. arguta* is probably comparable of the diet of *Eremias pleskei* which consumes various arthropods (ROGNER 1994).

***Eremias velox* (PALLAS, 1771)**

Number of examined specimens: 3 adults

Distribution:

Kazakhstan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Iran, Afghanistan, Pakistan, China, Russia, Azerbaijan, Georgia.

Dental morphology:

The right dentary of specimen SRK 00.212 bears 23 tooth positions. The teeth strongly resemble the teeth of *Eremias arguta* but they are less narrowly spaced in *Eremias velox*. The surfaces of the bicuspid teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.0:1.0. The resorption pits are circular in shape.

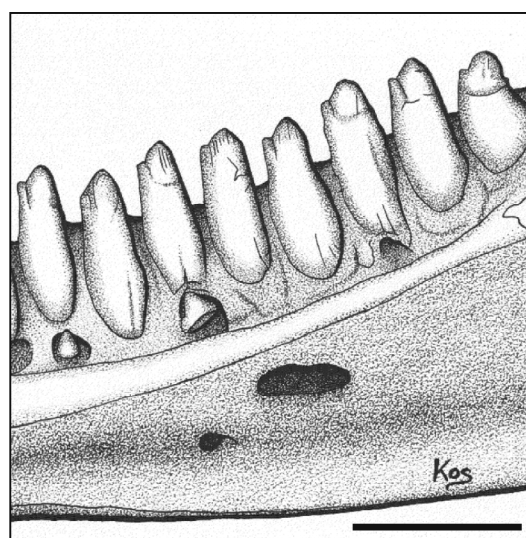


Fig. 31: *Eremias velox* (specimen SRK 00.212)
Posterior portion of a right dentary (tooth positions 16-23 from 23); lingual view
Scale bar: 1 mm

Remarks:

The filming of feeding mechanisms in *Eremias velox* enabled VOROBYEVA & CHUGUNOVA (1991) to observe that the propalinaric jaw movement is rarely used; it serves predominantly for the orientation of the prey within the mouth.

Gastropholis COPE, 1862

Gastropholis echinata (COPE, 1862)
(Pl. II, Figs. 18-19)

Number of examined specimens: 1 adult

Distribution:

Liberia, Ivory Coast, Ghana, Cameroon, Equatorial Guinea, Gabon, Democratic Republic of the Congo.

Dental morphology:

The right dentary of specimen BMNH 1903.7.28.4 bears 22 tooth positions. The teeth of *Gastropholis echinata* are robust and transversally expanded in occlusal view. The tooth crowns are lingually concave and unicuspid in the anterior teeth whereas the central and posterior teeth are bicuspid with a distally situated main cusp and a mesially situated and smaller lateral cusp. The anterior teeth are extremely pointed and their tips are recurved. The central and posterior teeth are relatively blunt and their main cusps show a tendency for the development of a separated cuspis lingualis and a cuspis labialis. The culmines lateres are distinctly pronounced. The lingual surfaces of all tooth crowns are heavily striated. Up to eight striae are found in each tooth. These prominent striae are straight and run parallel to each other; they converge only in their most apical portions. In most teeth, an isolated stria crosses the lingual surface of the lateral cusp. Apically, this stria reaches the tip of the lateral cusp. All labial tooth surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 2.8:1.0. The resorption pits are circular in shape.

Diet:

Literature about African lacertids is rare, hence the dietary preferences of *G. echinata* are unknown.

Holaspis GRAY, 1863

Holaspis guentheri GRAY, 1863

Number of examined specimens: 1 adult

Distribution:

Sierra Leone, Ghana, Nigeria, Cameroon, Gabon, Equatorial Guinea, Democratic Republic of the Congo, Uganda, Angola, Tanzania, Malawi, Mozambique, Ivory Coast.

Dental morphology:

The right dentary of specimen SRK 00.033 bears 22 tooth positions. The teeth are unicuspid without exception and show cylindrical tooth bases and tooth necks. The lingual surfaces of the tooth crowns are concave. The apices are recurved and moderately pointed. The apical thirds of the teeth rise above the labial parapet of the dentary. The cristae mesiales are longer than the cristae distales. The culmen lateris anterior is developed rather prominently whereas the culmen lateris posterior is less pronounced. Approximately five fine striae run across the concave lingual surfaces of the tooth crowns. The striae are arranged parallel to the longitudinal axes of the teeth and are relatively long. The labial surfaces and the entire enamel surfaces of the first two teeth of the tooth row are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.0:1.0. The resorption pits are perfectly circular.

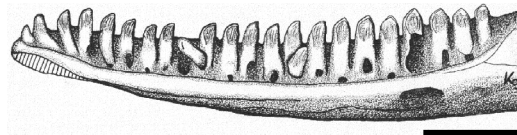


Fig. 32: *Holaspis guentheri*
(specimen SRK 00.033)
Right dentary; lingual view
Scale bar: 1 mm

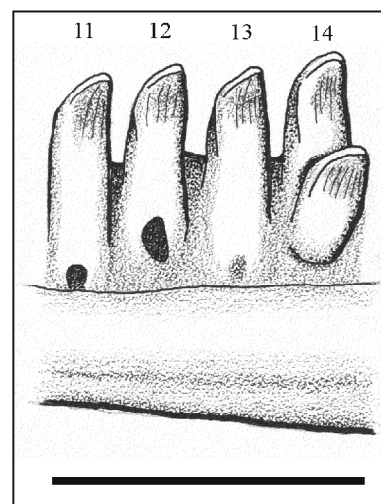


Fig. 33: *Holaspis guentheri*
(specimen SRK 00.033)
Central portion of a right dentary (tooth positions 11-14 from 22), demonstrating the ornamentation of the tooth crowns; lingual view
Scale bar: 1 mm

The tooth morphology of the gliding African lacertid *Holaspis guentheri* strongly resembles the tooth morphology of several cordylid species.

Diet:

The diet of *H. guentheri* consists of various small arthropods, which are actively hunted on tree trunks and vertical rock surfaces under captive conditions (pers. comm. H. STRAUSS, Los Angeles).

***Iberolacerta* ARRIBAS, 1997**

***Iberolacerta cyreni* (MÜLLER & HELLMICH, 1937)**

Number of examined specimens: 3 adults

Remark:

The investigated specimens of *Iberolacerta cyreni* are cataloged under the synonym *Lacerta monticola cyreni*.

Distribution:

Spain.

Dental morphology:

The teeth of *I. cyreni* are identical with the teeth of *Iberolacerta monticola*.

Diet:

The diet of *I. cyreni* is mostly comparable to the diet of *I. monticola*. Stomach contents of *I. cyreni* contained a high percentage of Formicidae (especially in juvenile lizards) (PÉREZ-MELLADO et al. 1991). PÉREZ-MELLADO et al. posited that "electivity scores for individual prey taxa were positively correlated with their length, and lizards preferentially consumed larger individuals belonging to the taxa containing smaller animals". The diet composition of *I. cyreni* underlies seasonal changes as a result of fluctuating prey availability.

***Iberolacerta monticola* (BOULENGER, 1905)**

Number of examined specimens: 6 adults

Remark:

All investigated specimens of *Iberolacerta monticola* are cataloged under the synonym *Lacerta monticola*.

Distribution:

Portugal, Spain.

Dental morphology:

The approximately 21 to 23 teeth in the dentaries of *I. monticola* are very slender and long. The apical halves of the teeth rise above

the labial parapet of the dentary. The shafts of the teeth are cylindrical and the lingual surfaces of the tooth crowns are only slightly flattened. The five or six anterior teeth are unicuspid whereas all following teeth are bicuspid with a posterior positioned main cusp and a smaller mesial lateral cusp. The teeth posterior of tooth position 9 show a tendency for tricuspidity since the angulus distalis in these teeth is very pronounced. However, true tricuspidity is not present in the investigated specimens of *I. monticola*. While the enamel surfaces of the central and posterior teeth are smooth and unwrinkled, some five striae are found on the lingual surfaces of the tooth crowns in the anteriormost teeth. These striae are very fine and they converge apically. The ratio toothlength:diameter of tooth neck is 5.0:1.0. The resorption pits are circularly.

Diet:

The diet of *I. monticola* is dominated by Coleoptera, Arachnida, and larvae of Diptera. In addition, the lizards consume smaller percentages of Orthoptera, Diptera, Dermaptera, Formicidae, Hymenoptera, Lepidoptera (and their larvae), Opiliones, Homoptera, Hemiptera, Myriapoda, Plecoptera, and Dictyoptera (BÖHME 1984).

***Ichnotropis* PETERS, 1854**

***Ichnotropis capensis* (SMITH, 1838)**
(Pl. II, Fig. 20)

Number of examined specimens: 2 adults

Distribution:

Tanzania, Namibia, Zambia, Zimbabwe, Mozambique, Botswana, Republic of South Africa, Democratic Republic of the Congo.

Dental morphology:

The teeth of *Ichnotropis capensis* are slender and have transversally expanded bases. The lingual surfaces of the tooth crowns are concave. All central and posterior teeth are bicuspid with a small mesial cusp and a distally situated main cusp. The anterior teeth are unicuspid. The cristae mesiales are longer than the cristae distales. Striations are restricted to the lingual surfaces of the tooth crowns in the central teeth. The parallel striae are rather fine and their number never exceeds five striae in one tooth. All anterior and posterior teeth are unwrinkled, as well as the labial surfaces of the central teeth. The ratio toothlength:diameter of

tooth neck amounts to 4.2:1.0. The resorption pits are circular in shape.

Diet:

The diet of *I. capensis* consists of small arthropods (AUERBACH 1985).

Ichnotropis squamulosa PETERS, 1854
(Pl. III, Fig. 1)

Number of examined specimens: 1 adult

Distribution:

Tanzania, Zambia, Angola, Zimbabwe, Botswana, Namibia, Republic of South Africa, Malawi.

Dental morphology:

The tooth morphology of *Ichnotropis squamulosa* is quite peculiar. The teeth are slender and conical with slightly flattened lingual surfaces of the tooth crowns. The anteriormost teeth are unicuspid whereas the central and posterior teeth are distinctly bicuspid with a mesial side cusp and a distally situated main cusp. Both cusps are moderately pointed. The most peculiar structure in the teeth of the investigated *I. squamulosa* specimens is a canal-like lingual notch which runs from the depression between the two cusps straight in basal direction and ends at the tooth neck. This notch is rather deep and it narrows in the basal direction. The notch is found in all bicuspid teeth throughout the tooth row. Aside from this, the tooth surfaces of *I. squamulosa* are perfectly smooth. The ratio toothlength:diameter of tooth neck is 4.0:1.0. The resorption pits are circularly shaped.

Diet:

The diet of *I. squamulosa* is dominated by termites and locusts (SCHMIDT 2001).

Lacerta LINNAEUS, 1758

Lacerta agilis LINNAEUS, 1758
(Pl. III, Fig. 2)

Number of examined specimens: 9 adults

Distribution:

Austria, Switzerland, Germany, France, Denmark, Sweden, Norway, Czech Republic, Hungary, Bulgaria, Greece, Albania, Balkan, Netherlands, Belgium, Luxemburg, England, Italy, Croatia, Bosnia-Hercegowina, Serbia, Macedonia, Bulgaria, Greece, Romania, Poland, Belorussia, Belarus, Russia, Ukraina, Armenia, Turkey, Kazakhstan, Kirgistan,

China, Georgia, Moldova, Latvia, Estonia, Lithuania, Azerbaijan, Mongolia.

Dental morphology:

The right dentary of specimen SRK 00.032 (*Lacerta agilis grusinica*) bears 20 tooth positions. The teeth are slender and cylindrical; they become more robust in the posterior portion of the tooth row. In most specimens, unicuspidity is restricted to the two anteriormost teeth whereas all following teeth are bicuspid with a distally situated main cusp and a smaller mesial side cusp. In specimen ZFMK 4090, several posterior teeth are tricuspid with an additional minute distal side cusp. The teeth of *L. agilis* are moderately pointed. The crista mesialis and the crista distalis of the main cusp are almost equal in length. The lingual surfaces of the tooth crowns are distinctly concave and are framed by prominent culmines lateres. Especially in the posterior teeth, some striations are found on these concave surfaces. There are nine or ten striae per tooth. The striae often form complex patterns including a stria dominans anterior and a stria dominans posterior, which together form an exposed cuspis lingualis. Framed by these dominant striae, the other shorter striae run parallel and often meet the striae dominantes. In many teeth, additional striae are found outside the system of the striae dominantes or on the lingual surfaces of the lateral cusps as well. These isolated striae diverge from the main striations and end apically at the tips of the lateral cusps. Complete patterns of striations are already found in embryonal teeth. The ratio toothlength:diameter of tooth neck amounts to 6.0:1.0 in the anterior and central teeth and is 3.6:1.0 in the posterior teeth. The resorption pits are of circular shape.

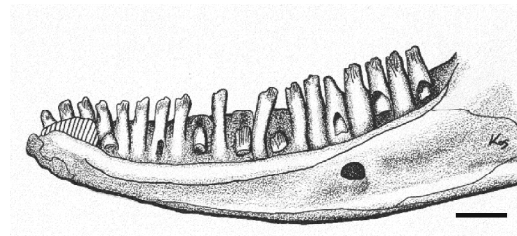


Fig. 34: *Lacerta agilis grusinica*
(specimen SRK 00.032)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

L. agilis is predominantly entomophagous. Arthropods and their larvae, earthworms, and small snails are reported as food items by ROGNER (1984). BÖHME (1984) mentions a prey spectrum made up by 2.64 % Oligochaeta, 2.18 % Gastropoda, 4.46 % Crustacea, 1.35 % Arachnida, 1.39 % Diplopoda, 0.46 % Chilopoda, 0.19 % Odonata, 0.10 % Blattaria, 0.23 % Mantodea, 19.55 % Orthoptera, 0.05 % Plecoptera, 0.79 % Dermaptera, 2.53 % Homoptera, 6.89 % Heteroptera, 34.17 % Coleoptera, 0.05 % Raphidioptera, 0.15 % Neuroptera, 17.82 % Hymenoptera, 0.20 % Mecoptera, 14.40 % Diptera, 0.05 % Trichoptera, 34.90 % Lepidoptera, 0.27 % Reptilia, 1.50 % plant matter, 1.60 % pebbles, and 0.03 % hairs.

Lacerta cappadocica WERNER, 1902
(Pl. III, Fig. 3)

Number of examined specimens: 1 adult

Remark:

The investigated specimen of *Lacerta cappadocica urmiana* (LANTZ & SUCHOW, 1934) is cataloged as *Lacerta cappadocica urmiana*.

Distribution:

Turkey, Iraq, Iran, Syria.

Dental morphology:

The teeth of *Lacerta cappadocica* are robust and cylindrical with lingually flattened tooth crowns. The lingual surfaces of the apices are distinctly concave in the immediate vicinity of the pronounced culmines lateres. Solely the anteriormost teeth are unicuspid whereas the central and posterior teeth are exceptionless bicuspid with distally situated main cusps and mesially situated lateral cusps. In most teeth, the main cusps are relatively blunt whereas the lateral cusps are pointed. Throughout the entire tooth row, the main cusps are separated into a cuspis labialis and a lower cuspis lingualis. As a result of this division of the main cusps, the anterior teeth are best referred to as being bicuspid sensu stricto. Accordingly, the central and posterior teeth are tricuspid sensu stricto. The cuspis labialis and the cuspis lingualis are connected by the straight ridge of the carina intercuspidalis. The cristae mesiales et distales are the same length. Two prominent striae (the striae dominantes anterior et posterior), which run parallel to the cristae mesialis et distalis form the cuspis lingualis. Additional isolated

striae are situated between the striae dominantes as well as outside this system of striations. These additional striae always run parallel to the striae dominantes and are distinctly shorter than these. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 2.7:1.0. The resorption pits are circular in shape.

Diet:

The diet of *L. cappadocica* probably consists of various arthropods. In contrast to the sympatric *Lacerta danfordi*, warmer and more humid microhabitats are preferred by *L. cappadocica*. It is unknown whether the different microclimatic conditions of the habitats result in different trophic structures.

Lacerta danfordi (GÜNTHER, 1876)

Number of examined specimens: 1 adult

Distribution:

Turkey, Greece (Samos).

Dental morphology:

The right dentary of specimen ZFMK 4066 bears 21 tooth positions. The teeth of *Lacerta danfordi* are narrowly spaced, robust, and almost cylindrical with a slight transversal expansion (visible in occlusal view). Solely the tooth crowns rise above the labial parapet of the dentary. The lingual surfaces of the tooth crowns are concave. The anteriormost teeth are unicuspid whereas the central and posterior teeth show a tendency for the development of a mesial side cusp. In contrast to most other lacertids, these lateral cusps are not separated from the main cusps but are formed more as sharp edges or extremely pronounced anguli mesiales. The anguli distales are less prominent. Both anguli transfer in the basal direction into the prominent culmines lateres which run to the transition zone between tooth crown and tooth neck. The main cusp is divided into a blunt cuspis labialis and a lower cuspis lingualis in *L. danfordi*; the cuspis lingualis is formed by the striae dominantes anterior et posterior. A maximum of three additional striae are situated between the striae dominantes. The labial enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.4:1.0. The resorption pits are circular in shape.

Diet:

The diet of *L. danfordi* probably consists of diverse arthropods and is assumed

to be comparable to the diet of *Podarcis muralis*.

***Lacerta graeca* BEDRIAGA, 1886**

Number of examined specimens: 1 adult

Distribution:

Greece (Peloponnese).

Dental morphology:

The right dentary of specimen SRK 00.263 bears 23 tooth positions. BÖHME (1984) mentions male individuals of *Lacerta graeca* with 27 tooth positions per dentary. The teeth in the anterior half of the tooth row are slender and cylindrical whereas the teeth in the posterior half of the tooth row are robust and barrel-shaped. The lingual surfaces of the tooth crowns are flattened or concave. The teeth which are situated anterior of tooth position eight are unicuspid; posterior of tooth position eight, all teeth are bicuspid. The bicuspid tooth crowns show a distal main cusp and a well developed mesial side cusp. In most teeth, the main cusps again are divided into a cuspis labialis and a lower cuspis lingualis; this separation is often not visible in older teeth as a result of extensive wear. The lingual surfaces of the tooth crowns are distinctly striated in the anterior and in several posterior teeth. Up to seven striae can be found in a single tooth crown. The striae run parallel to the longitudinal axes of the teeth and converge apically. The labial surfaces as well as the lingual surfaces of most posterior teeth are unwrinkled. The ratio toothlength:diameter of tooth neck amounts to 3.8:1.0 in the anterior teeth and is 2.4:1.0 in the posterior teeth. The resorption pits of *L. graeca* are shaped perfectly circular.

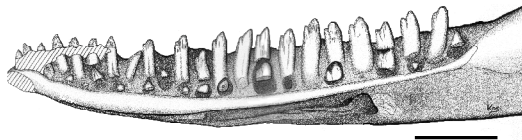


Fig. 35: *Lacerta graeca*
(specimen SRK 00.263)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

The diet of *L. graeca* at least partly consists of locusts (BÖHME 1984). The lizards usually forage for insects and other arthropods

on rocky surfaces (ROGNER 1994). More precisely, *L. graeca* consumes locusts, crickets, beetles, spiders, *Lithobius* sp., caterpillars, and worms (DIESENER & REICHHOLF 1985).

***Lacerta laevis* GRAY, 1838**

Number of examined specimens: 4 adults

Distribution:

Turkey, Syria, Lebanon, Israel, Jordan, Cyprus.

Dental morphology:

The right dentary of specimen SRK 00.090 bears 22 tooth positions. The dentition of *Lacerta laevis* is heterodont with rather slender and cylindrical anterior teeth which gradually transform into extremely massive posterior teeth. The lengths of the teeth are constant throughout the entire tooth row whereas the diameters of the teeth strongly increase the farther they are situated caudally. The eight anteriormost teeth are unicuspid; all following teeth are bicuspid, each showing a distally situated main cusp and a robust mesial side cusp. The lingual surfaces of the tooth crowns are concave in anterior teeth and are at best slightly flattened in posterior teeth. In most teeth, the main cusps are divided into a cuspis labialis and a lower cuspis lingualis; the latter is formed by the striae dominantes anterior et posterior. The entire lingual surfaces of the tooth crowns are heavily striated. About a dozen striae are found here, all of which converge at the tips of the main cusps. However, the surfaces of older teeth are sometimes unwrinkled, however this may be the result of wear. The labial surfaces of the teeth are smooth in *L. laevis*. The ratio toothlength:diameter of tooth neck amounts to 7.0:1.0 in the anterior teeth and is 2.5:1.0 in the posterior teeth. The resorption pits are circular or slightly elongated in the dorsal direction.

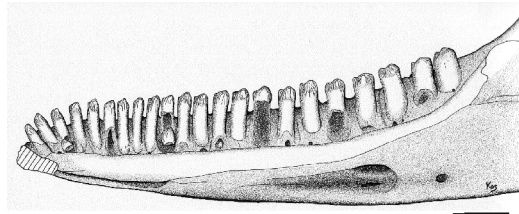


Fig. 36: *Lacerta laevis*
(specimen SRK 00.090)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

L. laevis is more ground dwelling than other rock lizards and therefore probably preys on arthropods, which are protected by a strong cuticula requiring a robust dentition for chewing.

Lacerta schreiberi BEDRIAGA, 1878

(Pl. III, Fig. 4)

Number of examined specimens: 1 juvenile, 3 adults

Distribution:

Spain, Portugal.

Dental morphology:

The right dentary of specimen SRK 00.035 bears 24 tooth positions. The teeth of *Lacerta schreiberi* are narrowly spaced and extraordinary robust in appearance. The tooth bases and the tooth necks are transversally expanded; the tooth crowns show distinct inward curvatures of the lingual surfaces. The teeth in the tooth positions 1 to 5 are unicuspid whereas all following teeth are bicuspid with a distal main cusp and a smaller mesially situated lateral cusp. All cusps are moderately pointed.

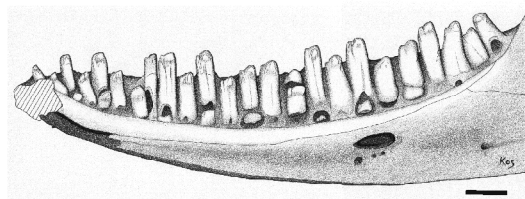


Fig. 37: *Lacerta schreiberi*
(specimen SRK 00.110)
Right dentary; lingual view
Scale bar: 1 mm

The lateral cusps are clearly separated from the main cusps. The main cusps of the majority of the teeth are divided into a cuspis labialis and a lower cuspis lingualis. The cuspis labialis is formed by the cristae mesialis et distalis which are equal in length; the cuspis lingualis is formed by very prominent striae dominantes anterior et posterior. Additional striae are often situated inside as well as outside the striae dominantes. These striae converge apically in the immediate vicinity of the cuspis labialis. In addition, the lingual surfaces of the lateral cusps are often distinctly striated (1 to 4 striae). These striae always converge at the tips of the lateral cusps. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter

of tooth neck is 4.6:1.0. The resorption pits of *L. schreiberi* are almost circular.

Diet:

The diet of *L. schreiberi* predominantly consists of Coleoptera, Orthoptera, Diptera, and Araneidae (LLORENTE & PÉREZ-MELLADO 1988).

Lacerta trilineata (BEDRIAGA, 1886)

(Pl. III, Figs. 5-6)

Number of examined specimens: 6 adults

Distribution:

Greece, Bulgaria, Turkey, Romania, Croatia, Montenegro, Albania, Israel.

Dental morphology:

The right dentary of specimen ZFMK 4059 (*Lacerta trilineata gica*) bears 23 tooth positions whereas even 28 tooth positions are present in the right dentary of specimen ZFMK 3509 (*Lacerta trilineata major*). The teeth of *Lacerta trilineata* are narrowly spaced and robust. The tooth bases and the tooth necks are slightly widened transversally. The lingual surfaces of the tooth crowns are concave. The teeth occupying tooth positions 1 to 5 are unicuspid and all following teeth are bicuspid with a relatively blunt distal main cusp and a smaller mesial lateral cusp. The lateral cusps are clearly separated from the main cusps. Striations are developed at the concave lingual surfaces of the tooth crowns in several specimens, but the patterns of striations strongly differ individually. In specimen SRK 00.092, some five to eight very fine striae run parallel to the longitudinal axes of the teeth. In specimen ZFMK 7869, a maximum of 18 striae are developed at the lingual surface of a sole tooth crown. The striae are relatively long and cover the entire inner apex. Most of these striae converge at the tip of the main cusp whereas several striae run across the lingual surface of the lateral cusp and converge at its tip. In contrast to the afore mentioned specimens, the striations in specimen ZFMK 3509 (*L. trilineata gica*) form a complex pattern: A dominant stria runs from the tip of the main cusp in the basal direction across the concave lingual surface of the tooth crown and ends at the transition zone between the tooth neck and the tooth crown. Additional striae are exposed on both sides of this main stria. These additional striae are restricted to the area between the culmines lateres and run in a bow before they unite with the dominant central

stria. The enamel surfaces of specimen ZFMK 4059 (*L. trilineata gica*) are unwrinkled and this specimen is peculiar since several posterior teeth are tricuspid, showing an additional small but well defined distal side cusp. The ratio toothlength:diameter of tooth neck is 3.6:1.0. The resorption pits of *L. trilineata* are circular in shape.

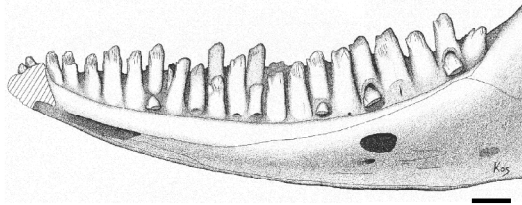


Fig. 38: *Lacerta trilineata*
(specimen SRK 00.092)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

Stomach contents analyses in *L. trilineata* showed a diet composition of 40.4 % ants, 21.6 % beetles and their larvae, 8.8 % flies, 5.5 % caterpillars, 8.8 % snails, 4.6 % Orthoptera, 2.2 % Heteroptera, 2.7 % Araneidae, and 2.9 % other arthropods. Occasionally, the lizards consume scorpions, lizards, snakes, and mice (BÖHME 1984).

Lacerta viridis (LAURENTI, 1768)
(Pl. III, Figs. 7-8)

Number of examined specimens: 10 adults

Distribution:

Austria, Poland, Switzerland, Germany, Czech Republic, Balkan Peninsula incl. Slovenia, Croatia, islands Cres and Trstenik, Turkey, Romania, Bulgaria, Greece, Moldova, Ukraina.

Dental morphology:

The dentaries of the investigated *Lacerta viridis* specimens bear 21 to 26 tooth positions. The teeth are robust and cylindrical or slightly expanded transversally and show lingually concave tooth crowns. The anteriormost teeth (approximately in tooth positions 1 to 5) are unicuspid and slightly inclined labially (prodonty sensu ROCEK (1980)); the following teeth are bicuspid. In specimen BMNH 1920.1.20.725, even tricuspid teeth are represented in the posterior portion of the tooth row. The posterior teeth are more robust than the anterior teeth (lizards of

high individual age probably possess “at least some permanent teeth which do not undergo replacement” (ROCEK 1980).). In general, the main cusps are only moderately pointed whereas the lateral cusps, especially the mesial ones, are often extremely acute. The crista mesialis is longer than the crista distalis. The patterns of striations greatly vary. In most specimens, the striae are most pronounced in the teeth, which are situated in the anterior half of the tooth row while the posterior teeth are unwrinkled. All striae are restricted to the concave inner surfaces of the tooth crowns. Usually, some five to seven parallel striae are found in one tooth; these striae converge apically and sometimes two dominating striae form an only slightly elevated cuspis lingualis. The striae are predominantly developed as relatively long and straight morphological ridges. The labial enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck amounts to 4.5:1.0 in anterior teeth and is 2.8:1.0 in posterior teeth. The resorption pits of *L. viridis* are circular in shape.

The appearance of tricuspid teeth in *L. viridis* was already mentioned by ROCEK (1980): “A limited number of posterior teeth may be tricuspid with a small third cusp distal to the main cusp.”. Bicuspidity and tricuspidity are not related to age or body size in *L. viridis*. This leads to the conclusion that the number of cusps is at least in this well known species an individual character rather than being of taxonomical value.

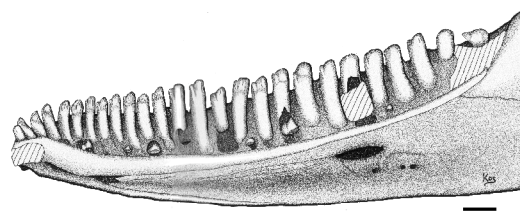


Fig. 39: *Lacerta viridis*
(specimen SRK 00.265)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

The diet composition of *L. viridis* underlies diverse seasonal changes. Insects, especially Coleoptera, are the dominating prey items of this large lizard. *L. viridis* consumes Scarabaeidae, Chrysomelidae, Isopoda, small snails, caterpillars and other larvae, *Gryllotalpa* sp., crickets (*Gryllus* sp.), locusts (Acrididae and Tettigoniidae), bumble-bees (*Bombus* sp.),

hornets (*Vespa crabro*), *Carabus* sp., *Calosoma* sp., juvenile mammals, lizards, snakes, eggs, red grapes, and blackberries (BÖHME 1984). The diet of *L. viridis* seems to be rather diverse, but captive bred juveniles of this species show individual preferences, which may correlate to the intraspecific variability in tooth morphology.

Meroles GRAY, 1838

Meroles suborbitalis (PETERS, 1869)
(Pl. III, Fig. 9)

Number of examined specimens: 1 adult

Distribution:

South Africa, Namibia, Botswana.

Dental morphology:

The teeth of *Meroles suborbitalis* show transversally widened bases and flattened flanks. The widths of the tooth crowns exceed the widths of the tooth shafts. The lingual surfaces of the tooth crowns are concave. The culmines lateres are only weakly developed. The anterior tooth crowns are unicuspid whereas the posterior teeth are bicuspid. The lateral cusps are situated mesially and are relatively large. The apical notch between the main cusp and the lateral cusp is only slightly concave, so that a true separation of the two cusps is not found. The main cusps are moderately pointed. The cristae mesiales of the main cusps are longer than the cristae distales, which leads to a recurvature of the apices. All enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.7:1.0. The resorption pits of *M. suborbitalis* are of circular shape or are slightly elongated in the apical direction.

Diet:

The desert dwelling *M. suborbitalis* is a sit-and-wait hunter. The diet of these lizards consists of beetles, locusts, and termites (ROGNER 1994).

Nucras NEUMANN, 1900

Nucras lalandii (MILNE-EDWARDS, 1829)

Number of examined specimens: 1 adult

Distribution:

South Africa, Swaziland.

Dental morphology:

The right dentary of specimen ZFMK 7830 bears 21 tooth positions. The two anteriormost teeth are unicuspid whereas all following teeth are bicuspid with robust main cusps and small but clearly separated and mesially situated lateral cusps. The cristae mesiales et distales are almost the same length and the tips of the main cusps are relatively blunt. The tooth shafts are cylindrical whereas the tooth crowns show concave lingual surfaces. All enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.4:1.0. The resorption pits of *Nucras lalandii* are circular in shape.

Diet:

The diet of the members of the nocturnal genus *Nucras* consists of insects (especially termites), beetles, and arachnids. Scorpions form a large percentage of the diet of *Nucras intertexta* (AUERBACH, 1985).

Omanosaura LUTZ, BISCHOFF & MAYER, 1986

Omanosaura jayakari (BOULENGER, 1887)

Number of examined specimens: 2 adults

Distribution:

Oman, United Arab Emirates.

Dental morphology:

The left dentary of specimen SRK 00.089 bears 25 tooth positions. The teeth are robust and stout. The tooth bases and tooth necks are transversally expanded. The inner surfaces of the teeth are concave. The five anterior teeth are unicuspid whereas all following teeth are bicuspid with a minute mesial side cusp and a large main cusp; the main cusps are blunt. The crista mesialis is always longer than the crista distalis and both encompass an extremely large angle of 150 degrees. In most teeth, the concave inner surfaces of the tooth crowns are heavily striated. The intensity of the striations decreases in the posterior teeth. Some ten striae are found per tooth. The striae are arranged in parallel and almost never converge apically. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 2.8:1.0. The resorption pits of *Omanosaura jayakari* are circular in shape.

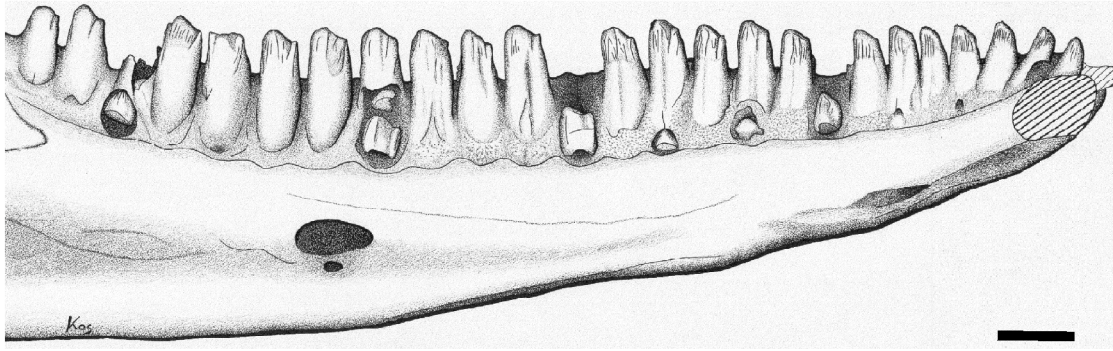


Fig. 40: *Omanosaura jayakari*
(specimen SRK 00.089)
Left dentary; lingual view
Scale bar: 1 mm

Diet:

Data concerning the diet of *O. jayakari* are not available.

Parvilacerta HARRIS, ARNOLD & THOMAS, 1998

Parvilacerta parva (BOULENGER, 1887)

Number of examined specimens: 1 adult

Distribution:

Armenia, Turkey.

Dental morphology:

The right dentary of specimen SRK 00.266 bears 21 tooth positions. The teeth of this dwarf lizard are slender with cylindrical shafts and lingually flattened tooth crowns. The seven anterior teeth are unicuspid; all following teeth are bicuspid with distinctly separated mesial side cusps and pointed main cusps.

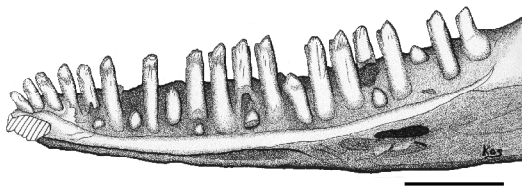


Fig. 41: *Parvilacerta parva*
(specimen SRK 00.266)
Right dentary; lingual view
Scale bar: 1 mm

The cristae mesiales of the main cusps are longer than the cristae distales so that the tooth tips are directed in the posterolingual direction. All cutting edges are sharp. The culmines lateres are short but prominent. Striations are restricted to the lingual surfaces of the tooth

crowns in *Parvilacerta parva*. The striae are rather fine and best developed in the anterior teeth. Up to six striae are found in a sole tooth. The striae are arranged parallel and converge apically. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.6:1.0. The resorption pits are circular or slightly elongated in the apical direction.

Diet:

P. parva consumes diverse insects and spiders. However, the dominating prey items of this small lizard are ants (ROGNER 1984).

Philochortus MATSCHIE, 1893

Philochortus hardeggeri (STEINDACHNER, 1891)
(Pl. III, Fig. 10)

Number of examined specimens: 1 adult

Distribution:

Somalia, Djibouti, Ethiopia.

Dental morphology:

The right dentary of specimen BMNH 1905.10.58.9 bears 23 tooth positions. The five most anterior teeth are unicuspid and of simple conical habitus with slightly recurved cusps. The following teeth show slightly transversally expanded tooth bases and lingually concave bicuspid tooth crowns. The main cusps of the erected central and posterior teeth appear blunt and rounded. The mesial side cusps are separated from the main cusps by notch-like inward curvatures of the apical cutting edges. The culmines lateres are well developed and especially the culmen lateris posterior is distinctly pronounced. In the immediate vicinity of the culmines lateres, the lingual surfaces of the tooth crowns are strongly

concave. The enamel surfaces of *Philochortus hardeggeri* are free of striations. The ratio toothlength:diameter of tooth neck is 2.8:1.0. The resorption pits are circular in shape.

Diet:

At present, the diet of this African lacertid is unknown.

Podarcis WAGLER, 1830

Podarcis bocagei (SEOANE, 1885)

(Pl. III, Fig. 11)

Number of examined specimens: 3 adults

Distribution:

Spain, Portugal (Berlenga Island).

Dental morphology:

The teeth of *Podarcis bocagei* are conical and predominantly unicuspid. Only a minor number of the teeth show minute mesial side cusps which are situated at the anguli mesiales. The cross-sections of the teeth are circular and the largest widths of the teeth are in the tooth necks. The tooth crowns are pointed and lingually flattened only slightly. The culmines lateres are only weakly pronounced. In many teeth, the tips are divided into a cuspis labialis and a lower cuspis lingualis. The separation of these two cusps is not advanced since the two cusps are situated close to each other and the cuspis lingualis is scarcely elevated above the concave lingual surface of the tooth crown. The cristae mesialis et distalis are the same length. The enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.5:1.0. The resorption pits are circular or slightly expanded in the apical direction.

Diet:

P. bocagei preys on arthropods (ROGNER 1984). The dominating prey items are Araneae (18.52 %), followed by Homoptera (17.45 %), Curculionidae (15.00 %), and other Coleoptera (10.87 %, predominantly Hydrophilidae, Elateridae, and Meloidae), and Diptera (9.03 %, predominantly Limnobiidae, Bibionidae, Anthomidae, and Muscidae) (MELLADO 1986).

Podarcis erhardii (BEDRIAGA, 1882)

Number of examined specimens: 2 adults

Distribution:

Greece, Albania, Macedonia, Bulgaria.

Dental morphology:

The right dentary of specimen SRK 00.214 bears 22 tooth positions. The seven anterior teeth are unicuspid whereas all following teeth are bicuspid with a recurved main cusp and a smaller mesial side cusp. The tooth shafts are cylindrical and the tooth crowns are lingually concave. The main cusps are pointed and directed in the posterolingual direction. The cristae mesiales are longer than the cristae distales. The culmines lateres are pronounced. Striations are found only in the teeth of the anterior half of the tooth row and are also restricted to the lingual surfaces of the tooth crowns. The striae are arranged in parallel and converge at the tips of the main cusps. The striae are rather fine and maximally five striae per tooth are present. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.0:1.0. The resorption pits of *Podarcis erhardii* are almost perfectly circular.

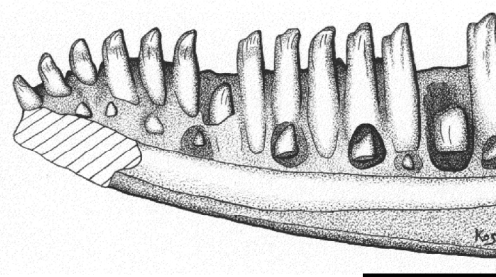


Fig. 42: *Podarcis erhardii* (specimen SRK 00.214) Anterior region of a right dentary (tooth positions 1-13 from 22); lingual view Scale bar: 1 mm

Diet:

The diet of *P. erhardii* consists of Lepidoptera, Orthoptera, Diptera (here, locusts dominate during the summer), Scorpiones, Araneae, and juvenile geckos (*Cyrtodactylus kotschy*) (GRUBER 1986). In island populations of *P. erhardii*, % of the total diet comprised of ants (QUAYLE 1983). In these diet analyses, which are based on fecal pellets of *P. erhardii* specimens from the island of Ios in the southern Aegean Sea, the following percentages were made up by other food items: 7 % Coleoptera, 7 % Hemiptera, 3 % Orthoptera, 3 % Scorpiones, 1 % Diptera, and 1 % Araneae. ADAMOPOULOU et al. (1999) record Coleoptera as the dominant prey group (26.53 %) of *P. erhardii*. Accordingly, the

composition of the diet of *P. erhardii* strongly depends on seasonal and local changes; the lizards seem to be opportunistic feeders.

Podarcis filfolensis (BEDRIAGA, 1876)
(Pl. III, Fig. 12)

Number of examined specimens: 1 adult

Remark:

Specimen BMNH 1909.10.30.56 is cataloged as *Lacerta filfolensis*.

Distribution:

Malta Archipelago, Filfla Island (Filfolia), Fungus Island (General's Island), Selmunett Island (San Paul), Italy, Pelagian Islands (Linosa and Lampione), Gozo and Kemmuna (Comino).

Dental morphology:

The right dentary of specimen BMNH 1909.10.30.56 bears 21 tooth positions. The teeth are cylindrical and the width of the tooth crown is identical with the width of the tooth base. The lingual surfaces of the teeth are flattened. The tooth crowns are slightly rotated in the posterior direction. The anterior teeth are unicuspid, the central and posterior teeth are bicuspid, and the posteriormost teeth show a tendency to tricuspidity with an additional distal side cusp which is still strongly connected to the main cusp. The crista mesialis is slightly longer than the crista distalis. Striations are restricted to the lingual surfaces of the tooth crowns. The number of striae is relatively low; in most teeth only a solely central stria is developed. This prominent stria runs straight from the transition zone between the tooth neck and the tooth crown to the tip of the main cusp. In several teeth, additional striae are found on the lingual surfaces of the mesial side cusps. The ratio toothlength:diameter of tooth neck is 3.0:1.0. The resorption pits are circular in *Podarcis filfolensis*.

The low tooth number is assumed to be a differentiating character which separates *P. filfolensis* from other species of the genus (VOROBYEVA & CHUGUNOVA 1991). This observation cannot be confirmed here since similar tooth numbers are found in several other lacertids.

Diet:

The arthropod diversity and especially the prey density are extremely low on the islands inhabited by *P. filfolensis*. Accordingly, the lizards largely depend on ants and weaker

individuals of their own species (BISCHOFF 1986).

Podarcis hispanica (STEINDACHNER, 1870)
(Pl. III, Fig. 13)

Number of examined specimens: 2 adults

Remark:

The investigated specimens are cataloged as *Lacerta hispanica*.

Distribution:

Portugal, Spain, France, Morocco, Algeria, Tunisia.

Dental morphology:

The teeth of *Podarcis hispanica* are relatively robust and the central and posterior teeth are transversally broadened in occlusal view, whereas the anterior teeth are cylindrical or slightly conical. The anteriormost four or five teeth are unicuspid; the following teeth are bicuspid and in the posterior portion of the tooth row several tricuspid teeth with an additional minute distal side cusp are found. The tips of the teeth are relatively pointed. The lingual surfaces of the tooth crowns are flattened and in the immediate vicinity of the lateral cusps concave in shape. The culmines lateres are distinctly pronounced. The enamel surfaces of most teeth are unwrinkled; some irregular and often hardly visible striations are developed only in several tricuspid posterior, as well as in several unicuspid, anterior teeth. The number of these fine striae is restricted to a maximum of five striae per tooth in the investigated *P. hispanica* specimens. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.0:1.0. The resorption pits are circular.

Diet:

Research on the *P. hispanica* population from Benidorm Island showed a highly stenophageous diet, which included a high proportion of clumped prey and a high percentage of plant matter as well (PÉREZ-MELLADO & CORTI 1993). The diet is dominated by Formicidae, Hymenoptera, Homoptera, Diptera, Pseudoscorpionida, vegetable matter, Araneae, and Dytioptera. To a lesser degree the lizards consume Heteroptera, insect larvae, Lepidoptera, and Coleoptera (PÉREZ-MELLADO & CORTI 1993).

Podarcis lilfordi (GÜNTHER, 1874)

Number of examined specimens: 2 adults

Remark:

Specimen ZFMK 21648 is cataloged under the synonym *Lacerta hispanica*.

Distribution:

Balearic Islands, Cabrera Archipelago.

Dental morphology:

The right dentary of specimen SRK 00.095 bears 18 tooth positions; almost one half of the tooth positions are represented as empty loci. The teeth are widely spaced, rather robust and cylindrical or slightly conical in shape. All teeth anterior of tooth position 7 are unicuspid; the following teeth are bicuspid with a small mesial side cusp and a distal main cusp. The lingual surfaces of the tooth crowns are flattened in posterior teeth or concave in anterior teeth. The cristae mesiales are longer than the cristae distales. Up to six striae are found at the lingual surfaces of the apices. The numbers of striae decrease in the posterior teeth, where the striae often are arranged in a slightly irregular manner. The striae run almost parallel to the longitudinal axes of the teeth and they converge apically. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 2.8:1.0. The resorption pits are circular.

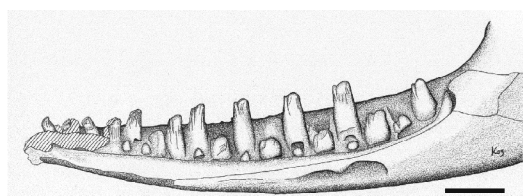


Fig. 43: *Podarcis lilfordi*
(specimen SRK 00.095)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

P. lilfordi captures flies which are attracted by the particular odour of the plant *Dracunculus muscivorus*. Occasionally, the lizards detect trapped flies in the spathe-tubes and they even eat the fruits of *D. muscivorus*. 53 % of all fecal pellets from *P. lilfordi* were exclusively composed of seeds from this plant. The dominating arthropod prey groups are Formicidae and Coleoptera (PÉREZ-MELLADO et al. 2000). In the summer, *P. lilfordi* feeds almost exclusively on nectar and pollen of *Crithmum maritimum*. The *P. lilfordi* populations on Nitge (and possibly other

Balearic islets) consume flowers of *Allium ampeloprasum* when arthropods become rare on the dry island. But even crustaceans (Amphipoda) are consumed on rare occasions, although usually malacophagy seems to be uncommon. Adult male *P. lilfordi* show cannibalistic tendencies (PÉREZ-MELLADO & CORTI 1993).

Podarcis melisellensis (BRAUN, 1877)

Number of examined specimens: 1 adult

Distribution:

Croatia, Italy, Slovenia, Montenegro (including many Adriatic Islands), Albania.

Dental morphology:

The right dentary of specimen SRK 00.082 bears 22 tooth positions. The teeth of *Podarcis melisellensis* are noticeably slender and they are of cylindrical habitus. The apical halves of the teeth rise above the labial margin of the dentary. The posterior teeth (tooth positions 14 to 21) are more robust than the anterior teeth. The unicuspid tooth crowns of teeth numbers 1 to 8 are pointed, distinctly recurved, and lingually concave. The following teeth are bicuspid with small mesial side cusps and relatively straight main cusps. The lingual surfaces of the tooth crowns are only slightly flattened in the posterior teeth. A maximum of six parallel striae are situated on the lingual surfaces of the tooth crowns whereas all other enamel surfaces are smooth. The striations are more pronounced in anterior teeth than they are in posterior teeth. Several posterior teeth of *P. melisellensis* are perfectly smooth. The ratio toothlength:diameter of tooth neck is 4.4:1.0. The resorption pits are dorsally expanded at the beginning of the replacement process and they become circular later.

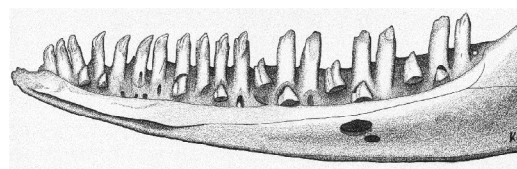


Fig. 44: *Podarcis melisellensis*
(specimen SRK 00.082)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

The diet of *P. melisellensis* consists of small insects, spiders, isopods, *Lithobius* sp., and snails (DIESENER & REICHHOLF 1985). More precise data are recorded by TIEDEMANN & HENLE (1986). These authors describe a diet consisting of terrestrial isopods, beetles, terrestrial snails, spiders, ants, cicadas, locusts, mosquitoes, flies, plant matter (in island populations), fruits of *Capparis rupestris*, food remains and ectoparasites of sea gulls, and smaller conspecific lizards.

Podarcis muralis (LAURENTI, 1768)
(Pl. III, Fig. 14)

Number of examined specimens: 8 adults

Distribution:

Austria, Czechia, Slovakia, Hungary, Romania, Italy, Slovenia, Croatia, Bosnia-Herzegovina, Croatia, Cres Island, Serbia, Macedonia, Albania, Bulgaria, Greece, Turkey, Spain, France, Belgium, Netherlands, Germany, Switzerland.

Dental morphology:

The right dentary of specimen SRK 00.037 bears 20 tooth positions. The four anterior teeth of this specimen are unicuspid whereas all following teeth are bicuspid with a moderately pointed main cusp and a well developed mesial side cusp. The tooth necks and tooth bases are cylindrical. The tooth crowns are lingually flattened. The culmines lateres are prominent and they cause inward curvatures of the lingual surfaces in their immediate vicinities. The cristae mesiales are only slightly longer than the cristae distales. The enamel surfaces of *Podarcis muralis* lack true striations apart from some irregular wear facets. The tooth morphology is almost similar in all investigated specimens even if the subspecific level is taken into consideration. The ratio toothlength:diameter of tooth neck is 3.6:1.0. The resorption pits of *P. muralis* are perfectly circular in shape.

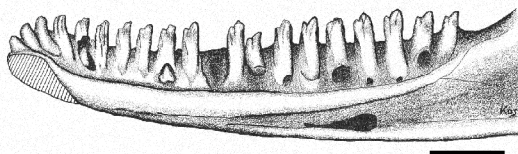


Fig. 45: *Podarcis muralis nigriventris*
(specimen SRK 00.037)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

The diet of *P. muralis* varies depending on location, season, and prey availability. The dominating prey items are insects, and here especially Diptera (Tipulidae, Syrphidae, Muscidae) with 52 %, and Hymenoptera with 31 %. In addition, Coleoptera are an important prey group for *P. muralis*. Arachnida, Oligochaeta, Gastropoda, Isopoda, Orthoptera, Dermaptera, Heteroptera, Lepidoptera, Opiliones, and Acari play a minor role in the composition of the lizards diet (GRUSCHWITZ & BÖHME 1986). *P. muralis* hunts actively for small crustaceans in coastal regions of France. Cannibalistic behavior and the consumption of plant matter by wall lizards was observed only on rare occasions (GRUSCHWITZ & BÖHME 1986).

Podarcis peloponnesiaca (BIBRON & BORY, 1833)
(Pl. III, Fig. 15)

Number of examined specimens: 5 adults

Distribution:

Greece.

Dental morphology:

The teeth of *Podarcis peloponnesiaca* show transversally expanded shafts and lingually flattened tooth crowns. The anterior teeth are unicuspid, but in the posterior direction they gradually transfer into bicuspid teeth with a blunt main cusp and a mesial side cusp. The side cusps are closely connected to the main cusps. The cristae mesialis et distalis are almost the same length; in most teeth these cutting edges are abraded and the tooth crowns are extensively worn. Some five parallel striae are found at the lingual surfaces of the tooth crowns. The striae are fine and many teeth completely lack striations. The striations do not converge apically; this is probably a result of the abrasion of the occlusal portions of the teeth. The labial tooth surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 2.8:1.0. The resorption pits of *P. peloponnesiaca* are of circular shape.

Diet:

The lizards prey on locusts, flies, winged individuals of the ant *Messor barbarus*, spiders (Tomisidae), Lycaenidae, and Coleoptera. In captivity, even earthworms are consumed (BRINGSOE 1986). In addition to the former food items, ROGNER (1994) also records Isopoda as prey items for *P. peloponnesiaca*.

Podarcis pityusensis (BOSCA, 1883)

Number of examined specimens: 7 adults

Distribution:

Balearic Islands (Pityuses).

Dental morphology:

The right dentary of specimen SRK 00.024 bears 21 tooth positions; all of these are represented as fully erected teeth. The six anterior teeth are unicuspid whereas all following teeth are bicuspid with pointed main cusps and small mesial side cusps; the later are closely connected to the main cusps. The teeth in tooth numbers 14 and 15 show a tendency to tricuspidity as the anguli distales of these teeth are extremely prominent. The robust and narrow spaced teeth of *Podarcis pityusensis* show cylindrical shafts and tooth crowns with lingually concave or at least flattened surfaces. The tips of the main cusps are posterolingually directed. The culmines lateres are well developed and stretch in the basal direction to the transition zone between the tooth neck and the tooth crown. Striations are developed rather irregularly on several teeth of the anterior, the central, and the posterior portions of the tooth row. However, most teeth are unwrinkled. If striations are present, they are restricted to the lingual surfaces of the tooth crowns. The striae converge apically at the tips of the main cusps as well as at the tips of the lateral cusps. A maximum of eight striae are found in one tooth. The striae are extremely fine. All labial enamel surfaces are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.3:1.0. The resorption pits of *P. pityusensis* are circular or slightly elongated in the apical direction.

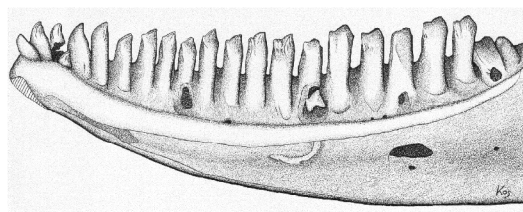


Fig. 46: *Podarcis pityusensis*
(specimen SRK 00.024)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

The diet of *P. pityusensis* includes not only various arthropods, but additionally large amounts of plant matter (ROGNER 1994). This herbivorous tendencies correspond to the island

habitat of this lizard. The populations from Ibiza feed almost exclusively on insects whereas the percentage of plant matter increases in populations from smaller islets. The lizards consume flowers of *Rosmarinus officinalis*, fruits of *Juniperus phoenicea*, flowers of *Convolvulus althaeoides*, leaves of *Crithmum maritimum*, seeds of *Cuscuta epithymum*, lizard eggs, and show coprophageous tendencies by feeding on the feces of *Larus audouini* (SALVADOR 1986). The dominating arthropods in the diet of *P. pityusensis* are Formicidae, Coleoptera and their larvae, Gastropoda, and Hymenoptera. Other prey groups as Arachnida, Hemiptera, Lepidoptera larvae, Orthoptera, Myriapoda, Diptera, Tenebrionidae, and Isopoda make up a minor part of the diet of *P. pityusensis*. The dietary composition depends on seasonal changes and prey availability.

Podarcis sicula (RAFINESQUE-SCHMALTZ, 1810)

(Pl. III, Fig. 16)

Number of examined specimens: 10 adults

Distribution:

France, Switzerland, Italy, Montenegro, Croatia, Slovenia, Turkey.

Dental morphology:

The dentaries of *Podarcis sicula* bear 23 tooth positions on average. The tooth numbers seems to be rather constant in various individuals and even in different subspecies (*Podarcis sicula campestris* DE BETTA, 1857, *Podarcis sicula sicula* (RAFINESQUE-SCHMALTZ, 1810)); however, the dental morphology strongly varies within this species.

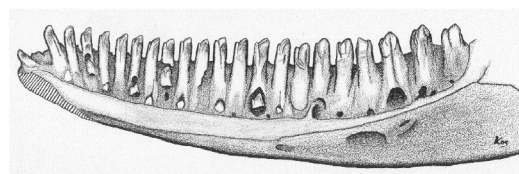


Fig. 47: *Podarcis sicula*
(specimen SRK 00.029)
Right dentary, demonstrating the slightly heterodont condition found in this species; lingual view
Scale bar: 1 mm

The dentition of specimen SRK 00.029 is slightly heterodont with slender anterior teeth and distinctly robust teeth in the posterior

portion of the relatively short mandible. In strong contrast, the dentition of specimen SRK 00.035 is homodont with the posterior teeth lacking any modification for a robust habitus.

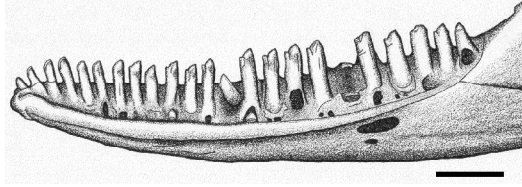


Fig. 48: *Podarcis sicula*
(specimen SRK 00.035)
Right dentary, demonstrating the homodont morphotype; lingual view
Scale bar: 1 mm

The teeth of all investigated specimens show cylindrical tooth shafts and lingually flattened tooth crowns. The four to eight anterior teeth are unicuspid whereas all following teeth are bicuspid with small mesial side cusps. A deep occlusal notch is situated between the two cusps. Hence, the lateral cusps are strongly separated from the main cusps. The crista mesialis is slightly longer than the crista distalis in most teeth. The tips of the main cusps, as well as the tips of the lateral cusps, are pointed. In specimen SRK 00.029, a distal side cusp is found instead of the mesial side cusp in tooth number 20. This situation is interpreted here as a pathological abnormality. Striations are extremely faint if they are present at all. The intensity of the striations gradually changes among the investigated specimens. In most specimens, the striae are restricted to the lingual surfaces of the anterior teeth whereas the posterior teeth are unwrinkled. The striae run parallel; not more than five striae are found in a single tooth. In specimen SRK 00.029, the surfaces of the robust posterior teeth show extensive wear facets which are arranged irregularly. The labial surfaces of the teeth of all investigated specimens are unwrinkled. The ratio toothlength:diameter of tooth neck is 4.0:1.0 on average. The resorption pits of *P. sicula* are of almost circular shape.

Diet:

The dietary composition varies in various populations of *P. sicula*. In general, the lizards consume Colcoptera, Lepidoptera larvae, Hymenoptera, Araneidae, Amphipoda, Formicidae, and other arthropods. Ants (Formicidae) become an important prey item when the availability of other prey animals

decreases. In addition to this arthropod prey, *P. sicula* feeds on ripe sweet fruits (*Opuntia ficus-indica*, *Solanum nigrum*, figs, grapes, cherries, and plums) and licks the nectar of flowers. On rare occasions, the lizards prey on scorpions (*Euscorpis italicus*), wasps (*Paravespula germanica*), and members of their own species (HENLE & KLAVER 1986).

Podarcis taurica (PALLAS, 1814)
(Pl. III, Fig. 17)

Number of examined specimens: 1 adult

Distribution:

Ukraine, Crime Peninsula, Romania, Hungary, Macedonia, Bulgaria, Greece, Turkey, Albania, Moldova.

Dental morphology:

The left dentary of specimen ZFMK 7865 bears 21 tooth positions. The tooth shafts of *Podarcis taurica* are cylindrical and the tooth crowns are lingually concave in shape. The anterior teeth are unicuspid whereas the central and posterior teeth are bicuspid. The bicuspid teeth show relatively blunt main cusps and minute mesial side cusps which are strongly connected to the main cusps. The culmines lateres are pronounced. About a dozen fine striae are situated at the concave lingual surfaces of the tooth crowns. The striae are fine and arranged in parallel. The spaces between two striae are always of constant width. The striae are perfectly straight and lack any signs of an apical convergence. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.5:1.0. The resorption pits of *P. taurica* are circular in shape and covered by mucosa in the solely available specimen.

Diet:

The diet of *P. taurica* consists predominantly of ground dwelling arthropods and underlies seasonal changes. The diet contains Araneae as well as various Coleoptera (Carabidae, Elateridae, Chrysomelidae, Curculionidae, and Scarabaeidae), Hymenoptera, Isopoda, Millepoda, Gastropoda, Formicidae, and other invertebrates (KABISCH 1986). The amount of locusts in the diet of *P. taurica* is lower than formerly assumed (KABISCH & ENGELMANN 1969).

Takydromus DAUDIN, 1802

Takydromus formosanus (BOULENGER, 1894)
(Pl. III, Fig. 18)

Number of examined specimens: 1 adult

Distribution:

China (Taiwan), Pescadores Islands.

Dental morphology:

The teeth of *Takydromus formosanus* are slender and show cylindrical shafts and lingually flattened tooth crowns. The anteriormost teeth are unicuspid. However, the majority of the teeth are tricuspid with a central main cusp and smaller mesial and distal side cusps. These lateral cusps are clearly separated from the main cusp by deep notches of the occlusal cutting edges. In lingual view, the tooth crowns of *T. formosanus* appear strongly symmetrical with both lateral cusps being of equal size. The cristae mesialis et distalis are blunt and the culmines lateres are only weakly developed and short. In contrast to the acute tips of the lateral cusps, the apices of the main cusps are only moderately pointed. All enamel surfaces lack striations. The ratio toothlength:diameter of tooth neck is 3.8:1.0. The resorption pits of *T. formosanus* are circular in shape.

Diet:

T. formosanus is assumed to be insectivorous. However, no exact data concerning the diet of this species are available.

Remark:

The genus *Takydromus* has an uncertain taxonomic status (HARRIS et al. 2001).

Takydromus septentrionalis (GÜNTHER, 1864)
(Pl. III, Fig. 19)

Number of examined specimens: 3 adults

Distribution:

China (Taiwan).

Dental morphology:

The right dentary of specimen ZFMK 14830 bears 26 tooth positions. The tooth morphology of *Takydromus septentrionalis* strongly resembles the tooth morphology of *Takydromus formosanus*. The occlusal cutting edges of the tricuspid tooth crowns are even more deeply notched in *T. septentrionalis* and appear V-shaped. From each of these notches, a depression runs across the apical surface in basal direction. The tips of the main cusps, as

well as the smaller lateral cusps, are pointed. The flanks of the teeth are slightly flattened in the investigated specimens of *T. septentrionalis*. In specimen ZFMK 14831, the lateral cusps are smaller than they are in other individuals and they appear less separated from the main cusps. The enamel surfaces of all teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.5:1.0. The resorption pits of *T. formosanus* are circular in shape.

Diet:

In captivity, *T. septentrionalis* preys on small arthropods (personal observation).

Takydromus sexlineatus DAUDIN, 1802
(Pl. III, Fig. 20; Pl. IV, Fig. 1)

Number of examined specimens: 3 adults

Distribution:

India, China, Burma, Thailand, Laos, Cambodia, Vietnam, Malaysian Peninsula, Indonesia (Sumatra, Java, Borneo).

Dental morphology:

The right dentary of specimen SRK 00.096 bears 30 tooth positions; almost the half of these are represented as empty loci due to the high individual ages of the specimens (captive kept individuals). The tooth bases of many teeth are covered by mucosa. The anterior half of the tooth row bears pointed unicuspid teeth whereas the teeth in the posterior half of the tooth row are tricuspid in *Takydromus sexlineatus*. The tooth shafts are cylindrical and relatively short. The tooth crowns are lingually flattened. The lateral cusps are clearly separated from the main cusps. The distal cusps are the same size as the mesial cusps, which results in a perfectly symmetrical appearance of the tooth crowns in the lingual view. In specimen SRK 00.269, the main cusps of the tricuspid teeth are additionally separated into a cuspis labialis and a lower situated cuspis lingualis. The cuspides linguales are more pointed than the cuspides labiales, and the two cusps are connected by the narrow ridge of the carina intercuspidalis. Several posterior teeth of this specimen show mesially expanded tooth crowns which have a candelabra-shaped appearance. The lingual surfaces of the lateral cusps are almost always concave. The anterior teeth are slightly recurved. Striations, if at all present, are found only in the anterior teeth and are restricted to the lingual surfaces of the tooth crowns. These

striations are very fine and the striae run parallel to the longitudinal axes of the teeth. The labial surfaces of the teeth are unwrinkled in *T. sexlineatus*. The ratio toothlength:diameter of tooth neck amounts to 2.8:1.0. The resorption pits are circular in shape.

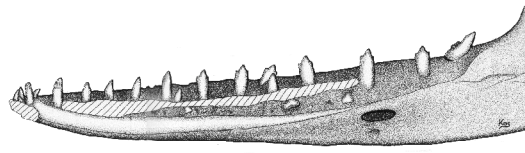


Fig. 49: *Takydromus sexlineatus*
(specimen SRK 00.096)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

These long-tailed lizards move snake-like through dense grass and forage for small arthropods. In captivity, *T. sexlineatus* consumes spiders, crickets, *Tenebrio* larvae, and occasionally flies and mosquitoes (ROGNER 1994).

Teira MAYER & BISCHOFF, 1996

Teira dugesii (MILNE-EDWARDS, 1829)
(Pl. IV, Figs. 2-3)

Number of examined specimens: 3 adults

Remark:

All investigated specimens are cataloged under the synonym *Podarcis dugesii*.

Distribution:

Madeira, Desertas Islands, Portugal, Porto Santo Island, Salvagens Islands.

Dental morphology:

The teeth of *Teira dugesii* show cylindrical tooth bases and tooth necks and lingually flattened or concave tooth crowns. The seven or eight anterior teeth are unicuspid and recurved whereas all following teeth are bicuspid. The small mesial cusps of these teeth are closely connected to the main cusps. The notch of the occlusal cutting edge between the main cusp and the lateral cusp is only slightly concave. The tooth bases and the tooth necks are cylindrical. The tooth crowns are lingually flattened or concave. The tips of the anterior teeth are divided into a cuspis labialis and a lower cuspis lingualis. These two cusps are connected by a straight carina intercuspidalis. The culmines lateres are short. Striations are

found in the anterior teeth and decay gradually within the tooth row. Hence, the posterior teeth are unwrinkled. The striae are restricted to the lingual surfaces of the tooth crowns and are arranged in parallel. Apically, the striae converge at the cuspides linguales. About a dozen striae can be found in a sole tooth. The lengths and intensities of the striae vary and several striae bifurcate in the basal direction. The ratio toothlength:diameter of tooth neck is 3.0:1.0. The resorption pits are circular in shape.

Diet:

QUAYLE (1983) records ants as the preferred prey of *T. dugesii*. Gut examinations made by SADEK (1981) showed a preference of special food items by lizards of particular habitats (beach, open ground, cultivated land, woodland, etc.). In general, the diet of *T. dugesii* consists of Formicidae (predominantly females) and other Hymenoptera, Coleoptera, Diptera, and Dermaptera. Occasionally, the lizards consume Homoptera, Hemiptera, Lepidoptera, Thysanoptera, Psocoptera, Collembola, Thysanura, Othoptera, Neuroptera, Isopoda, Araneida, Acarina, Diplopoda, Chilopoda, Pseudoscorpionida, Mollusca, various larvae, fruits, seeds, and other plant material (SADEK 1981). Additionally, the composition of the diet depends upon the individual age of the lizards.

Timon MAYER & BISCHOFF, 1996

Timon lepidus (DAUDIN, 1802)
(Pl. IV, Figs. 4-7)

Number of examined specimens: 1 juvenile, 16 adults

Remark:

The majority of the investigated specimens are cataloged under the synonym *Lacerta lepida*.

Distribution:

Spain, Portugal, France, Italy.

Dental morphology:

The dentaries of the investigated specimens bear 21 to 26 tooth positions. The teeth are relatively long and their apical halves rise above the labial parapet of the dentary. Almost all teeth of the entire tooth row are tricuspid; unicuspid teeth are restricted to the anteriormost one to three tooth positions. The tooth shafts are cylindrical; the lingual surfaces of the tooth crowns are flattened and they are

strongly concave in the immediate vicinity of the culmines lateres. In the lingual view, the tooth crowns appear strongly symmetrical with both lateral cusps being of equal size. In older specimens, the lateral cusps are often extensively worn and the main cusps appear blunt; however, the lateral cusps are pronounced and the central cusps are pointed in the juvenile specimen (K 17 Priv. Coll. EVANS). The cristae mesialis et distalis of the main cusps are the same length in all investigated specimens of *Timon lepidus*. Striations are restricted to the lingual surfaces of the tooth crowns. The patterns of striations greatly vary individually. In most specimens, the striae run parallel and converge apically. In specimen ZFMK 7800, the striae are concentrated on the mesolingual surfaces of the tooth crowns whereas the distolingual surfaces of the tooth crowns are almost unwrinkled. The striations are sometimes arranged in complex patterns. In specimen ZFMK 7801, two dominating striae, the striae dominantes anterior et posterior, form a prominent cuspis lingualis, which is clearly separated from the cuspis labialis by the concave antrum intercristatum. Approximately six additional striae are situated between the stria dominans anterior and the stria dominans posterior as well as between the striae dominantes and the prominent culmines lateres. Occasionally, one of these additional striae bifurcates with a stria dominans in specimen ZFMK 7801. In all investigated specimens, the labial enamel surfaces of the teeth are unwrinkled; the entire tooth surfaces of the juvenile specimen lack striations as well. The ratio toothlength:diameter of tooth neck is 4.3:1.0. The resorption pits of *T. lepidus* are perfectly circular.

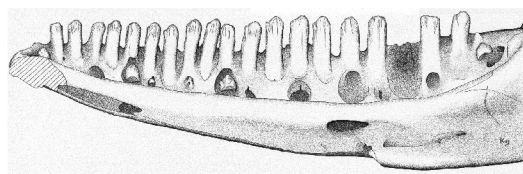


Fig. 50: *Timon lepidus*
(specimen SRK 00.088)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

T. lepidus is recorded as being a "habitual omnivore" by SOKOL (1967). Indeed, the lizards show seasonal changes in their diet which consists predominantly of insects (85 % Coleoptera) but additionally includes Gastropoda, Isopoda, Myriapoda, Araneae, Scorpionones, and occasionally vertebrates (rodents, songbirds, amphibiae (*Blanus cinereus*), geckos (*Tarentola mauritanica*), and conspecific juveniles) (BISCHOFF et al. 1984).

Timon pater (LATASTE, 1880)

(Pl. IV, Figs. 8-11)

Number of examined specimens: 4 adults

Remark:

Two specimens are cataloged under the synonym *Lacerta ocellata* (BMNH 1974.24.91 and IFSZ 27816) and two additional specimens are cataloged under the synonym *Lacerta pater* (ZFMK 4060 and ZFMK 7870).

Distribution:

Algeria, Tunisia, Morocco.

Dental morphology:

The right dentary of specimen BMNH 1974.24.91 bears 29 tooth positions. The teeth are rather robust and show transversally expanded tooth bases and tooth necks. In the lingual view, the widths of the tooth crowns appear larger than the widths of the tooth shafts. The flanks of most teeth are concave. The lingual surfaces of the tooth crowns are flattened; in the immediate vicinity of the culmines lateres, the tooth surfaces are concave. The anterior teeth are unicuspid; the central and posterior teeth are bicuspid with smaller lateral cusps which are situated in mesial positions. In several teeth of specimen BMNH 1974.24.91, a tendency to tricuspidity is seen. However, the distal side cusps are only slightly prominent and more resemble modified anguli distales. The cristae mesiales et distales of the main cusps are the same length and the tips of the teeth are blunt and often extensively worn. The lingual surfaces of the tooth crowns are heavily striated. A maximum of 12 striae is developed in the 25th tooth of specimen BMNH 1974.24.91. The striae are very pronounced and converge apically. In many teeth, two striae dominantes form a cuspis lingualis connected with the cuspis labialis by a prominent ridge, the carina intercuspidalis. In *Timon pater*, the apical angle of the cuspis lingualis is always smaller than the apical angle of the cuspis

labialis. In many teeth, some additional striae are situated at the lingual surfaces of the lateral cusps. The labial surfaces of the teeth are unwrinkled. Specimen ZFMK 7870 represents a completely different tooth crown morphology. Here, the majority of teeth are tricuspid and the distal side cusps are the same size as the mesial side cusps. The tips of the teeth are more pointed than in the remaining specimens of *T. pater*, and the lingual surfaces of the tooth crowns are less heavily striated. The ratio toothlength:diameter of tooth neck is 4.0:1.0. The resorption pits are circular in shape.

Diet:

The diet of *T. pater* is assumed to be comparable to the diet of *Timon lepidus*.

Timon princeps (BLANFORD, 1874)
(Pl. IV, Figs. 12-13)

Number of examined specimens: 1 adult

Remark:

Specimen ZFMK 7877 is cataloged under the synonym *Lacerta principes kurdistanica*.

Distribution:

Iran, Turkey, Syria, Iraq.

Dental morphology:

The tooth morphology of *Timon princeps* strongly resembles the tooth morphology of *Timon pater*. The teeth are robust and show transversally expanded tooth bases and tooth necks. The tooth crowns are relatively blunt and unicuspid in the anterior teeth and bicuspid in the posterior teeth. The lingual surfaces of the tooth crowns are concave. The culmines lateres are distinctly pronounced and they stretch from the anguli mesialis et distalis in the basal direction to the transition zone between tooth neck and tooth crown. The flanks of the teeth are flattened. The concave apical surfaces of the teeth are heavily striated with about twelve striae per tooth. These striae are straight, long, and prominent. They are arranged parallel and end apically in the immediate vicinity of the crista mesialis, the crista distalis, or the central cusp. The spaces between the striae are almost constant. The labial surfaces of the teeth are perfectly smooth. The ratio toothlength:diameter of tooth neck is 3.3:1.0. The resorption pits are circular or slightly elongated in the apical direction.

Diet:

The diet of *T. princeps* is assumed to be comparable to the diet of *Timon lepidus*.

Zootoca MAYER & BISCHOFF, 1996

Zootoca vivipara (VON JACQUIN, 1787)
(Pl. IV, Fig. 14)

Number of examined specimens: 3 adults

Remark:

Specimen ZFMK 4063 is cataloged under the synonym *Lacerta vivipara*.

Distribution:

Norway, Sweden, Finland, Switzerland, Germany, France, Austria, Denmark, Poland, Czech Republic, Hungary, Croatia, Slovenia, Bosnia, Hercegowina, Monte Negro, Macedonia, Serbia, Belgium, Netherlands, Luxembourg, England, Ireland, Spain, Italy, Russia, Estonia, Latvia, Lithuania, Ukraine, Japan, China.

Dental morphology:

The right dentary of specimen SRK 00.245 bears 22 tooth positions. The tooth bases and tooth necks are cylindrical. The lingual surfaces of the tooth crowns are flattened and concave in the immediate vicinity of the culmines lateres. The teeth of *Zootoca vivipara* are slender and become more robust in the posterior portions of the tooth row. The six or seven anteriormost teeth are unicuspid whereas all following teeth are bicuspid with distal main cusps and small mesial side cusps. The occlusal cutting edge between the two cusps is cut by a deep V-shaped notch. The tips of the main cusps are moderately pointed and often separated into a cuspis labialis and a lower cuspis lingualis. These two cusps are connected by the sharp and straight ridge of the carina intercuspidalis. Several posterior teeth show a tendency towards tricuspidity. In these teeth, the angulus distalis is swollen. The cristae mesiales et distales are almost the same length. The teeth lack striations apart from the two lingual ridges which form the cuspides linguales; occasionally, some extremely fine irregular striations are found at the lingual surfaces of the tooth crowns. The ratio toothlength:diameter of tooth neck is 3.3:1.0. The resorption pits of *Z. vivipara* are circular.

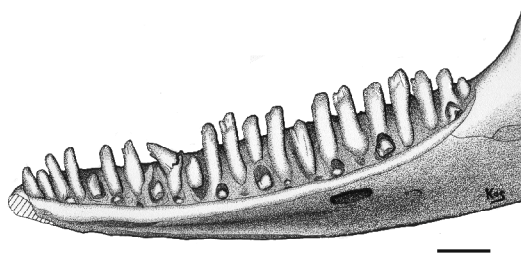


Fig. 51: *Zootoca vivipara*
(specimen SRK 00.245)
Right dentary; lingual view
Scale bar: 1 mm

Diet:

The diet of *Z. vivipara* includes Araneae (29.6 %), Diptera (20.5 %), Homoptera (16.9 %), and, to a lesser degree, Lepidoptera (mostly larvae) as well as needles from coniferophytes and pieces of grass (ITÄMIES & KOSKELA 1971). The plant matter was probably ingested involuntarily. In the composition of the diet, some differences exist between habitats, seasons, and sexes. Gravid females consume larger prey items than do non-gravid females and males. The lizards even consume flies and earthworms, but they avoid brightly colored animals. ITÄMIES & KOSKELA assume that differences exist in feeding habits between males and females of *Z. vivipara* since the prey group composition is almost similar in both sexes whereas differences in average numbers and volume of prey occur. Stomach contents analyses made by KOPONEN & HIETAKANGAS (1972) showed a diet composition dominated by spiders and insects, mainly Homoptera, Diptera, Hymenoptera, and Corrodentia. These prey groups made up about 95 % of the prey individuals and 97 % by weight. Juvenile *Z. vivipara* individuals preferred Corrodentia, Collembola, Homoptera, and small Gastropoda.

4.1.4 Family Scincidae GRAY, 1825

Consists of four subfamilies (Acontinae, Feylininae, Lygosominae, Scincinae).

(Diagnosis: see ESTES 1983, GREER 1970, READ 1986, and RIEPPEL 1980)

4.1.4.1 Subfamily Acontinae GRAY, 1845

(Diagnosis: see GREER 1970)

Acontias CUVIER, 1817

Acontias gracilicauda (ESSEX, 1925)
(Pl. IV, Fig. 15)

Number of examined specimens: 1 adult

Distribution:

Two isolated populations in Little Namaqualand and eastern Cape Province, Oranje Free State and southern Transvaal.

Dental morphology:

The solely available specimen of this species, AMNH 48507, belongs to the subspecies *Acontias g. gracilicauda*. The teeth of the lower jaw are heterodont with pointed and fang-like anterior teeth and strongly rounded or blunt teeth in the posterior part of the tooth row. The cross-sections of all teeth are round. The labial surfaces of the teeth are convex and smooth. The only exceptions are the lingual surfaces of the apices which are flattened or lightly concave and framed by the culmines lateres. Two additional cutting edges are running lingually parallel to the cristae mesialis et distalis. Those lingual cutting edges will be referred to as “Crista lingualis anterior” and “Crista lingualis posterior” in the following passages. The two cristae linguales are separated from the cristae mesialis et distalis by a deeply cut depression, the antrum intercristatum. At their point of intersection, the crista mesialis and the crista distalis form the cuspis labialis, which is directed posterolingually due to of a lightly torsion of the tooth crown. The cuspis labialis is relatively blunt. A second tip, the cuspis lingualis, is formed by the cristae linguales anterior et posterior. The cuspis lingualis is situated more deeply than the cuspis labialis; nevertheless it is morphologically elevated. In growing teeth, which are still non-functional, the separation into two parallel cutting edges and the connected arrangement of the antrum intercristatum have not yet occur. In functional teeth several striae are situated between the culmines lateres. These striae do not apically reach the cristae linguales anterior et posterior in younger teeth. Only in older teeth, which are in use for a long time and have therefore strongly worn cutting edges, the strong striae can reach the cristae linguales. All striae are running parallel and do not form any complex patterns. The surfaces of the teeth of anterior and posterior tooth-positions are smooth and absolutely free of striations. Only teeth in the middle of the tooth row are developing the

striking striae. The ratio tooth length:diameter of tooth neck is 3.2:1.0. The resorption pits are of semicircular shape.

Diet:

The mountain-dwelling South African burrowing scincid *A. g. gracilicauda* is like most species of the genus preying upon beetle larvae and termites (BROADLEY & GREER 1969).

Acontias meleagris LINNAEUS, 1758
(Pl. IV, Fig. 16)

Number of examined specimens: 2 adults

Distribution:

Southeastern Cape Province and Cape of Good Hope.

Dental morphology:

The South African burrowing skink *Acontias meleagris* bears 13 to 15 tooth positions in each jaw ramus. The teeth are slender, cylindrical and have round cross-sections. In several specimens (SRK 00.042, BMNH 63.2.21.21) the strongest teeth are situated in the symphyseal region of the jaw. Most individuals are typically homodont however. The lingual surfaces of the tooth crowns are concave or flattened, whereas the labial surfaces are of the apices are convex. The tooth tips are directed posterolingually as the result of a torsion of the entire tooth crown. The culmines lateres anterior et posterior are only weakly developed and don't form any sharp edges like they do in many other scincomorphans. The crista mesialis is longer than the crista distalis, so that the cuspis labialis shifts to a more posterior position. The cristae linguales anterior et posterior are distinctly developed. The two cristae linguales are forming the pointed cuspis lingualis, which is positioned far posteriorly underneath the cuspis labialis. Between the lingual and the labial cutting edges runs the notch of the antrum intercristatum. In older teeth this distinct relief of the apex is adjusted by wearing. Striations are only subordinately developed. At the lingual surfaces of the tooth crowns of several teeth, some very fine parallel striae running apically can be distinguished. Those striae do not form any complex patterns. In the anterior part of the tooth row, the teeth are oblique and anterolaterally adjusted, which makes them appear fang-like whereas the teeth of the middle and posterior parts of the tooth row are straightened in a line. The relation of

the tooth length to diameter of the tooth neck is 3.7:1.0. The resorption teeth are nearly circular.

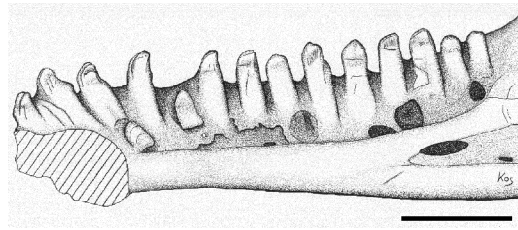


Fig. 52: *Acontias meleagris*
(specimen SRK 00.042)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

Although *A. meleagris* was the object of many scientific investigations by different authors (BELLAIRS 1949, BROADLEY 1968, BROADLEY & GREER 1969, BROCK 1941, DE VILLIERS 1939, MERWE 1944, RIEPPEL 1981), only little is known about the feeding behavior of the species. Foraging takes place directly underneath the ground surface. *A. meleagris* feeds upon earthworms, beetle larvae, millipedes, amphibians, and worm snakes (*Typhlops* sp.); additionally it will consume juveniles of its own species (HAUSCHILD & GABNER 1995). Water is acquired from the prey items.

Remarks:

The fossil equivalent within this study resembling the dental morphology of this species is the Upper Jurassic quadruped species *Saurillodon henkeli* from the Guimarota mine.

Acontias percivali LOVERIDGE, 1935

Number of examined specimens: 1 adult

Distribution:

Republic of South Africa, Transvaal, Zimbabwe, Namibia, Angola, and SE Kenya.

Dental morphology:

The jaw ramus of *Acontias percivali* contains approximately ten tooth positions. The teeth are very strong and lightly conical because the diameters of the teeth increase in the direction of the bases. The cross-sections are circular. The tooth crowns show a light rotation posteriorly, which makes the teeth posterolingually directed. The largest teeth are situated in the symphyseal region of the lower jaw. These teeth are pointed and oblique in an anterolabial direction. The teeth in the back of the jaw are straight and standing in line. The

lingual surfaces especially of the anterior teeth are flattened or lightly concave shaped. The crista mesialis is longer than the crista distalis, which leads to a relatively far posterior position of the cuspis labialis. Within the tooth row, the length of the crista distalis approaches the length of the crista mesialis from anterior to posterior tooth positions so that the cuspis labialis of the posterior teeth takes a central position. Like in *Acontias meleagris*, the cristae linguales anterior et posterior of *A. percivali* are well developed. The antrum intercristatum, which is sunken between the labial and the lingual cristae, separates the cuspis labialis from the more deeply positioned cuspis lingualis. The culmines lateres anterior et posterior reach across the apical third of the anterior teeth and frame the inner area of the apex. In this area, which is surrounded by the culmines lateres, striations are developed in most teeth. Those striae are arranged in parallel, but converge apically in the immediate vicinity of the cuspis lingualis. Striae are barely recognizable on the replacement teeth and the teeth in the posterior part of the tooth row. The labial surfaces of all teeth are also smooth. The resorption pits are large. During tooth replacement the old tooth often falls out very late when the replacement tooth has reached more than half of its final size.

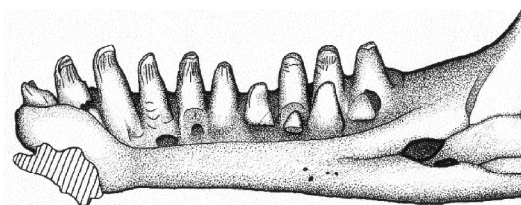


Fig. 53: *Acontias percivali*
(specimen SRK 00.054)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

A. percivali dwells in fallen leaves under trees and beneath rotten wood where it hunts for insects and worms (ROGNER 1994); maggots are also in the prey spectrum of this species.

Acontias plumbeus BIANCONI, 1849
(Pl. IV, Figs. 17-20)

Number of examined specimens: 1 adult

Distribution:

Northern and eastern Transvaal, Swaziland, Natal, Mozambique, isolated relict populations occur on catsren escarpment of Zimbabwe and at East London, Republic of South Africa.

Dental morphology :

The right mandible of the only available specimen of this species, BMNH 49.6.29.-38, shows 13 tooth positions. Within the tooth row a distinct tendency for heterodonty is apparent.

The anterior teeth are unicuspid and very pointed. Tooth base and tooth neck are cylindrical. The lingual surface of the tooth crown is lightly concave. The crista mesialis and the crista distalis are of equal length even though the tooth tip is directed posterolingually as a result of the torsion of the apex. The lata are distinctly flattened. The labial surfaces of the teeth are convex and smooth. Up to nine very prominent striae are developed between the culmines lateres, which themselves run in a wide sinus. The striae are running continuously in an exactly parallel manner. The teeth in the middle of the tooth row are blunt. The tooth crowns distinctly contrast with the tooth necks. The angle between the crista mesialis and the crista distalis, which forms the cuspis labialis, measures 150 degrees. The large size of this angle causes the blunt habitus of the cuspis labialis.

In contrast to the anterior teeth, the teeth in the middle of the tooth row have a cuspis lingualis with a 160° to 170° angle, which is formed by the morphological distinctly elevated and converging cristae linguales. Each of the culmines lateres of the central teeth forms a pronounced sinus whose surface is concave in immediate vicinity of the flanks. Up to eight striae are developed at the lingual surface of the tooth crown. These striae converge lightly in an apical direction and reach the cristae linguales. The antrum intercristatum is a deep notch which extends laterally from the sinus of the culmen lateris anterior to the sinus of the culmen lateris posterior.

The posterior teeth strongly differ from the anterior and central teeth. They are very short and stocky. Only one cutting edge is developed, which frames the tooth in a bow-like fashion occlusally. The lata are flattened. The lingual surface of the crown is concave especially close to the sinus of both culmines lateres. Up to three striae are running from the cusp to the culmen lateris posterior. A

prominent ridge is stretching straight from the cusp across the lingual surface of the crown to the neck of the tooth.

This pronounced heterodonty and the variability of the ultrastructures on the teeth of *A. plumbeus* separate the species from other species of the genus *Acontias*.

Diet:

The prey spectrum of *A. plumbeus* reflects the uniqueness of the dental morphology of this taxon; as the largest acontine skink, *A. plumbeus* consumes beetles and millipedes, but does not disdain from earthworms and larger vertebrates such as other burrowing skinks and frogs (BROADLEY 1969).

Remarks:

A. plumbeus proved to be the most primitive member of the genus (RIEPEL 1981).

4.1.4.2 Subfamily Feylininae CAMP, 1923
(Diagnosis: see GREER 1970)

Feylinia GRAY, 1845

Feylinia currori GRAY, 1845
(Pl. V, Fig. 1)

Number of examined specimens: 1 adult

Distribution:

Central and western Africa.

Dental morphology:

The numerous homodont teeth in the jaw ramus of *Feylinia currori* are slender and cylindrical. The teeth rise far above the margin of the labial wall of the dentary. The cross-sections of the teeth are circular at the tooth necks and widen transversally at the tooth bases. The tooth crown is lingually flattened or even concave, whereas it is convex labially. The tooth crowns are directed posterolingually as the result of torsions of the entire apical parts of the teeth. The cristae mesialis et distalis are of equal length and meet at the cuspis labialis at a 70° angle. The cristae linguales are well developed and separated from the cristae mesialis et distalis by a deeply cut antrum intercratum. The crista lingualis anterior is longer than the crista lingualis posterior. Both cristae linguales decrease in basal direction parallel to the culmines lateres, which stretch alongside the lata far to the basis. The tooth crown is generally more slim than the tooth neck and only slightly wrinkled on its

lingual surface. Striations *sensu stricto* are absent. The ratio tooth length:diameter of tooth neck is 3.6:1.0. The resorption pits are round or dorsally elongated.

Diet:

F. currori forages subterraneously for termites and scolopenders (HAUSCHILD & GABNER 1995).

Remarks:

Feylinia currori represents one of the four species of the legless and underground dwelling genus *Feylinia*, which comprise the Central African subfamily Feylininae. The phylogenetic position of the Feylininae has been disputed for a long time; the specializations of the genus are explained by RIEPEL (1981) as paedomorphosis.

Feylinia is a highly derived representative of a burrowing skink lineage, which evolved from the *Scelotes-Melanoseps-Scoleoseps* line of scincines (GREER 1985).

4.1.4.3 Subfamily Lygosominae

MITTLEMAN, 1952

(Diagnosis: see GREER 1970)

Ablepharus LICHTENSTEIN, 1823

Ablepharus grayanus BOULENGER, 1887
(Pl. V, Fig. 2)

Number of examined specimens: 1 adult

Remark:

Ablepharus boutoni was synonymized with *Cryptoblepharus boutoni*. Therefore specimen BMNH 1947.3.3.34 (cataloged as *Ablepharus boutoni*) will be dealt with in the chapter regarding the genus *Cryptoblepharus*. The taxon *Ablepharus lineo-ocellatus* is not valid. Therefore, specimen BMNH XI.4A (*A. lineo-ocellatus*) will not be described in this thesis and is treated as a nomen dubium. The dentition of this individual strongly resembles the dentition of *Ablepharus grayanus*.

Distribution:

India, Pakistan, Afghanistan, mountain regions of the eastern former Soviet central Asia.

Dental morphology:

Each jaw ramus of this species contains approximately 18 tooth positions. The teeth of this small skink are homodont and poor in characteristic features. All teeth are simple,

sharp, and pointed, the teeth of the symphyseal region bend forward whereas the teeth in the middle and posterior part of the tooth row are straight in line. The tooth crowns do not contrast with the tooth necks. The labia are lightly compressed so that the cross-sections of the teeth are transversally broadened. The labial cutting edge runs straight between the predominantly well developed angulus mesialis and the angulus distalis. A rudimentary crista lingualis, which is only slightly prominent, is running parallel to this cutting edge. All enamel surfaces are smooth. The ratio the tooth length:diameter of tooth neck amounts to 2.2:1.0. The resorption pits of the single available specimen BMNH 91.9.14.8 are covered by mucosa.

Diet:

All *Ablepharus* species prey on small arthropods, their larvae, and earthworms. They have a strong preference for spiders. GREENE (1982) mentions ants as the preferred diet of *Ablepharus grayanus*.

Remarks:

The genus *Ablepharus* returned secondary to the ground surface. The ancestors of these skinks were burrowers what is proved by the brille of recent *Ablepharus* species.

Anomalopus DUMÉRIL & DUMÉRIL, 1851

Anomalopus leuckartii WEINLAND, 1862

Number of examined specimens: 1 adult

Distribution:

Australia; New South Wales and Queensland.

Dental morphology:

The ophiomorph Australian burrowing skink *Anomalopus leuckartii* bears 14 to 15 tooth positions in each mandible. The teeth are strong and stocky. The cross-sections are circular. The apices of the anterior teeth are directed posterolingually and curved inward. The crista mesialis and the crista distalis are of equal length. Those two labial cristae form the cuspis labialis, which encompasses an angle of 80 to 100°. Lingually two additional cutting edges (cristae linguales anterior et posterior) have developed which run parallel to the labial cutting edges and form the cuspis lingualis. The two cusps are separated from each other by a deep antrum intercristatum. The bicuspidity of the anterior teeth is developed more conspicuously than it is at the posterior teeth.

The culmines lateres are short but strong. Striae are visible on the concave areas between the culmines at most teeth. There are a maximum of four striae. The striae converge apically. There are only very few striae developed on the posterior teeth. Replacement teeth are smooth. The ratio tooth length:diameter of tooth neck is 3.3:1.0. The resorption pits of *A. leuckartii* are round during the first stages of tooth replacement and become more dorsally elongated in shape during the course of further resorption.

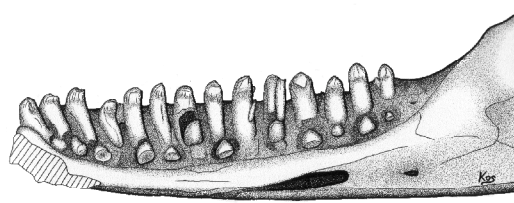


Fig. 54: *Anomalopus leuckartii* (specimen SRK 00.332) Right dentary; lingual view Scale bar: 1.0 mm

Diet:

A. leuckartii is a fossorial species which is found in loose soil, in decaying logs, or under shallowly-embedded rocks in warm temperate to subtropical woodland. Members of this species are sometimes active on the ground surface at night (HUTCHINSON, pers. comm.). Therefore, a diet dominated by small arthropods can be assumed for this skink.

Carlia GRAY, 1845

Carlia fusca (DUMÉRIL & BIBRON, 1839) (Pl. V, Fig. 4)

Number of examined specimens: 2 adults

Distribution:

Admiralty Islands, Kai Islands, Bismarck Archipelago, Papua New Guinea, Solomon Islands.

Dental morphology:

Carlia fusca, with its up to 36 tooth positions in each jaw ramus, belongs to the taxa with the largest tooth count within the scincomorpha. The teeth are homodont, very slender and cylindrical. The tooth crowns only slightly contrast with the tooth necks. The labial surface of the teeth is convex and smooth. The apex is pointed lingually. The crista mesialis and the crista distalis are of equal length. With an inner angle of 70° to 80°,

the cuspis labialis is relatively acute. The crista mesialis transforms without interruption into the culmen lateris anterior at a wide sinus. The transitions between the crista distalis and the culmen lateris posterior also take place without gradation. The striae dominantes anterior et posterior emerge distinctly and build up the cuspis lingualis, which is formed very acutely with an inner angle of 40° . The ace between the stria dominans anterior and the culmen lateris anterior is curved inward just like the surface between the stria dominans posterior and the culmen lateris posterior. Isolated striae can be developed in this concave area as well as on the flattened surface between the two main striae. The ratio tooth length:diameter of tooth neck is 6.0:1.0. The resorption pits are dorsally elongated.

Diet:

C. fusca is assumed to be insectivorous.

Carlia storri KIKKAWA, MONTEITH & INGRAM, 1981

Number of examined specimens: 1 adult

Distribution:

Australia (Queensland), possibly Indonesia (W Irian Jaya).

Dental morphology:

There are 31 tooth positions in the extended right jaw ramus of the only available specimen of *Carlia storri*, SRK 00.193. The teeth are homodont and are slender and cylindrical in shape. The cross-sections are circular and the tooth crowns contrast with the tooth necks. The most stout teeth are situated in tooth positions 20 to 28. The labial surfaces are smooth. The apices are lingually lightly concave and the ones in the anterior and central parts of the tooth row are lightly rotated to a posterolingual direction. The cristae mesiales of the anterior teeth are a little bit longer than the cristae distales. At their point of intersection both cristae meet at an angle of 70° and build up the cuspis labialis, which is the highest elevation of the entire tooth. Underneath these two main cutting edges and lingual to them, the cristae linguales run parallel. The crista lingualis anterior is, in most cases, shorter than the crista lingualis posterior. The cristae linguales form the morphologically elevated cuspis lingualis, which is always situated underneath the cuspis labialis. The antrum intercristatum is notched in between the lingual and the labial cutting edge systems.

This notch is especially striking at the anterior teeth and causes a distinct morphological raising of the cusps (serves to grasp the prey and penetrate the chitinous cuticula). On the inner surface of the apex, there are fine striae developed in several teeth. Those striae converge apically and show no tendency for complex patterns. The relation of the tooth length to the diameter of tooth neck amounts to 4.4:1.0. The resorption pits are circular or dorsally elongated. Some teeth lingually show longitudinal fissures which reach from the tooth bases to the apices and can gape widely.

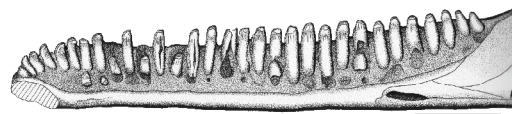


Fig. 55: *Carlia storri*
(specimen SRK 00.193)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

C. storri is highly active in leaf litter and low grass in tropical woodland (not in rainforests) and feeds on small invertebrates (HUTCHINSON, pers. comm.).

Corucia GRAY, 1855

Corucia zebrata GRAY, 1855
(Pl. V, Figs. 5-6)

Number of examined specimens: 1 neonate, 6 adults

Distribution:

Solomon Islands (Bougainville, Choiseul, New Georgia, Isabel, Guadalcanal, Nggela, Malaita, San Cristobal, Ugi, Santa Ana, and Shortlands).

Dental morphology:

There are between 15 and 19 tooth positions developed in each jaw ramus of *Corucia zebrata*. The tooth necks and the bases are slender and cylindrical. The tooth crowns distinctly contrast with the tooth necks. The morphology of the tooth crowns is exceptional. The outer shape of a tooth resembles a rhombus which is standing on one of its acute angles. Because of this tooth crown morphology, the tooth gets a lanceolate or blade-like habitus. The crista mesialis and the crista distalis are of equal length. Both meet at an angle of 90° and

thereby form the single cusp. The apices are mesially flattened. The labial surfaces of the tooth crowns are smooth and convex whereas the lingual surfaces are curved inward. Within this concave area, a prominent ridge runs from the cusp to the tooth neck where it declines at the convex surface of the shaft. The flanks of this morphologically outstanding ridge laterally taper off gently to the concave inner surfaces of the tooth crown. Parallel to this ridge are occasional light wrinkles of the enamel on the anterior teeth, whereas the lingual surfaces of most posterior teeth are smooth. The ratio tooth length:diameter of tooth neck is 5.8:1.0. The resorption pits are dorsally elongated.

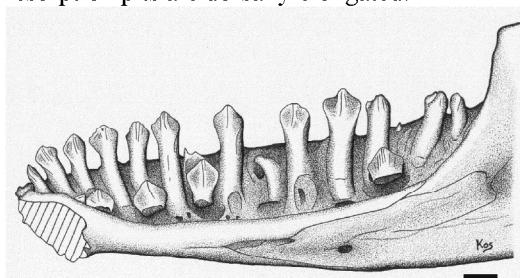


Fig. 56: *Corucia zebrata*
(specimen SRK 00.174)
Right dentary of a juvenile individual; lingual view
Scale bar: 1.0 mm

Diet:

The arboreal prehensile tailed skink *C. zebrata* is a highly specialized herbivore. In its natural environment, *C. zebrata* strongly prefers the epiphytic *Piper* sp. and *Epipremnum pinnatum* as its food source, (HONEGGER 1975). In captivity the skinks of HONEGGER only accepted pieces of apples in the beginning. After a while, three females also took pears, cherries, lettuce, boiled eggs, and raw and cooked mincemeat. Fish and insects were investigated by the skinks, but never eaten. *Tradescantia* sp., *Philodendron scandens*, and *Codiaeum* sp. were also refused. Instead, the lizards developed a preference for fresh creepers of *Monstera* sp. und *Scindapsus aureus*. The latter mentioned is also a component in the diet of this species in its natural habitat (HAUSCHILD & GABNER 1995). At Taronga Park Zoo in Sydney, *C. zebrata* specimens fed on cockroaches, caterpillars, *Tenebrio* larvae, and other insects. HONEGGER believes that this insectivore behavior is an exception. The species shows a tendency for coprophagy.

Remarks:

The differences in dental morphology between the two large scincid island species, *Corucia* (unicuspid) and *Macroscincus* (multicuspid), can be explained under functional morphological aspects as an adaption to different components in the diets of the two taxa. *Corucia*, which is inhabiting a humid tropical archipelago, feeds on soft plant material like fruits, blossoms, and leaves. The subfossil *Macroscincus*, in contrast, was endemic to the small islets Branco and Razo (Capeverde) which are characterized by an arid desert climate, and fed on very solid plant material.

Cryptoblepharus WIEGMANN, 1834

Cryptoblepharus boutoni MERTENS, 1928
(Pl. V, Fig. 7)

Number of examined specimens: 3 adults

Remark:

In 1969 the species *Ablepharus boutoni* was, like many other pacific species, transferred to *Cryptoblepharus boutoni* by FUHN. Therefore the specimen BMNH 1947.3.3.34, which is cataloged as *Ablepharus boutoni*, will be added to the description of *C. boutoni*. Before Fuhn published his revision of this group, all snake-eyed skinks were treated as a monophyletic group and put into the genus *Ablepharus*.

Distribution:

Republic of South Africa (northern Zululand), Mozambique (vicinity of Inhambane), Mascarenes (Mauritius, Round Island, Gunner's Quoin), Madagascar, Comoro Islands (Mayotte), Japan (*Cryptoblepharus boutonii nigropunctatus*), Tuamotus, Australs, Cook Islands, Marquesas, Pitcairn Islands, Society Islands, Niue, Samoas, Tonga, Fiji, Vanuatu, Solomon Islands, Bismarck Archipelago, Palau, Caroline Islands, Marianas, Phoenix, Tokelau, Hawaii, Peru (islands of Pacific coast), Chile.

Dental morphology:

The numerous teeth of *Cryptoblepharus boutoni* are poor in characters. The teeth are conically pointed and cutting edges are absent. All enamel surfaces are smooth. Many teeth show a torsion of the apices into the posterolingual direction. The tooth bases of the available specimens are

covered by mucosa so that the resorption pits are not to be seen.

Diet:

C. boutoni is an insectivorous hunter. The small skinks are voracious feeders. *Cryptoblepharus lineocellatus anomalus* is able to swallow grasshoppers of half of its own body size. The diet of *C. boutoni* is dominated by Copepoda (sand fleas) (POUGH et al. 2001).

Remarks:

C. boutoni is a coastal dweller which inhabits the rocks within the splashing zone of the surf and therefore is extraordinary resistant against seawater. This environmental adaption explains the large expansion of the inhabited area and the settlement on off shore oceanic islands.

Cryptoblepharus poecilopleurus WIEGMANN, 1836

(Pl. V, Fig. 8)

Number of examined specimens: 2 adults

Distribution:

Western Samoa, French Polynesia, New Britain, New Ireland vicinity (Ambitle, Malie), Solomon Islands, Gilbert Islands, USA (Hawaii: Kahoolawe), Easter Islands, Society Islands.

Dental morphology:

The numerous teeth in the mandible of *Cryptoblepharus poecilopleurus* are slender and cylindrical. The lingual surfaces of the tooth crowns are only weakly flattened. Most apices are blunt, but in some teeth a cusp is developed, which is positioned relatively far posteriorly. The tooth crowns don't contrast with the tooth necks. The culmines lateres are weakly developed and the culmen lateris anterior is longer than the culmen lateris posterior. All teeth of *C. poecilopleurus* are unicuspid. The relation of tooth length to diameter of tooth neck amounts to 2.4:1.0. The resorption pits form very narrow vertical caves in the middle of the lingual surface of the tooth bases.

Diet:

These very agile skinks hunt for small insects upon vertical surfaces of rocks und tree trunks.

Ctenotus STORR, 1964

Ctenotus regius STORR, 1971

Number of examined specimens: 1 adult

Distribution:

Australia; New South Wales, North Territory, Queensland, South Australia, Victoria.

Dental morphology:

The only available specimen of *Ctenotus regius*, SRK 00.170, shows 24 tooth positions in the right jaw ramus, of which tooth positions 8 to 17 are illustrated. The teeth are strong and cylindrical. The tooth crowns are only slightly contrasted with the tooth necks. The lingual surfaces of the apices are lightly concave. Those teeth, which are free of wear marks, show a crista mesialis that appears to be longer than the crista distalis. Both cristae meet at a 110° angle and form the cuspis labialis which is relatively far positioned posteriorly. The crista lingualis anterior runs parallel to the crista mesialis and meets the parallel to the crista distalis running crista lingualis posterior at the cuspis lingualis. The cuspis lingualis is distinctly morphological pronounced. A deep cut antrum intercristatum separates the lingual and the labial cutting edges. Inconspicuous striations are developed on the concave surface of several tooth crowns. The striae run parallel and are not arranged in complex patterns. The ratio tooth length:diameter of tooth neck is 3.0:1.0. The resorption pits of SRK 00.170 seem to be circular but are covered by mucosa.

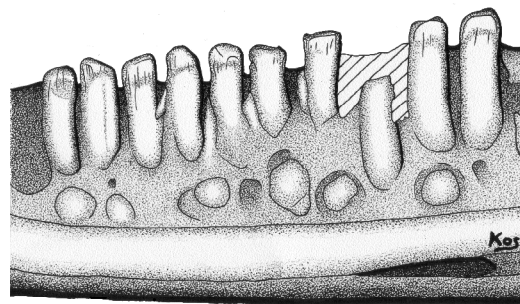


Fig. 57: *Ctenotus regius* (specimen SRK 00.170) Central portion of a right dentary (tooth positions 7-17 from 24); lingual view Scale bar: 1.0 mm

Diet:

Ctenotus regius is a surface dwelling species. The skinks are highly active in hot

sunlight, running rapidly across open spaces between bushes (HUTCHINSON, pers. comm.).

The species of the genus *Ctenotus* have specialized in a diversity of prey items. For example, the percentage of termites in the diet of *Ctenotus pantherinus* is extraordinary large, whereas *Ctenotus leonhardii* hardly ever preys on termites. Additionally, the composition of the prey spectrum underlies strong seasonal fluctuations. In the humid season or in very humid years in Australia, the major portion of the diet is made up of larvae. The main food source of most *Ctenotus* species is assumed to be spiders, termites, and grasshoppers (CRAIG 1991). It is assumed that the diverse saurofauna, which shows a great number of syntopic species (like *Ctenotus*) depending partly upon termite prey, could evolve because termites with their numerous guilds offer various types of prey (CRAIG 1991).

Cyclodomorphus FITZINGER, 1843

Cyclodomorphus melanops (STIRLING & ZIETZ, 1893)

Number of examined specimens: 1 adult

Distribution:

Isolated populations of three subspecies in several parts of Australia, excluding the eastern coastal region.

Dental morphology:

In the right dentary of *Cyclodomorphus melanops*, SRK 00.191, there are 14 tooth positions developed. The dentition shows a conspicuous grade of heterodonty. All teeth are bulky and relatively large compared to the size of the entire lower jaw. The 12th tooth is distinctly larger than the other teeth. This type of dentition, where one or more crushing teeth are present, draws a parallel to the durophagous species of the related genus *Tiliqua* and to the strongly molluscivore *Hemisphaeriodon gerrardi*, which also belongs to the *Tiliqua*-group *sensu lato*. The lower jaw of *C. melanops* represents a miniaturization of the *Tiliqua* bauplan. The teeth of *C. melanops* have short cylindrical tooth necks, and in some teeth the tooth crown contrasts with the tooth neck. The lingual surface of the apex is concave. The only exception of this character is the crushing tooth whose surfaces are exclusively convex. The crista mesialis is a little longer than the crista distalis. The cusps are directed posterolingually as a result of a

torsion of the tooth crowns. The cuspis labialis is situated in a posterior position. Two cristae linguales are developed parallel to the cristae mesialis et distalis. These lingual cutting edges form in their point of intersection the morphologically elevated cuspis lingualis. Especially in the anterior teeth, a deep notched antrum intercristatum is developed between the two systems of cutting edges. The culmines lateres are only weakly developed and transfer at the sinus into the labial cutting edges.

The morphology of the prominent crushing tooth on tooth position 12 greatly differs from all other teeth in the tooth row. The apex of the crushing tooth is dome-shaped and unicuspid. The cusp shows weak wear facets. The habitus of the entire tooth is of the shape of a mushroom since the apex is broadened and it strongly contrasts with the tooth neck. Numerous prominent striae are developed on the entire apex. The striations on the labial surfaces are less prominent than the ones on the lingual surface. The striae are arranged radially between the cusp and the transition zone of crown and neck where they end abruptly. Striations are also developed on the other teeth of the tooth row, but here the striae are limited to the concave inner surfaces of the tooth crowns and they are arranged in parallel. The apical half of the tooth crown surpasses the labial wall of the dentary. The ratio tooth length:diameter of tooth neck is 2.6:1.0. The resorption pits are circular and relatively large.

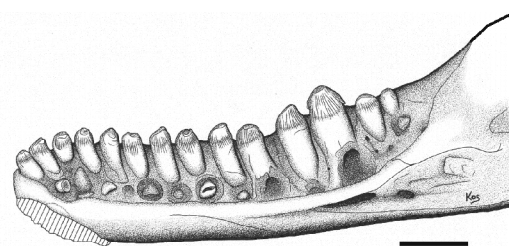


Fig. 58: *Cyclodomorphus melanops* (specimen SRK 00.191)
Right dentary, demonstrating the miniaturization of the *Tiliqua* bauplan; lingual view
Scale bar: 1.0 mm

Diet:

The prey spectrum of *Cyclodomorphus* species contains arthropods including insects and spiders. Stomach contents analyses proved that terrestrial snails were eaten (SHEA 2000). This observation consists well with the moist microhabitat the genus prefers. In captivity,

pinky mice, pieces of meat, and earthworms were also taken (DENNERT 2000).

Dasia GRAY, 1839

Dasia olivacea GRAY, 1839
(Pl. V, Fig. 9)

Number of examined specimens: 1 adult

Distribution:

Burma, Thailand, Cambodia, Laos, west Malaysia, Singapore, Borneo, Sumatra, Pulau Simeulue, Pulau Nias, Pulau Singkep, Sembilan Islands, Natuna Islands, Java.

Dental morphology:

The illustrated tooth of *Dasia olivacea* corresponds with tooth position 19. The numerous teeth of this species are homodont. All teeth are slender and cylindrical and the tooth bases of this solely available specimen are covered by the mucosa. The crista mesialis is only slightly longer than the crista distalis. These two labial cutting edges are framing an angle of 120° and forming the cuspis labialis in their point of intersection. In basal direction the two cutting edges are transferring via a prominent sinus into the culmines lateres, which finally comes to an end on the surface of the tooth neck. Underneath the crista mesialis and parallel to it a crista lingualis anterior is developed. This cutting edge forms a sharp-edged cuspis lingualis together with the crista lingualis posterior, which runs parallel to the crista distalis. Both cusps are connected by the ridge of the carina intercuspidalis, which runs transversally across the concave antrum intercristatum. The lingual surface of the tooth crown underneath the cuspis lingualis is shaped lightly concave. Within this concave area, the crista lingualis anterior transfers into the stria dominans anterior while the crista lingualis posterior transfers into the stria dominans posterior. Both main striae are strongly developed and rather long. Between the two main striae there are four to six additional striae present in most teeth. Another additional stria is developed between the stria dominans anterior and the culmen lateris anterior in several teeth. This striking pattern of striations is almost constant throughout the entire tooth row.

Diet:

In captivity this arboreal Southeast Asian skink consumes crickets, house-crickets, moths, butterflies, caterpillars, locusts, flies,

and spiders. A special preference for flying insects was observed (ROGNER 1994).

Egernia GRAY, 1838

Egernia cunninghami (GRAY, 1832)

Number of examined specimens: 1 neonate, 2 adults

Distribution:

Australia; south of Queensland along the coast of New South Wales to Victoria, and South Australia (Mt. Lofty Ranges).

Dental morphology:

There are 25 tooth positions in the right dentary of *Egernia cunninghami*, SRK 00.138. The teeth of this species are homodont, very slender and transversally broadened at their bases. The tooth crowns are lingually flattened and distinctly contrasted with the tooth necks. The lata also are distinctly flattened. The tooth crowns are mesially widened so that they nearly contact each other at their sinus. The crista mesialis and the crista distalis are running almost horizontal, what makes the cuspis labialis only lightly pronounced morphologically. The cuspis labialis is situated in an approximately central position. The cristae linguales which form the cuspis lingualis, run parallel to the labial cutting edges. The distances between the inner and outer cutting edges and also between the cuspis lingualis and the cuspis labialis are very small. Some very weak striations are developed at the anterior teeth, but they are not arranged in complex patterns. The relation of the tooth length to the diameter of tooth neck amounts to 5.4:1.0. The resorption pits are very narrow and dorsally elongated.

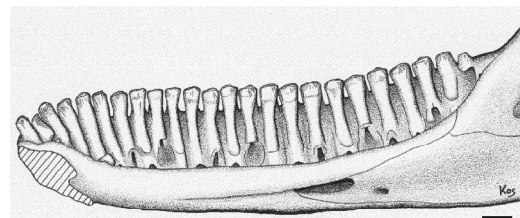


Fig. 59: *Egernia cunninghami*
(specimen SRK 00.138)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The major component of the diet of *E. cunninghami* is vegetarian. The species prefers clover of the genus *Trifolium*. In the natural habitat in Australia diverse insects, small-sized vertebrates and plant matter, including fruits, are consumed. In captivity these lizards proved to be omnivorous with a tendency for coprophagy (NIEKISCH 1980). Even cases of cannibalism are common; the weaker individuals were eaten by the strongest individual of the group. To a large extent, the juveniles are protected from harm by their characteristic coloration and their mother's defense.

Remarks:

The morphology of the teeth, which shows conspicuous similarities with herbivore lizards of other genera, indicates a functional-morphological adaptation of the dentition to a plant-dominated diet.

Egernia depressa (GÜNTHER, 1875)

Number of examined specimens: 1 adult

Distribution:

West Australia with the exception of the southernmost part.

Dental morphology:

The only available specimen of this species, SRK 00.198, bears 22 tooth positions in its right jaw ramus. In labial view, only the tooth crowns tower above the labial margin of the dentary. Tooth necks and tooth bases are transversally widened in *Egernia depressa*. The tooth crown is distinctly contrasted with the tooth neck and widened mesially. The lingual surfaces of the tooth crowns are flattened. The cristae mesialis et distalis are of equal length. Both cristae enclose the cuspis lingualis at an angle of 140°. The culmines lateres are well developed and frame the flattened lingual portion of the tooth crown, in which there are numerous striae. Those striae converge apically. Some teeth show two central striae which are especially pronounced. These striae dominantes form the cuspis lingualis in their point of intersection. This cusp is morphologically only lightly elevated and is situated directly underneath the cuspis labialis. The ratio tooth length:diameter of tooth neck is 5.7:1.0. Younger resorption pits are vertically elongated, older resorption pits are circular.

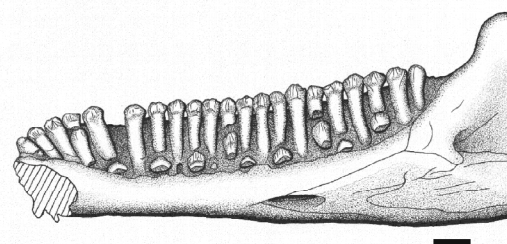


Fig. 60: *Egernia depressa* (specimen SRK 00.198)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

E. depressa consumes crickets, locusts, spiders, ants, termites, and snails in its natural habitat. In captivity this species also accepts sweet fruits (HAUSCHILD & GABNER 1995). Plant matter is probably also a dietary addition to the natural food of this species.

Egernia dorsalis nomen dubium
(Pl. V, Fig. 10)

Number of examined specimens: 1 adult

Remark:

The name of the species, *Egernia dorsalis*, is not valid. Despite this, the specimen BMNH 1908.2.25.9 is cataloged under this name and therefore will be described here as *Egernia dorsalis*.

Dental morphology:

The teeth of BMNH 1908.2.25.9 are rather slender and transversally widened at their bases and necks. The apical third of the tooth necks and the tooth crowns rise above the labial margin of the dentary. The crowns are flattened. The lingual and labial surfaces of the teeth are convex and smooth. The tooth crowns, which distinctly contrast with the tooth necks, are strongly widened mesially. In some cases, the sinus of successive teeth overlap. The length of the crista mesialis is equivalent to the length of the crista distalis. These two cutting edges spread at an angle of 130° and build up the central positioned cuspis labialis in their point of intersection. Directly underneath the cuspis labialis, the relatively pointed cuspis lingualis is situated. Both cusps are separated from each other by a narrow antrum intercrisatum. The culmines lateres are developed as morphologically pronounced ridges which frame the concave surface at the lower part of the tooth crown. Apart from that, the enamel surfaces are smooth. The relation of

tooth length to diameter of tooth neck amounts to 5.4:1.0.

Diet:

Since *E. dorsalis* is treated as a nomen dubium, no data concerning the diet of this "species" can be given.

Egernia inornata (ROSEN, 1905)

Number of examined specimens: 2 adults

Distribution:

Australia; south of West Australia, South Australia, northwestern Victoria.

Dental morphology:

The relatively stout right dentary of *Egernia inornata* bears 19 tooth positions (SRK 00.176). The teeth are slender and slightly widened in transversal direction. The tooth crowns do not contrast with the tooth necks. The lingual surfaces of the tooth crowns are only lightly flattened. The crista mesialis is always longer than the crista distalis, which makes the cusp shift to a more posterior position. The entire apex is rotated caudally. In several teeth of the tooth row a cuspis lingualis is developed, which is situated directly underneath the cuspis labialis. The original tooth crown morphology is blurred by wear in many teeth. Teeth can be worn so intensively that only a horizontal facet remains on their occlusal side. Culmines lateres are developed only at anterior teeth. Complex patterns of striations are absent. In some teeth faint striations parallel to the longitudinal axis are developed, which never converge apically. The ratio tooth length:diameter of tooth neck is 4.4:1.0. The resorption pits are circular and only slightly deepened into the tooth bases.

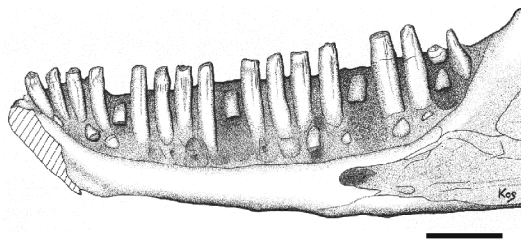


Fig. 61: *Egernia inornata*
(specimen SRK 00.176)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The desert dwelling *E. inornata* is digging out burrows from where it hunts insects and even smaller lizards. The species is a nocturnal hunter (HAUSCHILD & GABNER 1995).

Egernia kingii (GRAY, 1838)

Number of examined specimens: 1 juvenile, 2 adults

Distribution:

West Australia to Geraldton in the north, Houtman Abrolhos Islands, and to Esperance in the east.

Dental morphology:

The Dental morphology of *Egernia kingii* underlies great intraspecific variation. Juveniles bear 14 tooth positions (SRK 00.107) in their slender and elongated dentary, whereas there are developed up to 27 tooth positions (SRK 00.151) in the stout dentaries of adult specimens. The tooth bases and the tooth necks are transversally widened in *E. kingii*. In contrast, the tooth crowns distinctly show a mesial widening in which the lingual surfaces even can be shaped concavely. The teeth of adult specimens are very narrowly spaced, and this can lead to an overlap of the sinus of successive teeth. In contrast to this, the teeth of the juvenile specimen are conspicuously wide-spaced. The crista mesialis is of equal length as the crista distalis. Therefore, the cuspis labialis is situated in a central position and only slightly inclined posterolingually. A second system of cutting edges runs parallel to the crista mesialis et distalis. These cristae linguales are forming the cuspis lingualis which is situated directly underneath the cuspis labialis. A vertical ridge run across the inward bent lingual surface of the tooth crown from the tip of the tooth to the tooth neck. This structure was also noticed in *Corucia zebrata*. In the *E. kingii* specimen SRK 00.107, this ridge is extraordinary well defined. The lingual surfaces of the tooth crowns are covered by very fine striations which converge apically. In all investigated specimens of *E. kingii*, there are cavities in the bony material of the dentary around the tooth bases which strongly resemble identical structures in anguimorphans. The ratio of the tooth length to the diameter of tooth neck is 4.9:1.0. The resorption pits are dorsally elongated.

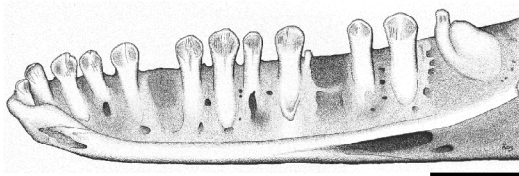


Fig. 62: *Egernia kingii*
(specimen SRK 00.107)
Right dentary of a juvenile individual; lingual view
Scale bar: 1.0 mm

Specimen SRK 00.107 shows a pathological feature in tooth position 14. This tooth is developed as a globular form with a vertical notch. The anterior part of this tooth developed a rudimentary tooth crown, which reaches the level of the other tooth crowns in the tooth row, but has a minor diameter. Possibly two teeth united here.

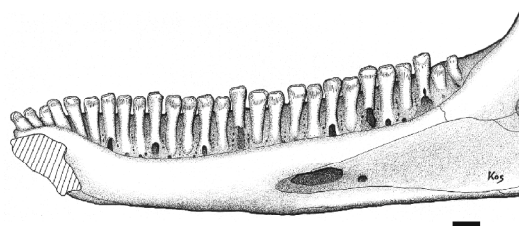


Fig. 63: *Egernia kingii*
(specimen SRK 00.151)
Right dentary of an adult individual; lingual view
Scale bar: 1.0 mm

Diet:

E. kingii is not only spread on the Australian mainland, but it also dominates the saurofauna of many islands at the coast of Australia. The skinks feed on carrion washed ashore, flowers, fruits, insects, small mammals, and eggs and chicks of seabirds (MEATHREL 1990). In captivity fish and snails are also consumed (HAUSCHILD & GABNER 1995). The diet is dominated by plant matter.

Egernia stokesii (GRAY, 1838)
(Pl. V, Fig. 11)

Number of examined specimens: 3 adults

Distribution:

Three subspecies inhabiting continental Australia, Baudin Island, and the Houtman Abrolhos Islands.

Dental morphology:

The tooth morphology of *Egernia stokesii* is extremely unusual and strongly contrasting all other species of this genus. Each jaw ramus bears about 14 tooth positions. The teeth are cylindrical and show a mesially depressed tooth crown. The crista mesialis and the crista distalis are of equal length. Both cristae do not run straight, but instead in a concave bow making the tooth cusp appear strangled from anterior and posterior. The angle of the triangular cusp is 40°. All enamel surfaces are convex and completely smooth. There are no cunines lateres, no additional cristae or cusps, and no striations present. The relation of tooth length to diameter of tooth neck amounts to 4.1:1.0. The resorption pits are dorsally elongated.

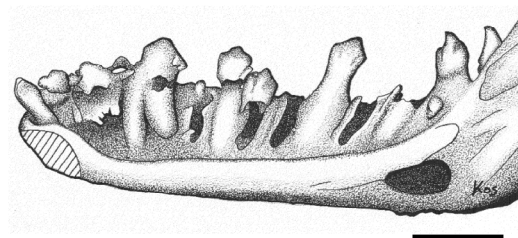


Fig. 64: *Egernia stokesii*
(specimen SRK 00.073)
Right dentary of an individual showing deficiency symptoms in calcium; lingual view
Scale bar: 1.0 mm

Diet:

The dietary spectrum of *E. stokesii* comprises arthropods (grasshoppers, moths, beetles, spiders) as well as plant matter. Stomach contents analyses showed a high percentage of seeds of diverse plants (*Enchylaena tomentosa*, *Portulaca oleracea*, *Carrichtera annua*, *Medicago minima* and *Lycium ferocissium*) (DUFFIELD 1998). There are seasonal fluctuations in the dietary composition of this species. There are also differences in the dietary compositions of different age groups and sexes. In specimens with a higher individual age, the percentage of plant matter is increasing proportional. In captivity snails were also consumed by *E. stokesii* (NIETZKE 1998).

Remarks:

The lower jaw of specimen SRK 00.073 was strongly deformed (especially the articular complex) by a rhachitic disease.

Egernia striolata (PETERS, 1870)
(Pl. V, Fig. 12)

Number of examined specimens: 2 adults

Distribution:

Australia; eastern and central Queensland across New South Wales (excluding the coast and areas of higher altitudes) to Victoria and the east of South Australia.

Dental morphology:

The right mandible of *Egernia striolata* (SRK 00.173) bears 19 tooth positions. The teeth are cylindrical and therefore barely widened transversally. The tooth crowns only lightly contrast with the tooth necks and rise above the labial wall of the dentary. A concave portion of the tooth surface stretches lingually from the sinus-like angulus mesialis to the likewise blunt angulus distalis. The crista mesialis and the crista distalis are of equal length. As the result of an apical torsion the anterior teeth are directed posterolingually. The cuspides labiales of the anterior teeth are more pointed than the cuspides labiales of the posterior teeth. In comparison to other species of the genus, the culmines lateres are very short. Lingually underneath the cuspis labialis a cuspis lingualis is developed, which is separated from the main cusp by a lightly deepened mesial running antrum intercrisatum. The labial enamel surfaces are smooth. Striations are developed at the lingual surfaces of the tooth crowns. The striae converge apically. Many teeth, especially in the posterior part of the tooth row, are characterized by two striae dominantes, which enclose at an angle of 40° and in most cases lead into the cuspis lingualis. In addition to these striae dominantes, there can be up to twelve subordinate striae. The total number of striae is much larger in anterior teeth than it is in posterior teeth. The ratio tooth length:diameter of tooth neck is 3.8:1.0. The resorption pits are perfectly circular.

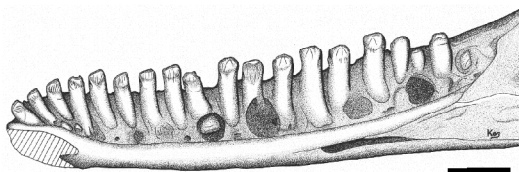


Fig. 65: *Egernia striolata*
(specimen SRK 00.173)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The diet of *E. striolata* is made up by beetles, cockroaches, grasshoppers, large ants, and soft fruits. The individual's shedded skin is also eaten.

Egernia whitii (LACÉPÈDE, 1804)
(Pl. V, Fig. 13)

Number of examined specimens: 1 adult

Distribution:

Southeastern Australia and northern Tasmania.

Dental morphology:

The teeth of *Egernia whitii* are strong and stocky. The tooth bases are lightly broadened transversally which leads to a compression of the flanks. The tooth crowns do not contrast with the tooth necks. The lingual surface of the tooth crown is only lightly flattened. The angulus mesialis and the angulus distalis are distinctly developed. Therefore the apex appears rectangular. The cristae mesialis et distalis are equal in length, they run parallel to the dorsal margin of the dentary, and they form a straight labial cutting edge. The morphological low cuspis labialis is directed lingually. Two additional cutting edges, the crista lingualis anterior and the crista lingualis posterior, are developed at the lingual side of the apex. These two cutting edges run parallel to the labial cutting edges and form the less elevated cuspis lingualis. The antrum intercrisatum, which represents the most pronounced character in the dental morphology of *E. whitii*, runs mesially between the labial and the lingual systems of cutting edges. The antrum intercrisatum is wide and deeply notched into the apex. All enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 2.1:1.0.

Diet:

E. whitii preys on diverse insects with a special preference for ants. Additionally, this species hunts for beetles, bugs, and spiders (HICKMAN 1960). As being the smallest of the *Egernia*-group species, the vegetable component of the diet is of minor importance in *E. whitii* in comparison to the larger *Egernia* species, which usually consume large amounts of plant matter.

Emoia GRAY, 1845

Emoia aneityumensis MEDWAY, 1974

Number of examined specimens: 1 adult

Distribution:

Vanuatu (New Hebrides).

Dental morphology:

The right dentary of specimen BMNH 1956.1.3.63 bears 35 tooth positions. All teeth of the Vanatu endemic *Emoia aneityumensis* are very slender and transversally broadened at their bases and necks. The tooth crowns distinctly contrast with the tooth necks and tower far above the labial wall of the dentary. Additionally, the tooth crowns are directed posterolingually as a result of torsions of the entire apices. The culmines lateres are very prominent. The culmen lateris anterior transfers in a wide bow into the crista mesialis, whereas the culmen lateris posterior runs straight apically and forms the direct elongation of the crista distalis. The cuspis labialis is situated in a far posterior position. The cuspis lingualis is separated from the cuspis labialis by a wide antrum intercristatum. In occlusal view, the antrum is running S-shaped from the culmen lateris anterior to the culmen lateris posterior. On the lingual surfaces of the tooth crowns up to seven striae are developed, two of which are morphologically more prominent than the others. These two striae form the cuspis lingualis. The remaining striae show regular distances to each other and do not converge. The relation of tooth length to diameter of tooth neck amounts to 4.3:1.0.

Diet:

The widespread *Emoia* species of the South Asian islands are preying upon diverse arthropods. One species, *Emoia atrocostata*, hunts in tidepools for small crabs, shrimps, and fishes during low tide (MANTHEY & GROSSMANN 1997).

Emoia caeruleocauda (DE VIES, 1892)

(Pl. V, Figs. 14-15)

Number of examined specimens: 2 adults

Distribution:

Widespread from S Indonesia through New Guinea and the Solomon Islands northward into the Marianas, Carolines, and Marshall Islands, Fiji Islands (Viti Levu, Taveuni), Vanuatu, New Caledonia (Loyalty Islands, excluding the mainland), Papua New

Guinea, Philippines, Indonesia (Moluccas, Celebes, Irian Jaya), Admiralty Islands.

Dental morphology:

The teeth of *Emoia caeruleocauda* are slender cylindrical and pointed. The cross-sections of the teeth are circular, only the lingual surfaces of the tooth crowns are often concave (USNM 122578). In contrast, the lingual apex-area of specimen USNM 323699 is only lightly flattened. The tooth crowns of the anterior teeth show a torsion into a posterolingual direction. The prominent culmines lateres transfer directly into the cristae mesialis et distalis, which converge at a 60° angle and form the cuspis labialis. Parallel to these labial cutting edges two shorter lingual cutting edges (cristae linguales anterior et posterior) are found. Those sharp-edged cristae linguales construct the cuspis lingualis at their point of intersection. Aside from that, all enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 3.0:1.0. The resorption pits are circular.

Diet:

E. caeruleocauda probably preys on small arthropods.

Emoia cyanura (LESSON, 1826/1830)

(Pl. V, Fig. 16)

Number of examined specimens: 3 adults

Distribution:

Common and broadly distributed in the Pacific, occurring from the Bismarcks through the Solomons and Vanuatu eastward to and including Polynesia; Society Islands, Fiji Islands, Western Samoa, Admiralty Islands, New Caledonia, Vanuatu, Solomons, Papua New Guinea, Tonga, Wallis, Niue, Tuvalu, Tokelau, Cook Islands, French Polynesia, Pitcairn Islands, Kiribati, Marshalls, Carolines, Marianas, USA (Hawaii).

Dental morphology:

The teeth of *Emoia cyanura* are unicuspid and basally much more broadened transversally. The surfaces of the latera are curved inward. Only the apical halves of the tooth crowns rise above the dorsolabial margin of the dentary. The tooth crowns distinctly contrast with the tooth necks and are slightly rotated posterolingually. The lingual surfaces of the tooth crowns are concave. The crista mesialis and the crista distalis are the same length. Together these two cutting edges form the cusp. The culmines lateres are very long

and distinctly pronounced morphologically. Close to the sinus, the culmines lateres are transforming into the cristae mesialis et distalis without interruption. Prominent striations are developed on the lingual surface that is framed by the culmines lateres. These striae converge apically but show very regular distances in the lower part of the tooth crown. There are approximately seven striae recognizable per tooth. The relation of tooth length to diameter of tooth neck amounts to 3.8:1.0. The resorption pits are circular shaped.

Diet:

E. cyanura probably preys on small arthropods. The lizards are very agile and always foraging during the day. While hunting, these skinks can climb up to one meter into the scrubs (ZUG 1991).

Remarks:

On Rotuma, *E. cyanura* is living syntopically with *Emoia trossula* and *Emoia nigra* (ZUG 1991).

Emoia jakati (KOPSTEIN, 1926)
(Pl. V, Fig. 17)

Number of examined specimens: 1 adult

Distribution:

Irian Jaya, Papua New Guinea, Solomons, Palau, Carolines, Marshalls, Bismarck Archipelago.

Dental morphology:

The teeth of *Emoia jakati* are very pointed and show a conical habitus. The cross-sections of teeth are circular. In several teeth a second internal cusp, the cuspis lingualis, is developed. The cutting edges, which build up the cuspis lingualis, run bow-like and parallel to the labial cutting edges. All cutting edges are blunt. All enamel surfaces are smooth and striations are absent. The ratio tooth length:diameter of tooth neck is 3.8:1.0. The resorption pits are shaped circularly.

Diet:

E. jakati probably preys upon small arthropods.

Emoia nigromarginata (ROUX, 1913)
(Pl. V, Fig. 18)

Number of examined specimens: 1 adult

Distribution:

Vanuatu, New Hebrides.

Dental morphology:

The teeth of *Emoia nigromarginata* are slender and cylindrical. The tooth crowns distinctly contrast with the tooth necks. Only the tip of the apex rises above the labial wall of the dentary. The tooth crowns are blunt, their lingual surfaces are concave. The short culmines lateres transform without gradation into the cristae mesialis et distalis, which form the posterolingually directed cuspis labialis. Underneath the cuspis labialis, the morphologically elevated, plateau-like cuspis lingualis is developed. While the labial surfaces of the teeth are perfectly smooth, prominent striations at the lingual surfaces of the tooth crowns can be developed. These striae are limited to the concave areas of the apices which are framed by the culmines lateres. The number of striae amounts up to five striae per tooth. All striae converge apically. The ratio tooth length:diameter of tooth neck is 3.8:1.0. The resorption pits of *E. nigromarginata* are circularly shaped.

Diet:

No exact data about the spectrum of prey items of *E. nigromarginata* are available. The related *Emoia nigra* preys upon insects and spiders, but even a frog was detected in the stomach of one specimen (HAUSCHILD & GABNER 1995). Probably the dietary spectrum of *E. nigromarginata* is comparable to the one of *E. nigra*.

Emoia sanfordi SCHMIDT & BURT, 1930
(Pl. V, Fig. 19)

Number of examined specimens: 1 adult

Distribution:

Vanuatu (Banks Islands and New Hebrides), Fauro, Solomon Islands.

Dental morphology:

The right dentary of *Emoia sanfordi* (AMNH R40169) bears 32 tooth positions. The teeth are robust and have transversally broadened tooth bases. The tooth crowns are rising above the labial wall of the dentary and do not contrast with the tooth necks. The lingual surfaces of the apices are curved inward. The crista mesialis is longer than the crista distalis which causes the shift of the cuspis labialis to a more posterior position. The culmines lateres of the only available specimen of this species, AMNH R 40169, are relatively short. Underneath the cuspis labialis a lower cuspis lingualis is developed, which transforms

into cutting edges that run parallel to the dorsal margin of the dentary. Between the labial and the lingual cutting edges a wide but shallow antrum intercristatum is stretching from the sinus mesialis to the sinus distalis. On the concave ace between the culmines lateres parallel arranged striations are developed. These striations are to be found on all teeth of the entire tooth row. There are up to eight striae developed on each tooth. The ratio tooth length:diameter of tooth neck is 2.6:1.0. The resorption pits of AMNH R 40169 are covered by the mucosa.

Diet:

E. sanfordi probably preys upon small arthropods.

Emoia slevini BROWN & FALANRUW, 1972
(Pl. V, Fig. 20)

Number of examined specimens: 1 adult

Distribution:

Mariana Islands.

Dental morphology:

The teeth of *Emoia slevini* are cylindrical and slightly thickset. The tooth crowns don't contrast with the tooth necks and only their apical halves rise above the labial wall of the dentary. The lingual surfaces of the apices are concave, whereas the labial surfaces are flattened. The crista mesialis is slightly longer than the crista distalis, which causes the shift of the position of the cuspis labialis to a more posterior position. The enclosed angle of the cuspis labialis is 80°. The culmines lateres are absent. Underneath the cuspis labialis and situated in the vortex of a bow-shaped lingual cutting edge the cuspis lingualis is found. The two cusps are separated from each other by a shallow but wide antrum intercristatum. The labial surfaces of the teeth are smooth, whereas up to three prominent striae can be developed at the concave inner surfaces of the tooth crowns. The ratio of the tooth length to the diameter of tooth neck is 2.3:1.0. The resorption pits are circular in shape.

Diet:

E. slevini probably preys upon small arthropods.

Emoia trossula BROWN & GIBBONS, 1986
(Pl. VI, Fig. 1)

Number of examined specimens: 3 adults

Distribution:

Fiji Islands, Rotuma Island,
Cook Islands, Tonga.

Dental morphology:

The right dentary of specimen USNM 249745 bears 32 tooth positions. The dental morphology of *Emoia trossula* shows great variability. The teeth are generally very slender and cylindrical. The tooth crowns are mesially broadened and distinctly contrast with the tooth necks. The lingual surfaces of the tooth crowns are concave. Most specimens show a posterolingual torsion of the tooth crowns. The crista mesialis is often longer than the crista distalis. Basally the cristae mesialis et distalis transform (across the sinus) into the sharp-edged and prominent culmines lateres. The cuspis labialis is relatively pointed and directed posterolingually. A prominent cuspis lingualis, which morphologically towers above the cuspis labialis (USNM 249744), is developed in all specimens. The cuspis lingualis is built by two striae dominantes which converge in a 40° angle. Between the two cusps of several teeth of USNM 249745 a carina intercuspidalis is developed. The total count of remaining striae varies. There are specimens without any striae (SDS 66261), specimens with few weak striations (USNM 249744), and specimens with numerous pronounced striations (USNM 249745). Interestingly, even in USNM 249745 there are teeth with perfectly smooth surfaces in the posterior part of the tooth row. The replacement teeth which are not yet functional are also free of striations and are of simple conical habitus in this specimen. The ratio of the tooth length to the diameter of tooth neck is 2.7:1.0. The resorption pits are relatively circular in shape.

Diet:

E. trossula probably preys upon small arthropods.

Remark:

On Rotuma *E. trossula* is living syntopically with *Emoia cyanura* and *Emoia nigra* (ZUG 1991).

Eremiascincus GREER, 1979

Eremiascincus richardsonii (GRAY, 1845)

Number of examined specimens: 2 adults

Remark:

Specimen BMNH 1908.5.28.54.-55 is cataloged under the synonym *Sphenomorphus monotropis*.

Distribution:

Australia; West Australia, Northern Territory, South Australia, New South Wales, Queensland.

Dental morphology:

The right dentary of specimen BMNH 1908.5.28.54.-55 bears 22 tooth positions whereas the right mandible of specimen SRK 00.172 bears 21 tooth positions. The teeth of *Eremiascincus richardsonii* are robust and cylindrical. The tooth diameter is larger in the anterior teeth than in teeth of the posterior part of the tooth row. The apical third of the teeth rises above the labial wall of the dentary. The tooth crowns only slightly contrast with the tooth necks and show a posterolingual torsion. The lingual surfaces of the apices are concave. The culmen lateris anterior is more prominent and longer than the culmen lateris posterior. The crista mesialis is longer than the crista distalis; this causes a shifting of the cuspis labialis from a central to a more posterior position. The cuspides labiales of the anterior teeth are distinctly more pointed than the cuspides labiales of the posterior teeth. Two lingual cutting edges, the cristae linguales anterior et posterior, run parallel to the labial cutting edges. These lingual cristae apically form the cuspis lingualis, which is more highly elevated in the anterior teeth than it is in the posterior teeth. In the 17th and 18th teeth of SRK 00.172, additional small anterior side cusps are present. Several weak striae are running across the lingual surface of the tooth crowns. The total number of these striae varies and complex patterns of striations are absent. Most striations are found in the anterior teeth. These striae converge apically. The labial enamel surfaces are smooth. The relation of the tooth length to the diameter of tooth neck is 2.2:1.0. The resorption pits are shaped circularly.

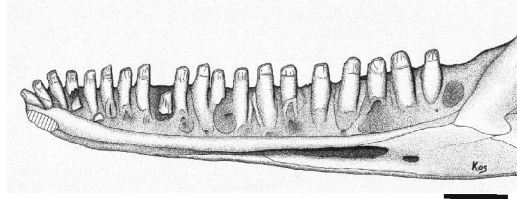


Fig. 66: *Eremiascincus richardsonii* (specimen SRK 00.172)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

E. richardsonii is a nocturnal skink, which is active on the ground surface. Nevertheless, these lizards “swim” into loose soil and sand or inhabit other animal burrows by day. It hunts on the surface at night for invertebrates and was observed eating smaller reptiles (*Lerista* sp., small *Ctenotus* sp.) by HUTCHINSON (pers. comm.). *E. richardsonii* is a widely foraging species, and foraging below the surface is recorded by HENLE (1989).

Eugongylus FITZINGER, 1843

Eugongylus albifasciolatus (GÜNTHER, 1872)
(Pl. VI, Fig. 2)

Number of examined specimens: 1 adult

Remark:

The only available specimen of *Eugongylus albifasciolatus*, BMNH 98.5.27.-13, is cataloged under the synonym *Lygosoma (Riopa) albifasciolata*.

Distribution:

Australia (Queensland), Solomon Islands, New Britain, New Ireland.

Dental morphology:

The tooth crowns of *Eugongylus albifasciolatus* distinctly contrast with the tooth necks. The tooth bases are conspicuously broadened transversally and therefore the surfaces of the flanks are flattened or even concave. The tooth crowns of this species are mesially widened and lingually curved inward. The cristae mesialis et distalis are of equal length and are forming a posterolingually directed cuspis labialis. A less pronounced cuspis lingualis is separated from the cuspis labialis by a wide antrum intercristatum. The labial enamel surfaces are smooth, whereas up to ten very prominent striae are developed on the lingual surfaces of the crowns between the short but morphologically pronounced culmines lateres. These striations converge fan-

like and are reaching the cuspis lingualis. The ratio tooth length:diameter of tooth neck is 4.6:1.0. The resorption pits are circular in shape. The pattern of striations is already fully developed in replacement teeth.

Diet:

E. albifasciolatus is a crepuscular species, dwelling on forest floors covered by dense undergrowth. The diet includes insects, spiders, small land crabs, and smaller lizards (MCCOY 1980).

***Eugongylus rufescens* (SHAW, 1802)**

(Pl. VI, Figs. 3-4)

Number of examined specimens: 1 adult

Remark:

The specimen BMNH 97.12.10.73 was cataloged under the synonym *Lygosoma (Riopa) rufescens*.

Distribution:

Australia (Queensland), Admiralty Islands, Indonesia (Irian Jaya), New Guinea, Solomon Islands.

Dental morphology:

In lingual view the teeth of *Eugongylus rufescens* appear to be very slender. In occlusal view the distinct transversal broadening of the tooth bases becomes apparent. The latera are flattened or even slightly concave. The lingual surfaces of the tooth crowns are curved inward. The tips of the apices are directed posterolingually. The crista mesialis is always longer than the crista distalis. The cuspis labialis is forming a sharp edge and is separated from the only slightly elevated cuspis lingualis by a moderate concave antrum intercristatum. The cristae mesialis et distalis transform basally in a wide sinus into the culmines lateres. The culmines lateres anterior et posterior are framing the concave inner surface of the apex, of which mostly six or seven very prominent striae protrude. Those striae are incipient at the transition between the tooth neck and tooth crown and run parallel to each other first in order to converge at the cuspis lingualis afterwards. This pattern of striations is already present in non-functional replacement teeth. All labial surfaces are smooth. Wear facets mostly concern the area of the antrum intercristatum so that in many teeth, the cuspis lingualis is worn out. The relation of the tooth length to the diameter of tooth neck is 4.3:1.0. The resorption pits are shaped circularly.

Diet:

E. rufescens is a crepuscular species, dwelling on forest floors covered by dense undergrowth. The diet is probably similar to the diet of *Eugongylus albifasciolatus* (HUTCHINSON, pers. comm.).

***Eulamprus* FITZINGER, 1843**

***Eulamprus tympanum* (L ÖNNBERG & ANDERSSON, 1915)**

Number of examined specimens: 1 adult

Distribution:

Australia; New South Wales, South Australia, Victoria.

Dental morphology:

The only available specimen of the Australian water skink *Eulamprus tympanum*, SRK 00.168, bears 22 tooth positions in its right dentary. The teeth are very slender and column-shaped. The apical third of the teeth is rising above the labial wall of the dentary. The apices show a posterolingually torsion and are lingually concave. The crista mesialis is always slightly longer than the crista distalis, which leads to a far posterior position of the cuspis labialis. Underneath the cuspides labiales, the often very pointed cuspides linguales are situated, which show intensive wear facets at several of the posteriormost teeth. Between cuspis labialis and cuspis lingualis a deep antrum intercristatum is notched. Culmines lateres are only developed in the anterior teeth. The culmen lateris anterior is longer than the culmen lateris posterior. Up to five parallel striae are running between the culmines lateres. The intensity of the striations is decreasing caudally within the tooth row. The ratio tooth length:diameter of tooth neck is 4.8:1.0. The resorption pits are shaped circular. Processes of tooth replacement are seen at nearly all tooth bases.

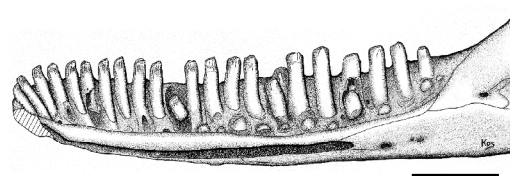


Fig. 67: *Eulamprus tympanum* (specimen SRK 00.168)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The genus *Eulamprus* is semiaquatic. The lizards are hunting on the banks of Australian rivers and lakes. Stomach contents analyses in *Eulamprus quoyii* proved that one quarter of the diet in the natural habitat consists of aquatic prey (dragonflies and their larvae, water beetles, and tadpoles) and three quarters consist of insects, spiders, terrestrial snails, and small lizards (DANIELS 1987). However, *Eulamprus* never hunts underwater; instead it captures the prey items at the water surface. Fishes and ground dwelling aquatic snails are rarely captured. *Eulamprus* is not choosy concerning the size of its prey. In captivity even sweet fruit pudding was accepted (HAUSCHILD & GABNER 1995). Brown (1991) describes this species as being aggressive; this author observed the occurrence of occasional skinks in the diet.

Eumecia BOCAGE, 1870

Eumecia anchietae BOCAGE, 1870
(Pl. VI, Figs. 5-7)

Number of examined specimens: 1 adult

Remark:

The only available specimen of this species, BMNH 1906.7.6.4., was cataloged under the synonym *Lygosoma anchietae*.

Distribution:

Angola, Democratic Republic of the Congo (Zaire), Kenya, Tanzania, Zambia.

Dental morphology:

The teeth of *Eumecia anchietae* are pointed and conical with a recurved and posterolingually directed tip. Only the lingual surfaces of the apices are flattened or concave in shape; apart from that, all surfaces of the teeth are convex. The teeth are typically fang-like. The tooth crowns are bicuspid; a low cuspis lingualis is developed in addition to a relatively pointed cuspis labialis. The antrum intercristatum is in some teeth exceptionally deep notched. The cristae mesialis et distalis gradually transform into the culmines lateres, which both stretch far upon the surface of the tooth neck. The labial surfaces of the teeth are smooth, whereas on their lingual surfaces, one or two short, but prominent, striae are mostly developed. The ratio of the tooth length to the diameter of tooth neck is 2.4:1.0.

Diet:

No data are available about the dietary spectrum of *Eumecia anchietae*.

Hemiergis WAGLER, 1830

Hemiergis decresiensis (CUVIER, 1829)
(Pl. VI, Fig. 8)

Number of examined specimens: 5 adults

Distribution:

Australia; New South Wales, South Australia, Victoria.

Dental morphology:

The ophiomorph Australian burrowing skink *Hemiergis decresiensis* bears approximately 16 to 18 tooth positions in each jaw ramus. In contrast to the African Acontinae, the teeth of *Hemiergis* species are mostly straight without curvature. Tooth bases and tooth necks of *H. decresiensis* are cylindrical. The tooth crowns of the symphyseal region are pointed whereas they are blunt in the posterior part of the tooth row. The apices alone are rising above the labial wall of the dentary. The labial surfaces of the tooth crowns are only slightly flattened. The cristae mesialis et distalis are the same length and form the pointed and posterolingually curved cuspis labialis. A short lingual cutting edge constructs the elevated and sharp-edged cuspis lingualis which is situated underneath the cuspis labialis and separated from this cusp by a deeply notched antrum intercristatum. The lingual cutting edge transforms anteriorly in a wide sinus into the culmen lateris anterior, whereas it transfers posteriorly into the culmen lateris posterior. Most enamel surfaces are smooth; isolated striae are developed only in a few teeth in the anterior third of the tooth row. The ratio of the tooth length to the diameter of tooth neck is 3.6:1.0. The resorption pits are shaped circular.

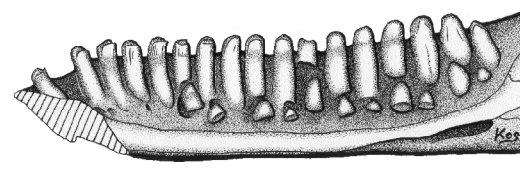


Fig. 68: *Hemiergis decresiensis*
(specimen SRK 00.280)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The members of the genus *Hemiergis*, whose extremities are distinctly reduced, are hunting small arthropods on the ground surface. *H. decresiensis* stays entirely under dense grass or inhabits cracks and holes in the soil (HUTCHINSON, pers. comm.). It shows a large percentage (7.6 %) of Annelida in its diet. The major part of its diet consists of Formicidae. Accordingly *H. decresiensis* is a myrmecophageous species. The remaining part of the diet is made up by small and soft-bodied food items (BROWN 1991).

***Hemiergis millewae* COVENTRY, 1976**

Number of examined specimens: 3 adults

Distribution:

Australia; New South Wales, South Australia, Victoria, West Australia.

Dental morphology:

The teeth of *Hemiergis millewae* strongly resemble the teeth of *Hemiergis decresiensis*. Each dentary of *H. millewae* bears up to 18 tooth positions. The teeth are robust and cylindrical. Only the outer tips are towering above the labial wall of the dentary. Several massive teeth are situated in the posterior part of the tooth row. The tooth crowns are hardly flattened lingually. The diameters of the anterior teeth are similar to the diameters of the posterior teeth. Bicuspidity is also developed in the posterior portion of the tooth row. The antra intercristata are deeply notched particularly in the anterior teeth. The culmines lateres are only weakly developed and end before reaching the tooth necks.

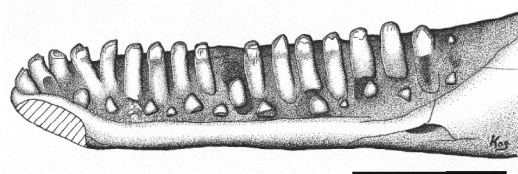


Fig. 69: *Hemiergis millewae* (specimen SRK 00.281)
Right dentary; lingual view
Scale bar: 1.0 mm

In specimen SRK 00.281 striations are developed in only a very few tooth crowns (tooth positions 9 and 11). The striations are restricted to the lingual surfaces of the apices and are only weakly developed. The ratio tooth

length:diameter of tooth neck amounts to 4.6:1.0 in the central and 2.5:1.0 in the posterior portion of the tooth row. The resorption pits are circular shaped. Replacement teeth are situated at the bases of most functional teeth.

Diet:

No data about the composition of the diet of *H. millewae* are available. These skinks are confined to porcupine grass tussocks (*Triodia irritans*) (HUTCHINSON, pers. comm.).

***Hemiergis peronii* (GRAY, 1831)**

(Pl. VI, Fig. 9)

Number of examined specimens: 2 adults

Distribution:

Australia; South Australia, Victoria, West Australia.

Dental morphology :

The dentary of *Hemiergis peronii* bears up to 18 tooth positions. The teeth of *H. peronii* largely resemble the teeth of the other species of *Hemiergis* described in this thesis. In *H. peronii* a cuspis labialis and a cuspis lingualis are developed, separated by a (in this species, shallow) antrum intercristatum. The labial cutting edges are running approximately horizontal, which makes the outlines of the teeth appear rectangular. Several posterior teeth show weak striations which are running parallel to one another. The ratio tooth length:diameter of tooth neck is 4.2:1.0. The resorption pits are circularly shaped.

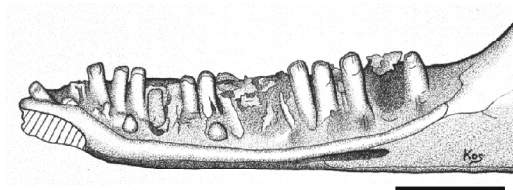


Fig. 70: *Hemiergis peronii* (specimen SRK 00.287)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

H. peronii stays entirely under dense grass or inhabits cracks and holes in the soil (HUTCHINSON, pers. comm.). The diet consists almost exclusively of arthropods (mainly beetles, ants, and other Hymenoptera), the only plant matter recorded are seeds of the lily *Dianella revoluta*, which might have been mistaken for insects (SMYTH 1968).

Hemisphaeriodon PETERS, 1867

Hemisphaeriodon gerrardi (GRAY, 1845)
(Pl. VI, Figs. 10-12)

Number of examined specimens: 4 adults

Distribution:

Australia; eastern coast from Sydney in the south of New South Wales to the Cape York peninsula in the north of Queensland.

Dental morphology:

The dentition of the Australian snail-eating skink *Hemisphaeriodon gerrardi* is highly specialized and adapted to a durophagous diet. The robust and massive dentaries bear 14 tooth positions on average. The teeth are very widely spaced. The penultimate tooth is enlarged and transformed into a prominent crushing tooth. The cross-sections of all teeth are circular, but the tooth necks of the anterior teeth are more slender compared to the posterior teeth. A transversal broadening of the tooth neck is obvious only in tooth positions 1 and 2. The tooth crowns are dome-shaped in lingual view and round in occlusal view. Only the anterior teeth show pointed apices with concave lingual surfaces. The cusps are directed posterolingually. The enamel surfaces of the tooth crowns are intensively wrinkled. These striations are covering the entire occlusal surfaces of the tooth crowns in the central and the posterior portion of the tooth row, whereas the tooth necks are perfectly smooth. More than 80 striae can be developed in one tooth. Some striae are bifurcated and converge at the centrally positioned and rounded cusp. Several striae are polyfurcated at their basal ends. The labial surfaces of the tooth crowns are smooth in tooth positions 1 to 3; from tooth position 4 on striae are developed, which are weak at first but become more prominent in the posterior teeth. All striae end abruptly at a particular level in the transition zone between tooth crown and tooth neck. The cristae mesialis et distalis are developed only in the anterior teeth (up to tooth position 4). The cristae are the same length and form the slightly elevated cusp. The ratio tooth length:diameter of tooth neck is from 3.3:1.0 in the central area to 1.1:1.0 in the posterior portion of the tooth row. The resorption pits are circular. Often more than one resorption pit is set up at a single tooth base in the first stage of tooth replacement. Those multiple resorption pits fuse during the replacement process. The

striations are already fully developed in growing and still non functional teeth.

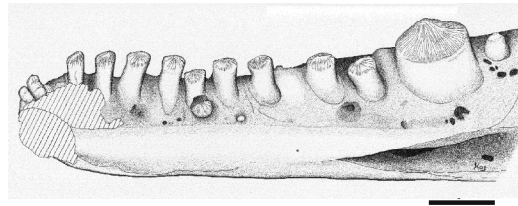


Fig. 71: *Hemisphaeriodon gerrardi*
(specimen SRK 00.081)
Right dentary, showing the prominent crushing tooth;
lingual view
Scale bar: 1.0 mm

Diet:

H. gerrardi is an unusual specialized molluscivore, which preys exclusively upon snails and slugs. Snails are crushed with the durophagous teeth in the back of the jaws. Sometimes the lizards additionally use a hard object. The soft parts of the snails are separated from the shell fragments with the tongue. If shell fragments are taken in accidentally, the skink pushes them out of its mouth with the tongue. Slugs are removed from the ground surface by rotation around the longitudinal axis of the body (LÖHR 2000).

Lamprolepis FITZINGER, 1843

Lamprolepis smaragdina (LESSON, 1826)
(Pl. VI, Figs. 13-15)

Number of examined specimens: 5 adults

Distribution:

Taiwan, Philippines, Palawan and Sulu-Archipelago, Micronesia (Palau Islands to Marshall Islands and Carolines), Indo-Australian Archipelago, New Guinea, Solomons and Santa Cruz Islands.

Dental morphology:

The slender dentaries of *Lamprolepis smaragdina* bear 25 tooth positions on average. The apical halves of the tooth crowns are rising above the labial wall of the dentary. The cross-sections of the teeth are circular and enlarged at the bases. Therefore the tooth bases appear to be very massive. The lingual surfaces of the tooth crowns of *L. smaragdina* are concave-shaped. The posterior teeth are distinctly more robust than the anterior teeth. The crista mesialis is longer than the crista distalis, which causes a slightly posteriorly situated cuspis

labialis. The inner angle of the cuspis labialis amounts to 130°. The cristae mesialis et distalis each transforms in a wide sinus into the prominent culmines lateres, which in one specimen nearly converge again basically (USNM 340061), or run parallel far across the tooth necks as in another specimen (ZFMK 14825). Parallel to the labial cutting edges, a crista lingualis anterior and a crista lingualis posterior are developed which are sharp-edged and construct an elevated cuspis lingualis. Between the two cusps, a deeply notched antrum intercristatum is found. While the labial surfaces of the teeth are smooth, the concave lingual surfaces of the crowns are covered by numerous striae. These striae can be developed as up to six thin parallel lines which are limited to a narrow belt-zone (USNM 340061) or as long prominent ridges which are running from the tooth necks to the cuspis lingualis where they converge (ZFMK 14825, SRK 00.080). The ratio tooth length:diameter of tooth neck is from 4.2:1.0 in the symphyseal region to 2.5:1.0 in the posterior part of the tooth row. The resorption pits are circular.

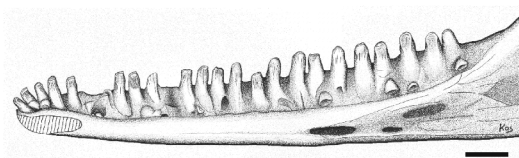


Fig. 72: *Lamprolepis smaragdina* (specimen SRK 00.080)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

L. smaragdina preys upon insects, spiders, and scorpions. Additionally, fallen and bursted fruits (*Carica papaya*), seeds, flowers, and nectar are consumed by this species (HAUSCHILD & GÄBNER 1995). In captivity, this tree skink develops a preference for lizard eggs and ant pupae; this may indicate a comparable diet in the natural habitat in Southeastern Asia.

Lampropholis FITZINGER, 1843

Lampropholis delicata (DE VIES, 1888)
(Pl. VI, Fig. 16)

Number of examined specimens: 4 adults

Distribution:

Australia; New South Wales, Queensland, South Australia, Victoria, Tasmania, New Zealand (introduced), USA (Hawaii).

Dental morphology:

The teeth of *Lampropholis delicata* are very slender and cylindrical. The apical third of the teeth towers above the dorsal margin of the labial wall of the dentary. Mostly the tooth bases are narrow compared to the tooth necks. The tooth crowns are only lightly flattened. An only modest torsion of the apices causes a posterolingual direction of the cuspis labialis. Despite this, the cristae mesialis et distalis are of equal length. Underneath the cuspides labiales only slightly elevated cuspides linguales are developed. All enamel surfaces are smooth. The relation of the tooth length to the diameter of tooth neck amounts to 4.8:1.0. The resorption pits are of circular shape.

Diet:

L. delicata is insectivorous.

Leiolopisma DUMÉRIL & BIBRON, 1839

Leiolopisma australcaledonicum nomen dubium
(Pl. VI, Fig. 17)

Number of examined specimens: 1 adult

Remark:

The species name of specimen ZFMK 14826 is a nomen dubium. This specimen probably belongs to *Leiolopisma alazon* ZUG 1985 or *Leiolopisma telfairi* (DESJARDIN 1831).

Dental morphology:

The teeth of ZFMK 14826 are slender and cylindrical. The tooth crowns distinctly contrast with the tooth necks. The lingual surfaces of the tooth crowns are concave. The cristae mesialis et distalis are the same length; both cristae transform via a wide sinus into the culmines lateres anterior et postererior. The crista lingualis anterior and the crista lingualis posterior run parallel to the above described labial cutting edges, which together form the cuspis labialis. The cuspis lingualis is situated

underneath the cuspis labialis and is only moderately elevated. The two cusps are separated from each other by a broadened but shallow antrum intercristatum. Apart from these structures, the enamel surfaces are smooth.

Diet:

The diet of this arboreal genus includes the regurgitated stomach contents of seabirds (GREER 1976). *Leiopisma* specimens are often very aggressive. The New Caledonian tree skink *Leiopisma nigrofasciolatum* often attacks other lizards, injures them, or eats their tails (HAUSCHILD & GABNER 1995). In captivity these skinks consume insects, spiders, and small snails. Sweet fruits are refused by *Leiopisma*.

Remarks:

The genus *Leiopisma* is probably ancestral to the genus *Lampropholis* (BROWN 1991).

Lerista BELL, 1833

Lerista bougainvillii (GRAY, 1839)

Number of examined specimens: 2 adults

Distribution:

Australia; New South Wales, South Australia, Victoria, Tasmania.

Dental morphology:

The elongated and stretched dentary of the ophiomorph Australian skink *Lerista bougainvillii* bears approximately 17 tooth positions. The teeth are relatively short and stout. There is a tendency for a heterodont condition since the posterior teeth are stronger than the anterior teeth. The apices alone tower above the labial wall of the dentary. The cusps of the anterior teeth are posterolingually directed and lingually concave whereas the apices of the posterior teeth are blunt. The anterior teeth are bicuspid, each showing a cuspis labialis and a cuspis lingualis which are separated by the notched antrum intercristatum. The culmines lateres are very short. The posterior teeth are unicuspid. On the lingual surfaces of the tooth crowns, very fine striae are visible. These striae do not form complex patterns; they run irregularly and converge apically. The ratio of the tooth length to the diameter of tooth neck is 3.0:1.0. The resorption pits are shaped circularly.

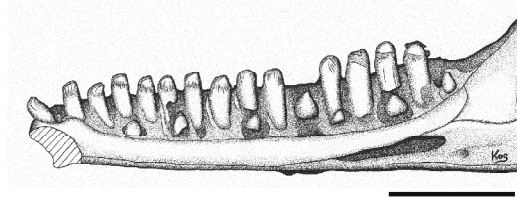


Fig. 73: *Lerista bougainvillii*
(specimen SRK 00.262)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The preferred diet of the genus *Lerista* is termites (CRAIG 1991). *L. bougainvillii* is semi-fossorial; the skinks hide in loose soil under rocks or logs. They forage within the litter layer (HUTCHINSON, pers. comm.).

Remark:

The extremities are gradually reduced within the genus *Lerista*. In many species only vestiges of the hind limbs are present.

Lerista planiventralis (LUCAS & FROST, 1902)
(Pl. VI, Fig. 18)

Number of examined specimens: 1 adult

Distribution:

Australia; West Australia.

Dental morphology:

The dentition of *Lerista planiventralis* strongly resembles the dentition of *Lerista bougainvillii*. The anterior tooth crowns of *L. planiventralis* are distinctly ornamentated lingually. The striations run parallel to one another. The surfaces of the conical posterior teeth are smooth. The ratio tooth length:diameter of tooth neck is 2.9:1.0. The resorption pits are shaped circularly.

Diet:

The preferred diet of the genus *Lerista* is termites (CRAIG 1991). The fossorial *L. planiventralis* is a specialized sand-swimmer (HUTCHINSON, pers. comm.).

Lerista punctatovittata (GÜNTHER, 1867)

Number of examined specimens: 2 adults

Distribution:

Australia; New South Wales, Queensland, South Australia, Victoria.

Dental morphology:

Each of the slender mandibles of *Lerista punctatovittata* bears approximately 14

tooth positions. The teeth are cylindrical and very robust. The anterior tooth crowns are recurved, whereas the mesially broadened tooth crowns of the posterior teeth are straight. The cristae mesialis et distalis are the same length and form the cuspides labiales, which are very pointed especially in the anterior teeth. The crista lingualis anterior and the crista lingualis posterior run parallel to the labial cutting edges. Furthermore, those cristae linguales build the distinctly elevated cuspis lingualis and they transform at the sinus into the prominent culmines lateres. The antrum intercristatum is deeply notched in several teeth. While the tooth crowns of the anterior teeth are only slightly flattened lingually, the tooth crowns of the posterior teeth are lingually often distinctly curved inwards. The lingual surfaces of most tooth crowns are covered by numerous fine striations which run approximately parallel to each other. The labial surfaces of the teeth are smooth. The relation of the tooth length to the diameter of tooth neck is 2.7:1.0. The resorption pits are circular. Striations are already developed in non functional replacement teeth.

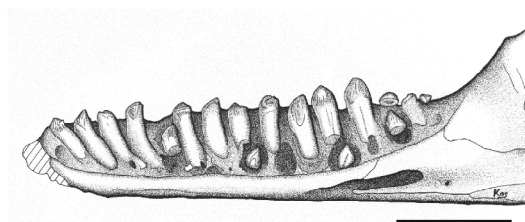


Fig. 74: *Lerista punctatovittata*
(specimen SRK 00.256)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The preferred diet of the genus *Lerista* is termites (CRAIG 1991). The fossorial *L. punctatovittata* is a specialized sand-swimmer, which hides in soft sand and forages within leaf litter. These skinks are active on the ground surface on warm nights (HUTCHINSON, pers. comm.). HENLE (1989) assumes underground foraging for *L. punctatovittata* since stomach contents analyses showed considerable amounts of sand, 44.7 % fossorial arthropods, and only 1.9 % flying insects.

Lipinia GRAY, 1845

Lipinia leptosoma (BROWN & FEHLMANN, 1958)

(Pl. VI, Fig. 19)

Number of examined specimens: 1 adult

Distribution:

Palau Island.

Dental morphology:

The teeth of these arboreal skinks are poor in characters. The cross-sections of the teeth are mesially slightly broadened in *Lipinia leptosoma*. The apices are conical and show very short cristae mesiales. The cuspides labiales are situated centrally. Lingually of this main cusp a low cuspis lingualis is developed, which is separated from the cuspis labialis by a deep antrum intercristatum. In occlusal view, the antrum bows to the lingual direction. The tooth surfaces are smooth without exception. The tooth length and the morphology of the resorption pits cannot be determined because the bases of the teeth of the only available specimen of *L. leptosoma*, USNM 507554, are covered by mucosa.

Diet:

The taxa of the Southeastern Asian genus *Lipinia* prey upon arthropods (MANTHEY & GROSSMANN 1997).

Lipinia noctua (LESSON, 1826)

(Pl. VII, Fig. 1)

Number of examined specimens: 2 adults

Distribution:

Cosmopolitan Pacific species occurring from Sulawesi eastward across the north of New Guinea through the Solomons and Vanuatu to Tuamotu Archipelago and Marquesas Islands and northward to Hawaii (USA), Fiji Islands, Tuamotu Atoll, Nukutipipi Atoll, Western Samoa, Admiralty Islands.

Dental morphology:

The teeth of *Lipinia noctua* are slender and cylindrical. Only the posterior teeth show slightly bulbous bases. The short cristae mesialis et distalis form a distinctly rounded cuspis labialis. As in *Lipinia leptosoma*, an additional low cuspis lingualis is developed, which separates from the cuspis labialis by a lingually curved antrum intercristatum. In contrast to *L. leptosoma*, the antra of *L. noctua* (SDS 18018) form an extensive plateau in several teeth. This apical plateau is absent in

another specimen (USNM 249758) and therefore suggests intraspecific variability. The enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 2.6:1.0. The resorption pits are circular.

Diet:

Like *Lipinia leptosoma*. The data in literature are very generalized and therefore no differentiated data are available. Probably the prey spectrum of the crepuscular and nocturnal *L. noctua* differs from the spectrum of the diurnal *L. leptosoma*.

Lipinia pulchella (GRAY, 1845)
(Pl. VII, Fig. 2)

Number of examined specimens: 1 adult

Distribution:

Philippine Islands (Luzon, Mindanao, Negros, Bohol, Pollillo, Panay).

Dental morphology:

The teeth of *Lipinia pulchella* are extraordinarily poor in characters. The tooth bases and tooth necks are cylindrical and transform fluently into the conical tooth crowns. All teeth of *Lipinia pulchella* are unicuspid. The enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 2.6:1.0. The resorption pits are of circular shape.

Diet:

Like *Lipinia leptosoma*.

Lipinia rabori (BROWN & ALCALA, 1956)

Number of examined specimens: 1 adult

Distribution:

Philippine Islands.

Dental morphology:

The teeth of *Lipinia rabori* are cylindrical and show slightly flattened tooth crowns lingually. The crista mesialis is slightly longer than the crista distalis. Both cristae converge at the pointed cuspis labialis. Parallel to these labial cutting edges, two shorter lingual cutting edges are running, forming the cuspis lingualis at their point of intersection. The antrum intercristatum is modestly concave and runs in a wide bow from the sinus mesialis to the sinus distalis. The enamel surfaces are smooth. The relation of the tooth length to the diameter of tooth neck is 2.6:1.0. The resorption pits are of circular shape.

Diet:

Like *Lipinia leptosoma*.

Lygosoma HARDWICK & GRAY, 1827

Lygosoma afra (PETERS, 1854)
(Pl. VII, Fig. 3)

Number of examined specimens: 3 adults

Distribution:

Somalia, Kenya, Tanzania, Mozambique, Sudan, Ethiopia, Uganda, Zambia, Malawi, Democratic Republic of the Congo (Zaire), Central African Republic.

Dental morphology:

The dentary of the quadruped burrowing skink *Lygosoma afra* bears 20 to 21 tooth positions. The teeth are slender and cylindrical, the tooth crowns only slightly contrast with the tooth necks. The crista mesialis is for the most part a little longer than the crista distalis. The cuspis labialis, which is formed by these two labial cristae, is very pointed (60°) and posterolingually directed. The cristae mesialis et distalis transform fluently into the culmines lateres, which stretch far basally. Two lingual cutting edges, the cuspides linguales anterior et posterior, run parallel to the labial cutting edges. At their point of intersection, the cuspides linguales form the only slightly elevated cuspis lingualis. In most specimens of this species, the antrum intercristatum is only slightly concave. On the lingual surfaces of the tooth crowns, five striae are developed between the culmines lateres. These striae converge near the cuspis lingualis. Some striations are longer and more prominent than others, but they never form complex patterns. The ratio tooth length:diameter of tooth neck is 2.9:1.0. The resorption pits are of circular shape.

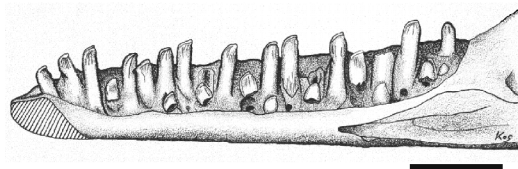


Fig. 75: *Lygosoma afra*
(specimen SRK 00.019)
Right dentary; lingual view
Scale bar: 1.0 mm

There are several (up to three) parallel tooth rows developed in the dentaries of two specimens of *Lygosoma afra* (SRK 00.018 und SRK 00.293) as a result of a pathological deformity. This unusual pathological feature was also detected in one individual of *Sphenomorphus variegatus* (SRK 00.297). The two *L. afra*-specimens which are characterized by this formerly unknown deformity demonstrably lived in captivity at BROSCINSKI for many years and reached a high individual age. The lifespan of these lizards exceeded by far the lifespans of wild conspecific lizards. The development of several parallel tooth rows will be referred to as "multiple replacement" in the following.

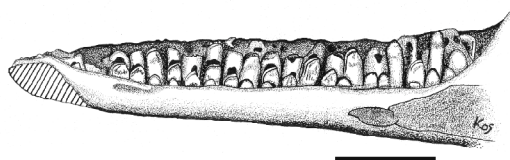


Fig. 76: *Lygosoma afra*
(specimen SRK 00.018)
Right dentary demonstrating "multiple tooth rows";
lingual view
Scale bar: 1.0 mm

Diet:

The three specimens which were available for this thesis lived in captivity and preferred larvae of the mealbeetle, *Tenebrio molitor*, (BROSCINSKI, pers. comm.). Because of the burrowing habits of *L. afra*, it can be assumed that this species preys on beetle larvae, maggots, woodlouses, and earthworms in its natural habitat. Observations on BROSCINSKI's captive individuals showed that with increasing age the animals had difficulties in chewing and biting their prey items (BROSCINSKI, pers. comm.).

Lygosoma bowringii (GÜNTHER, 1864)

Number of examined specimens: 1 adult

Distribution:

West Malaysia, Pulau Tioman, India (Andaman Islands), Philippines (Sulu Archipelago), Indonesia (Borneo, Java, Sulawesi), China (Hong Kong), Singapore, India, Indochina west to Burma, Vietnam, Thailand, Laos, Cambodia, Australia (Cook Islands).

Dental morphology:

The teeth of *Lygosoma bowringii* are very poor in characteristic features. The tooth bases and tooth necks are cylindrical and relatively robust. The conical apices are lingually slightly concave. Only the tooth crowns rise above the labial wall of the dentary. The tips of the teeth are posterolingually directed. The crista mesialis is a little longer than the crista distalis. The culmines lateres are only weakly developed. A slightly elevated cuspis lingualis is visible only in very few teeth. The antrum intercristatum is modestly concave and relatively narrow. The ratio tooth length:diameter of tooth neck is 3.0:1.0. The resorption pits are of circular shape.

Diet:

No data about the dietary spectrum of this species are available.

Mabuya FITZINGER, 1826

Mabuya affinis (GRAY, 1838)

(Pl. VII, Fig. 4)

Number of examined specimens: 1 adult

Distribution:

Angola, Gabon, Equatorial Guinea, Cameroon, Nigeria, Togo, Benin, Ghana, Ivory Coast, Liberia, Sierra Leone, Guinea, Guinea-Bissau, Senegal, Central African Republic, Gambia.

Dental morphology:

The teeth of *Mabuya affinis* are slender and show flattened latera. The tooth crowns are modestly pointed and show concave surfaces lingually. The cristae mesialis et distalis transform without interruption into the culmines lateres, which stretch far upon the tooth necks. A garland of striations has developed at the lingual surface of the basal part of the tooth crown in specimen ZFMK 9196. A maximum of seven parallel striae end already in the lower half of the tooth crown. The striae are short and robust. The apical half of the tooth crown shows a smooth surface. The teeth are predominantly unicuspid, only in older teeth a deep antrum intercristatum, and therefore also a cuspis lingualis, are developed as the result of wear.

Diet:

No data about the dietary spectrum of this species are available. Most *Mabuya* species are opportunistic insectivores.

Mabuya aureopunctata (GRANDIDIER, 1867)

Number of examined specimens: 1 adult

Distribution:

Madagascar.

Dental morphology:

The teeth of *Mabuya aureopunctata* are robust and slightly stocky. The tooth crowns tower above the labial wall of the dentary. The tooth bases and the tooth necks are broadened transversally. The teeth strongly resemble those of *Mabuya affinis*. However the culmines lateres of *M. aureopunctata* are shorter than the culmines lateres of *M. affinis*. The garland-like arrangement of striations is found in both species. In *M. aureopunctata*, up to twelve short striae can be developed in one tooth (tooth position 17 of specimen BMNH 95.11.12.70).

Diet:

No data about the dietary spectrum of this species are available. Most *Mabuya* species are opportunistic insectivores. Stomach contents analyses proved that locusts, cockroaches, termites, ants, and 20% plant matter are the food sources of *Mabuya aurata* (MOHAMMED 1987).

Mabuya bistrinata (SPIX, 1825)
(Pl. VII, Fig. 5)

Number of examined specimens: 2 adults

Distribution:

South America; Brazil, French Guiana, Bolivia, Jamaica.

Dental morphology:

The teeth of *Mabuya bistrinata* are cylindrical and very narrowly spaced. The tooth crowns are lingually concave. The cristae mesialis et distalis are the same length and both transfer in wide sinus into the relatively short and very prominent culmines lateres. The tips of the teeth are posterolingually directed. In addition to the cristae mesialis et distalis and parallel to them, two cutting edges, the cristae linguales anterior et posterior, are developed. These lingual cutting edges build an only slightly elevated cuspis lingualis. A maximum of eight striae, which are very prominent, is present at the concave lingual surfaces of the apices. These striae are longer than in *Mabuya affinis*, but also arranged in a garland-like fashion. However, there are also teeth which show very extended striations almost reaching the cuspis lingualis. Some striations are

bifurcated; the bifurcations can be directed apically and also basally. Partes furcatae are also developed in several teeth. The ratio tooth length:diameter of tooth neck is 4.2:1.0. The resorption pits are perfectly circular.

Diet:

No data about the dietary spectrum of this species are available. Most *Mabuya* species are opportunistic insectivores.

Mabuya brevicollis (WIEGMANN, 1837)

Number of examined specimens: 1 adult

Distribution:

Sudan, Ethiopia, Eritrea, Somalia, Kenya, Uganda, Tanzania, Yemen, Saudi Arabia.

Dental morphology:

The teeth of *Mabuya brevicollis* are identical to the teeth of *Mabuya affinis*.

Diet:

No data about the dietary spectrum of this species are available. Most *Mabuya* species are opportunistic insectivores.

Mabuya carinata (SCHNEIDER, 1801)

Number of examined specimens: 4 adults

Distribution:

India, Bangladesh, Maldives, Sri Lanka.

Dental morphology:

The teeth of *Mabuya carinata* are slender and transversally broadened at their bases; therefore the flanks appear flattened. The tooth crowns distinctly contrast with the tooth necks and tower completely above the labial wall of the dentary. The lingual surfaces of the apices are concave and the tooth tips are directed to posterolingually. The crista mesialis is longer than the crista distalis. The cuspis labialis is relatively pointed at an angle of 60-70°. Parallel to the cristae mesialis et distalis, and separated from them by a narrow antrum intercristatum run the cristae linguales anterior et posterior, which form the slightly elevated cuspis lingualis underneath the cuspis labialis. The culmines lateres are prominent and form a very wide sinus at the transition zone where they transform into the cutting edges. The concave lingual surfaces of the tooth crowns show up to seven striae. These parallel striations are very prominent and stretch from the tooth necks to the immediate vicinity of the

cuspides linguales. This pattern of striations is already fully developed in replacement teeth. The relation of the tooth length to the diameter of tooth neck is 5.0:1.0. The resorption pits are shaped circularly.

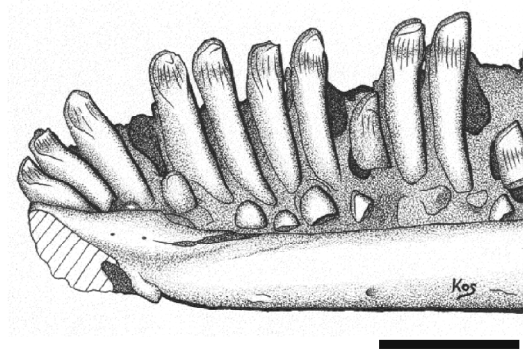


Fig. 77: *Mabuya carinata* (specimen SRK 00.197)
Anterior portion of a right dentary (tooth positions 1-11 from 29); lingual view
Scale bar: 1.0 mm

Diet:

No data about the dietary spectrum of this South American species are available. Since most *Mabuya* species are opportunistic insectivores, the diet of *M. carinata* is probably also dominated by insects.

Mabuya cumingi BROWN & ALCALA, 1980

Number of examined specimens: 1 adult

Distribution:

Philippine Islands (Luzon).

Dental morphology:

The teeth of *Mabuya cumingi* strongly resemble the teeth of *Mabuya affinis* in terms of morphology although they are mesially broadened. In addition, the antrum intercratum is distinctly notched in all teeth of *M. cumingi*.

Diet:

No data about the dietary spectrum of this species are available. The dietary spectrum of *M. cumingi* is probably comparable to its congenetics.

Mabuya elegans (PETERS, 1854)

Number of examined specimens: 1 adult

Distribution:

Madagascar.

Dental morphology:

The teeth of *Mabuya elegans* are cylindrical and show lingually flattened tooth crowns. As a result of rotation, the tooth crowns are posterolingually directed. The lingual surfaces of the teeth are concavely shaped in the immediate vicinity of the prominent culmines lateres. The crista mesialis is substantially longer than the crista distalis. The cuspid lingualis in replacing teeth has developed as a cusp with an inner angle of 100° whereas in older and worn teeth, only a horizontal ridge is visible. All enamel surfaces are smooth. Several teeth are intensively worn in the area of the antrum intercratum so that the lines between tooth enamel and dentine are exposed. The enamel of *M. elegans* is relatively thick. The ratio tooth length:diameter of tooth neck is 3.2:1.0. The resorption pits are shaped circularly.

Diet:

M. elegans is probably predominantly insectivorous. The species dwells in cultivated areas and settles in gardens and plantations

Mabuya gravenhorstii (DUMÉRIL & BIBRON, 1839)

(Pl. VII, Fig. 6)

Number of examined specimens: 2 adults

Distribution:

Madagascar.

Dental morphology:

The teeth of *Mabuya gravenhorstii* differ from the teeth of *Mabuya elegans* in only one character; this is the development of one or two very weak striae on the lingual surfaces of the tooth crowns in *M. gravenhorstii*. These striae are very long in some teeth and stretch from the tooth neck to the cuspid lingualis. The striations are developed only in the minority of the teeth. The surfaces of most teeth are smooth.

Diet:

The dietary spectrum of *M. gravenhorstii* probably resembles the one of *M. elegans*. *M. gravenhorstii* is the largest of the Madagascan *Mabuya* species and is adapted

more for forest habitation than the savanna-dwelling species like *Mabuya aureopunctata*.

Mabuya mabouya (LACÉPÈDE, 1788)

Number of examined specimens: 1 adult

Distribution:

Central America; Mexico, Guatemala, El Salvador, Nicaragua, Costa Rica, Honduras, Panama, Colombia, Trinidad, Tobago, Isla Mona, Isla Monito, Virgin Islands, Turks Islands, Caicos Islands, Lesser Antilles.

Dental morphology :

The right dentary of SRK 00.127 (*Mabuya mabouya alliacea*) bears 28 tooth positions. The teeth are slender and show slightly flattened latera. The tooth crowns are directed posterolingually as the result of an apical torsion and are lingually flattened. The crista mesialis is mostly slightly longer than the crista distalis. In addition to the relatively pointed cuspis labialis, a scarcely elevated cuspis lingualis is developed in the anterior teeth. Irregular striations are developed on the flattened lingual surfaces of the tooth crowns. These striations are arranged garland-like on the tooth numbers 19 and 20, resembling *Mabuya affinis*. The ratio tooth length:diameter of tooth neck amounts to 4.5:1.0. The resorption pits are shaped circularly.

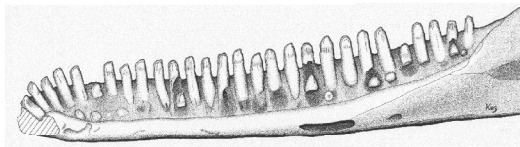


Fig. 78: *Mabuya mabouya alliacea* (specimen SRK 00.127)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

This Central American *Mabuya* is probably an opportunistic insectivore.

Mabuya macularia (BLYTH, 1853)

Number of examined specimens: 2 adults

Remark:

Specimen BMNH 77.8.9.8 was cataloged as *Mabuya macularis comorensis*. Since *Mabuya macularia* is not found on the Comoran Islands, the specific affiliation of this

specimen remains unsolved. *Mabuya macularis* is a nomen dubium.

Distribution:

Pakistan, India, Bhutan, Sri Lanka, Burma, Thailand, Laos, Cambodia, Vietnam, Malaysia.

Dental morphology:

The lower jaw of *M. macularia* (SRK 00.206) bears 34 tooth positions. The teeth are homodont and poor in characters. The tooth bases and the tooth necks are cylindrical. The tooth crowns do not contrast with the tooth necks. The Cristae mesialis et distalis are the same length and form the relatively pointed cuspides labiales. The tips are directed posterolingually. The cuspis lingualis is only slightly elevated and separated from the cuspis labialis by a narrow antrum intercristatum. The culmines lateres are only weakly developed. Most enamel surfaces are smooth, seldom isolated fine striae are visible. The ratio tooth length:diameter of tooth neck is 4.6:1.0. The resorption pits are shaped circularly in the beginning of replacement and become dorsally elongated later. The teeth of BMNH 77.8.9.8 agree with this description, but show distinct striae. These relatively long and prominent striae run across the lingual surfaces of the apices; there are six to seven striae per tooth developed.

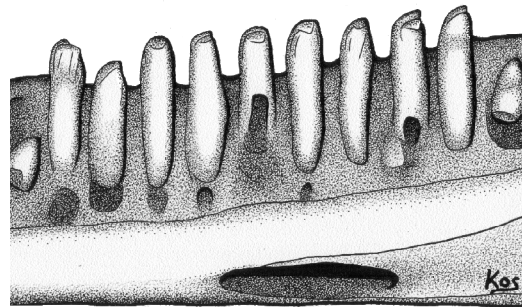


Fig. 79: *Mabuya macularia* (specimen SRK 00.206)
Central portion of a right dentary (tooth positions 18-28 from 34); lingual view
Scale bar: 1.0 mm

Diet:

No data about the dietary spectrum of this species are available. Like most *Mabuya* species, *M. macularia* probably is an opportunistic insectivore.

Mabuya madagascariensis (MOCQUARD, 1908)

Number of examined specimens: 3 adults

Distribution:

Madagascar.

Dental morphology:

The teeth of *Mabuya madagascariensis* are morphologically identical to the teeth of *Mabuya elegans*.

Diet:

No data about the dietary spectrum of this species are available. Like most *Mabuya* species, *M. madagascariensis* probably is an opportunistic insectivore.

Mabuya multifasciata (KÜHL, 1820)

Number of examined specimens: 9 adults

Distribution:

From India (Assam) to southern China, China (Taiwan, Hainan, Yunnan), Thailand, Burma, Laos, Cambodia, Vietnam, Malaysian Peninsula, Pulau Tioman, Singapore, Indonesia (Borneo, Sumatra, Java, Bali), New Guinea, Philippine Islands (Negros, Panay, Palawan, Calamian Islands, Luzon).

Dental morphology:

The dentary of *Mabuya multifasciata* bears 29 to 30 tooth positions. The teeth are strongly transversally broadened at their bases. In lingual view, the teeth appear to be slender. The lingual surfaces of the tooth crowns are curved inward. The tips of the teeth that are situated in the anterior half of the tooth row are posterolingually directed whereas the tooth crowns of the posterior half of the tooth row are blunt. The crista mesialis is slightly longer than the crista distalis. The teeth are predominantly unicuspid. Only in very few teeth a cuspis lingualis is present. The cutting edges transform over a wide sinus into the very prominent culmines lateres, which stretch to the tooth necks. While the labial enamel surfaces are generally smooth, very pronounced striae are visible at the lingual surfaces of the tooth crowns. The striae are arranged in parallel; they converge at the cusps in only a few teeth. A maximum of eight striae are developed on one tooth. A bifurcation of single striae in the basal direction is only rarely developed. The relation of the tooth length to the diameter of tooth neck amounts to 7.1:1.0. The resorption pits are dorsally elongated and sometimes become acute apically.

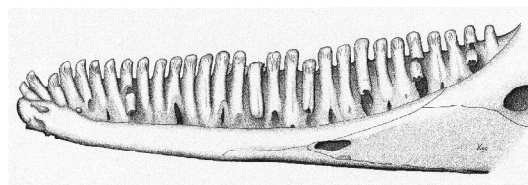


Fig. 80: *Mabuya multifasciata* (specimen SRK 00.050)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The Asian *M. multifasciata* lives close to lakes and rivers and preys on all kinds of insects. (HAUSCHILD & GABNER 1995, ZIEGLER & WEITKUS 1999). This observation was affirmed by own experiences with this species in captivity. Additionally, *M. multifasciata* consumes sweet fruits like papaya and mango, spiders, bird eggs, crabs, insect pupae, and smaller lizards.

Mabuya perrotetii (DUMÉRIL & BIBRON, 1839)

Number of examined specimens: 4 adults

Distribution:

Senegal, Gambia, Guinea-Bissau, Guinea, Sierra Leone, Liberia, Ivory Coast, Ghana, Togo, Benin, Nigeria, Cameroon, Central African Republic, Democratic Republic of the Congo (Zaire), Uganda, Mali.

Dental morphology:

The dentary of the West African *Mabuya perrotetii* bears 25 (SRK 00.074) to 31 (SRK 00.059) tooth positions; this indicates an intraspecific variability concerning the tooth count. The modus of tooth replacement also varies within the available specimens of *M. perrotetii*. The replacement waves of SRK 00.059 are very regular with every 5th tooth showing the same status of tooth replacement. In contrast to this, the tooth replacement within the tooth row of SRK 00.074 is more irregular.

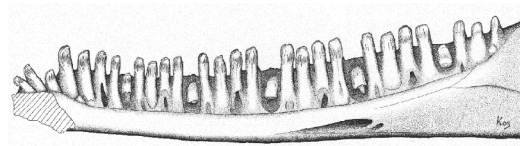


Fig. 81: *Mabuya perrotetii* (specimen SRK 00.059)
Right dentary, demonstrating regular tooth replacement throughout the tooth row; lingual view
Scale bar: 1.0 mm

Despite these differences in replacement patterns, the actual dental morphology is very constant within this species. The teeth are slender in shape and show transversally broadened tooth bases and tooth necks. The lata are flattened. The lingual surfaces of the tooth crowns are slightly concave. The crista mesialis is longer than the crista distalis. Both cristae include a 70° angle which represents the posterolingually directed cuspis labialis. Underneath the cuspis labialis, a cuspis lingualis is developed which is separated from the main cusp by a narrow antrum intercristatum. The labial enamel surfaces are smooth. At the lingual surfaces of the tooth crowns, up to ten parallel striae are developed. The striae are extended from the tooth necks to the immediate vicinity of of the cuspis lingualis. The ratio tooth length:diameter of tooth neck is 5.0:1.0. The resorption pits of *M. perrotetii* are dorsally elongated.

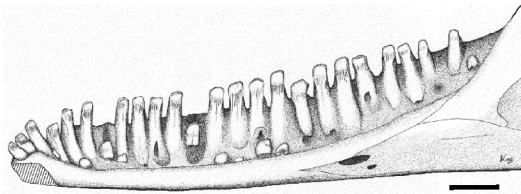


Fig. 82: *Mabuya perrotetii*
(specimen SRK 00.074)
Right dentary, demonstrating irregular tooth replacement throughout the tooth row; lingual view
Scale bar: 1.0 mm

Diet:

M. perrotetii is described as a voracious feeder (HAUSCHILD & GABNER 1995). The lizards consume diverse insects and pinky mice. Additionally, some individuals accept sweet fruits.

Mabuya quinquetaeniata (LICHTENSTEIN, 1823)

Number of examined specimens: 1 adult

Distribution:

Zimbabwe, Republic of South Africa (Natal, Transvaal lowveld, Swaziland), Angola, Zambia, Democratic Republic of the Congo (Zaire), Gabon, Equatorial Guinea, Cameroon, Mali, Central African Republic, Nigeria, Benin, Togo, Ghana, Ivory Coast, Liberia, Sierra Leone, Guinea, Guinea-Bissau, Senegal, Mauritania, Malawi, Niger, Chad, Algeria, Egypt, Eritrea, Ethiopia.

Dental morphology:

The right lower jaw of SRK 00.122 bears 24 tooth positions. The teeth of this West- and Central-African species are relatively robust and show transversally broadened bases. The tooth crowns are lingually curved inwards. The crista mesialis is longer than the crista distalis. The posterolingually directed cuspis labialis has an inner angle of 70°. Directly underneath this main cusp and separated from it by a narrow antrum intercristatum, the cuspis lingualis is developed although it is only slightly elevated. The cristae mesialis et distalis basally transform in a wide sinus into the prominent culmines lateres. Up to ten very pronounced striae are developed on the lingual surfaces of the tooth crowns whereas the labial surfaces are smooth. The ratio tooth length:diameter of the tooth neck is 3.2:1.0. The resorption pits of *M. quinquetaeniata* are circular or sometimes dorsally elongated.

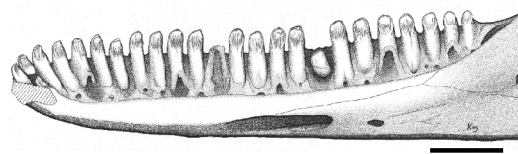


Fig. 83: *Mabuya quinquetaeniata*
(specimen SRK 00.122)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

M. quinquetaeniata is a hunter of spiders, earwigs, cockroaches, caterpillars, crickets, locusts, termites, flies, earthworms, and occasionally of smaller skinks (HAUSCHILD & GABNER 1995).

Mabuya striata (PETERS, 1844)

Number of examined specimens: 1 adult

Distribution:

Southern Africa and the Comoran Islands.

Dental morphology:

The dentary of *Mabuya striata* bears approximately 26 teeth, which are very poor in characters. The tooth bases are thickened and the tooth diameter becomes smaller in the apical direction. The apical third of the teeth towers above the labial wall of the dentary. The tooth necks are slender and cylindrical. The

tooth crowns are occlusally flattened. All surfaces are convex and smooth. The arrangement of teeth within the tooth row of SRK 00.202 is very unusual because the tooth pairs of tooth positions 12 and 13, as well as 15 and 16, show very narrowly spaced tooth bases although the teeth diverge V-like in the apical direction. It can not be determined whether this dental arrangement is pathological or characteristic for *M. striata* since only one specimen of this species was available. The ratio tooth length:diameter of tooth neck is 5.0:1.0. The resorption pits are circular in shape.

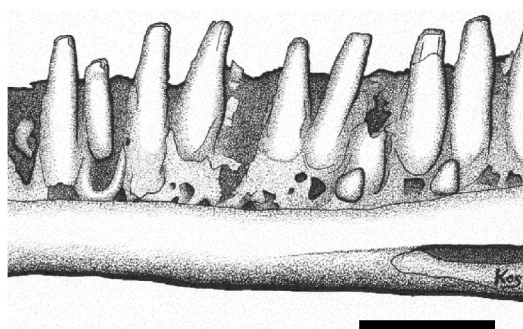


Fig. 84: *Mabuya striata* (specimen SRK 00.202)
Central portion of a right dentary (tooth positions 10-19 from 26); lingual view
Scale bar: 1.0 mm

Diet:

The diet of this species consists of insects and other small arthropods, plant matter, and carrion (AUERBACH 1985).

Mabuya vittata (OLIVIER, 1804)
(Pl. VII, Fig. 8)

Number of examined specimens: 2 adults

Distribution:

Turkey, Algeria, Tunisia, Egypt, Cyprus, Syria, Israel, Lebanon, Jordan, Iraq, Iran.

Dental morphology:

The teeth of *Mabuya vittata* are very slender and conical. Tooth bases and tooth necks are cylindrical in this species. The lingual surfaces of the apices are concave shaped between the prominent culmines lateres. The cristae mesialis et distalis are the same length and form a pointed, lingually recurved cuspis labialis. Underneath this main cusp, a small cuspis lingualis is developed whose

apical ending forms a small plateau running to the antrum intercristatum. This plateau resembles a structure which was described above in *Lipinia noctua*. The labial surfaces of the teeth are smooth. Isolated striae are developed on the lingual surfaces of several teeth. These striae are restricted to the area between the culmines lateres; they are short and only hardly protruding.

Diet:

No data about the dietary spectrum of this species are available. Like most *Mabuya* species, *M. vittata* probably is an opportunistic insectivore.

Mabuya wrightii BOULENGER, 1887
(Pl. VII, Fig. 9)

Number of examined specimens: 1 adult

Distribution:

Seychelles.

Dental morphology:

The tooth bases of *Mabuya wrightii* are very much broadened transversally. The surfaces of the labia are flattened or concave. The apical third of the teeth rises above the labial wall of the dentary. The tooth crowns distinctly contrast with the tooth necks and are flattened lingually. The cristae mesialis et distalis are the same length and build up a rounded cuspis labialis. A relatively long crista lingualis anterior runs parallel to the crista mesialis; at its point of intersection with the shorter crista lingualis posterior, the well defined cuspis lingualis is formed. Between the two systems of cutting edges, a relatively wide antrum intercristatum is developed. The culmines lateres are straight and short so that they hardly reach the tooth necks. All labial enamel surfaces are smooth. Up to eight morphologically quite prominent striae are developed at the lingual surfaces of the tooth crowns. The striae run parallel to each other and stretch from the transition zone between the tooth necks and the tooth crowns to the immediate vicinity of the cuspis lingualis. The ratio tooth length:diameter of tooth neck is 3.2:1.0. The resorption pits are shaped circularly.

Diet:

M. wrightii, which is endemic to the Seychelles, is specialized in its feeding habits. The skink consumes the eggs of the sea swallows, in whose colonies it predominantly settles (VESEY-FITZGERALD 1947). *M. wrightii*

presses the eggs out of the nests with its body so that the eggs roll against rocks and break (HENKEL & SCHMIDT 1995); the spilt contents are then consumed. Sometimes several lizards share one egg. Apart from that, *M. wrightii* preys on the freshly hatched chicks of the sea swallows (SCHAUENBERG 1978). During the breeding season of the birds, awards for killed skinks were paid by the government.

***Macrosцинus* BOCAGE, 1873**

***Macrosцинus coctei* DUMÉRIL & BIBRON, 1837**

Number of examined specimens: 1 adult

Distribution:

Raso and Branco (Cape Verde).

Dental morphology:

The right dentary of the single examined specimen of *Macrosцинus coctei* from University College London bears 24 tooth positions. The specimen originated from the Cape Verde Island Branco. The teeth are slender and show transversally broadened tooth necks. The lata are flattened or concave. The tooth bases are slightly bulbous. The multicuspoid tooth crowns are mesially widened and distinctly contrast with the tooth necks. There is a maximum of seven cusps in a tooth; these cusps diverge fan-like in the apical direction and are arranged in a mesial row. Within this row, the central cusp is generally the largest one. A tooth with 11 cusps was formerly illustrated by GREER (1975: p.696). Probably this specimen was older than the examined specimen from UCL. The enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 6.5:1.0. The resorption pits are dorsally elongated.

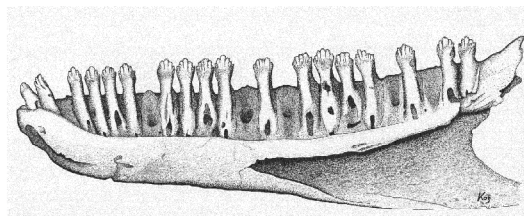


Fig. 85: *Macrosцинus coctei*
(non cataloged subrecent specimen from Branco;
UCL (London))
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The subrecent Cape Verde prehensile tailed skink *M. coctei* was often dealt with as exclusively vegetarian. Actually, the lizards thrived very well in captivity on an exclusively herbivore diet. In addition, a specimen of *M. coctei* consumed fruits, which makes a partially frugivore diet in their natural environment plausible. Observations in the wild in 1875 proved that in addition to mallow seeds, the eggs of sea-birds, and in one case a still living petrel, were also eaten (GREER 1975). Local fishermen also reported that *M. coctei* consumes eggs as well as chicks of sea birds. Despite this, it is probable that animal food sources account for a minor percentage of the total food intake since eggs and juvenile birds were available on the Cape Verde Islands only during certain seasons of the year.

Remarks:

M. coctei probably was not driven to extinction by anthropogenic influences until the 20th century. This crepuscular and nocturnal species was endemic to the small islands Raso and Branco (Cape Verde).

M. coctei was spread on arid islands, which were inhabited by plants with a solid cuticula. The serrations of the teeth were used for chopping up the resistant plant matter as a preliminary stage of the chemical break down of its ingredients during the process of digestion.

***Mochlus* GÜNTHER, 1864**

***Mochlus fernandi* (BURTON, 1836)**
(Pl. VII, Fig. 10)

Number of examined specimens: 1 adult

Remark:

Specimen BMNH 88.829.-3 was cataloged under the synonym *Riopa fernandi*.

Distribution:

Guinea, Ivory Coast, Ghana, Togo, Benin, Nigeria, Cameroon, Central African Republic, Democratic Republic of the Congo (Zaire), Angola, Uganda, Gabon, Sierra Leone, Burundi, Rwanda, Kenya.

Dental morphology:

The right dentary of the forest dwelling *Mochlus fernandi* (BMNH 88.829.-3) bears 25 tooth positions. The teeth are compressed laterally and broadened transversally. The lingual surfaces of the tooth crowns are distinctly concave. The crista mesialis is

slightly longer than the crista distalis. Both cutting edges are situated approximately horizontal and form the posterolingually directed cuspis labialis. Characteristic for *M. fernandi* are the far extended anguli mesialis et distalis. These are the origins of the culmen lateris anterior, which is connected via a sweeping sinus with the angulus mesialis, and the culmen lateris posterior, which runs relatively straight to the tooth basis. Both culmines lateres are distinctly pronounced. Underneath the cuspis labialis, a protruding cuspis lingualis is developed whose accessory cutting edges run parallel to the cristae mesialis et distalis. The antrum intercristatum, which separates the two cusps, is narrow and only slightly concave in younger teeth; in older teeth, the antrum becomes wide and deep as a result of wear so that the dentine finally becomes visible. The entire lingual surfaces of the tooth crowns are coated by long and very prominent striae. These striae run parallel and stretch apically to the immediate vicinity of the cristae linguales anterior et posterior. A maximum of 14 striae can be developed in a single tooth. The labial enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 2.7:1.0 in *M. fernandi*.

Diet:

In captivity *M. fernandi* consumes crickets, slugs, earthworms, mealbeetle larvae, and strips of meat and fish (ROGNER 1994).

Remarks:

M. fernandi is a forest dweller and digs deep burrows into the moist forest floor. This behavior is ecologically convergent to *Sphenomorphus muelleri*, which differs significantly from *M. fernandi* in terms of dental morphology.

***Mochlus sundevalli* (SMITH, 1849)**

(Pl. VII, Figs. 11-12)

Number of examined specimens: 1 adult

Remark:

The only available specimen of this species, AMNH 40723, was cataloged under the synonym *Lygosoma s. sundevalli*.

Distribution:

Namibia, Botswana, Zimbabwe, Republic of South Africa, Swaziland, Mozambique, Angola, Democratic Republic of the Congo (Zairc), Zambia, Malawi, Tanzania, Kenya, Somalia, Ethiopia.

Dental morphology:

The teeth of the quadruped African burrowing skink *Mochlus sundevalli* are cylindrical and their apical thirds tower above the labial wall of the dentary. The tooth crowns show slightly concave lingual surfaces. The crista mesialis is 30% longer than the crista distalis. At their point of intersection, these two cutting edges form the relatively pointed cuspis lingualis, whereas in basal direction the cutting edges transfer into the culmines lateres. In the transition zone between the crista mesialis and the culmen lateris anterior, a distinct sinus is developed. In contrast, the crista distalis drops steeply and transfers fluently into the culmen lateris posterior. Underneath the cuspis labialis, an elevated cuspis lingualis is developed. Between the cuspides linguales and the antra intercristata of the central and posterior teeth, there are extensive plateaus visible which resemble the structures formerly described in this thesis for *Lipinia noctua*. On the lingual apical surfaces of *M. sundevalli* very prominent striae are developed which run parallel to each other and converge only slightly in apical direction. The number of these striae is relatively constant and is up to six in most teeth. The anterior teeth (up to tooth position 3) are unicuspid. All labial enamel surfaces are smooth. The relation of the tooth length to the diameter of the tooth neck is 2.9:1.0.

Diet:

The prey of *M. sundevalli* consists of small insects. Termites and beetle larvae which are caught subterraneous are preferred by this burrowing skink (AUERBACH 1985). But additional crickets, caterpillars, sowbugs, slugs, and snails are also consumed (PATTERSON 1997).

Remarks:

BROADLEY (1966) worked very extensively on the systematics of this species, which shifted continuously between the genera *Lygosoma*, *Mochlus* and *Riopa*.

***Morethia* GRAY, 1845**

***Morethia obscura* STORR, 1973**

Number of examined specimens: 1 adult

Distribution:

Australia; New South Wales, South Australia, Victoria, West Australia.

Dental morphology:

The right dentary of *Morethia obscura* (SRK 00.190) from Australia bears 23 tooth positions. The teeth are pin-shaped and cylindrical. The tooth crowns are relatively pointed and lingually only slightly flattened. The tooth crowns are posterolingually directed as a result of an apical torsion. The cristae mesialis et distalis are approximately the same length and form the pointed cuspis labialis. The tooth tip is only blunt in the posteriormost teeth. Parallel to the cristae mesialis et distalis at the inner surface of the tooth crown the cristae linguales anterior et posterior are running. These lingual cutting edges construct the only slightly pronounced cuspis lingualis. Between both systems of cutting edges, the narrow but deep antrum intercrisatum is notched. The labial enamel surfaces are smooth. Striations are restricted to few teeth in the symphyseal region. These striae are developed at the lingual surfaces of the tooth crowns and even there they are very weak. A maximum of three short and parallelly arranged striae per tooth is recognizable. The ratio tooth length:diameter of tooth neck is 4.4:1.0 in *M. obscura*. The resorption pits are circularly shaped.

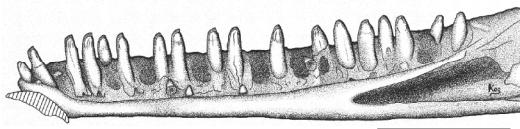


Fig. 86: *Morethia obscura*
(specimen SRK 00.190)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

M. obscura preys on small invertebrates (probably termites and other small insects). The skinks are active on the ground surface and inhabit semiarid areas with heavy litter layers (HUTCHINSON, pers. comm.).

***Panaspis* COPE, 1868**

***Panaspis africana* (GRAY, 1845)**
(Pl. VII, Fig. 13)

Number of examined specimens: 1 adult

Distribution:

Principe, Rolas, Sao Tome (Gulf of Guinea, western Africa).

Dental morphology:

Panaspis africana bears approximately 24 tooth positions in each jaw ramus. The relatively short teeth of this *Ablepharus*-like skink are cylindrical and show roughly conical apices. The cristae mesialis et distalis are scarcely prominent and form a blunt cuspis labialis. In the basal direction, the cristae transform into the very short culmines lateres. The lingual ace is slightly concave underneath the cuspis labialis. Because of its position, this extensive inward curvature can be identified as a distinctly restructured and widened antrum intercrisatum. This assumption is proven by the development of a convex step-like structure in the transition zone between tooth crown and tooth neck which represents the modified cuspis lingualis. All enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 2.9:1.0. The resorption pits are circular in shape.

Diet:

No data about the dietary spectrum of *P. africana* are available. Probably the small agile skink preys upon small arthropods.

***Pseudemoia* FUHN, 1967**

***Pseudemoia entrecasteauxii* (DUMÉRIL & BIBRON, 1839)**

Number of examined specimens: 1 adult

Distribution:

Australia; New South Wales, South Australia, Tasmania, Victoria.

Dental morphology :

The right mandible of specimen SRK 00.254 bears 24 tooth positions. The teeth are very slender, cylindrical, and directed to the anterior. The apical third of the teeth towers above the labial wall of the dentary. The tooth crowns are lingually slightly concave-shaped. The cristae mesialis et distalis are the same length and form a cuspis labialis which is directed posterolingually as a result of the torsion of the entire tooth crown. With an inner

angle of 50-60°, the cuspis labialis of *Pseudemoia entrecasteauxii* appears relatively pointed. The crista lingualis anterior runs parallel to the crista mesialis, while a short crista lingualis posterior is developed parallel to the crista distalis. The cuspis lingualis is only slightly elevated and the antrum intercrisatum is narrow. *P. entrecasteauxii* shows isolated striae on the lingual surfaces of the tooth crowns. These striae are fine and irregular. A maximum of three striae per tooth can be counted. The ratio tooth length:diameter of tooth neck is 5.0:1.0. The resorption pits are circular. Replacement teeth are developed on the basis of each tooth, suggesting extraordinary fast replacement waves in this species.

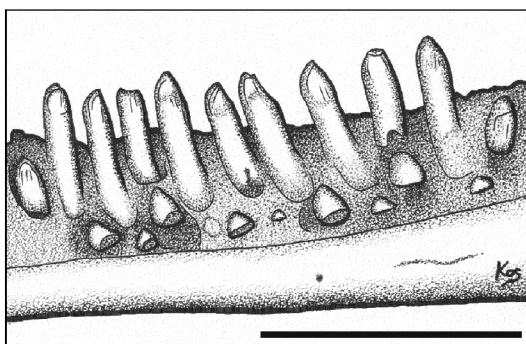


Fig. 87: *Pseudemoia entrecasteauxii* (specimen SRK 00.254) Central portion of a right dentary (tooth positions 10-18 from 24); lingual view Scale bar: 1.0 mm

Diet:

No data about the feeding habits of *P. entrecasteauxii* are available. The skinks are active on the ground surface in grassland and grassy woodland in cool temperate habitats (HUTCHINSON, pers. comm.).

***Saiphos* GRAY, 1831**

***Saiphos equalis* (GRAY, 1825)**

Number of examined specimens: 2 adults

Distribution:

Australia; New South Wales, Queensland.

Dental morphology:

Specimen SRK 00.333 bears 22 tooth positions in the right dentary. The teeth of this Australian burrowing skink are very robust and blunt. The tooth necks and tooth bases are

cylindrical, while the tooth crowns are lingually slightly concave. The teeth appear rectangular in lingual view since the cutting edges are perfectly flattened (like in *Mochlus fernandi*). The crista mesialis is always longer than the crista distalis. The cuspis labialis is directed posterolingually. All teeth also show a horizontally running lingual cutting edge which forms an elevated cuspis lingualis. The antrum intercrisatum is deeply notched and more broadened in anterior teeth than in posterior teeth. The apical cutting edges of all teeth of the entire tooth row are in line. Striations are restricted to the lingual surfaces of the tooth crowns. The striae are fine and are absent in several teeth. In one tooth, there is a maximum of four striae developed. These striae run parallel and sometimes reach the lingual cutting edge. The ratio tooth length:diameter of tooth neck is 6.0:1.0. The resorption pits are shaped circularly or are dorsally elongated. In several tooth bases, fissures are visible which can stretch to the tooth necks. These fissures are interpreted as secondary shrinkage structures which arise from the drying process of the bone.

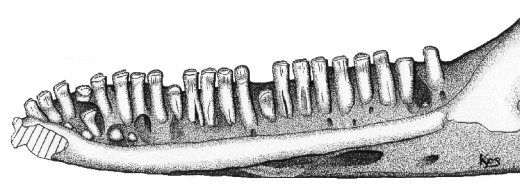


Fig. 88: *Saiphos equalis* (specimen SRK 00.333) Right dentary; lingual view Scale bar: 1.0 mm

Diet:

No data about the feeding habits of *S. equalis* are available. The skinks stay entirely under dense grass or in cracks and holes in the soil (HUTCHINSON, pers. comm.).

***Saproscincus* WELLS & WELLINGTON, 1984**

***Saproscincus mustelinus* (O'SHAUGHNESSY, 1874)**
(Pl. VII, Figs. 14-15)

Number of examined specimens: 1 adult

Distribution:

Australia; New South Wales, Victoria.

Dental morphology:

The teeth of the Australian *Saproscincus mustelinus* are strong and cylindrical. The surface of the lingual area of the tooth crown is flattened or concave. All labial enamel surfaces are smooth. The cristae mesialis and distalis are of equal length. The entire apex was rotated so that the tip of each tooth is directed posterolingually. The cuspis labialis is pointed. A second system of cutting edges is developed underneath the cuspis labialis. Those cutting edges, the cristae linguales anterior et posterior, stretch across the inwardly curved area of the inner tooth crown and form the cuspis lingualis, which is morphologically elevated. The crista lingualis anterior diverge from the crista mesialis and the crista lingualis posterior diverge from the crista distalis. A straight carina intercuspidalis runs from the cuspis lingualis to the cuspis labialis. In some teeth, only the crista lingualis posterior is present whereas there is no developed crista lingualis anterior. In this case, the crista lingualis posterior apically meets the cuspis labialis and the cuspis lingualis is absent. In *S. mustelinus*, a maximum of one stria per tooth can be present, but in most teeth even this stria is missing. The stria is straight and very protruding. It originates directly beyond the cuspis lingualis and reaches downward to the neck of the tooth. The ratio tooth length:diameter of tooth neck is 2.2:1.0. The resorption pits of the only available specimen are covered by mucosa.

Diet:

S. mustelinus shows cryptic habits, staying in cover during the day but it forages in the open on overcast days or warm evenings. *S. mustelinus* feeds on small invertebrates (HUTCHINSON, pers. comm.).

Scincella MITTLEMANN, 1950

Scincella lateralis (SAY, 1823)
(Pl. VII, Figs. 16-17)

Number of examined specimens: 2 adults

Distribution:

From New Jersey and Nebraska southwards through Florida and Texas to the Rio Grande.

Dental morphology:

The numerous homodont teeth of *Scincella lateralis* are of simple conical shape, with only the lingual surfaces of the tooth

crowns being slightly flattened. The tooth necks are long and slender. The apices are only slightly rotated in the posterior direction. The crista mesialis and the crista distalis are the same length and both form the relatively pointed cuspis labialis apically. The crista lingualis anterior is often longer than the crista lingualis posterior. These two cutting edges form the cuspis lingualis at the apical point of their intersection; it is always lower than the cuspis labialis. A deep and relatively wide antrum intercristatum runs mesially between the two cusps. All enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 3.5:1.0. The resorption pits are circularly shaped and relatively large.

Diet:

S. lateralis preys on diverse small sized-insects, spiders, and earthworms (HAUSCHILD & GABNER 1995). These lizards show cannibalistic tendencies by eating their younger conspecifics.

Remarks:

S. lateralis is the first scincid lizard with thoroughly described dentition (TOWNSEND et al. 1999). These authors observed no ontogenetic or sexual variation in tooth crown morphology; however, ontogenetic changes in tooth size and tooth number were noticed, with significantly more teeth in the dentaries of adults than in the dentaries of juveniles. In contrast to other lizards, in which tooth size increases with body size, and a reduction in tooth number occurs, the tooth number in the dentary of *S. lateralis* increases ontogenetically. An ontogenetic increasing of the tooth number was observed during research for this thesis in many taxa (e.g. *Corucia zebrata*).

Sphenomorphus FITZINGER, 1843

Sphenomorphus aignanus nomen dubium
(Pl. VII, Fig. 18)

Number of examined specimens: 1 adult

Remark:

The name *Sphenomorphus aignanus* is not valid, but because of the striking characters in the dentition of specimen BMNH 1946.8.15.48 and the uncertainty in grouping this specimen with another taxon, the name is maintained in this thesis.

Dental morphology:

Specimen BMNH 1946.8.15.48 bears 36 tooth positions in its right dentary. The teeth are extensively expanded transversally. The flanks are concave and the cross-sections show a narrowing in the lingual direction. The crista mesialis and the crista distalis are the same length and form a blunt cuspis labialis. Both cristae transform into the culmines lateres which approach in the basal direction. Striations are developed on the concave lingual surfaces of the tooth crowns. Two prominent main striae (the striae dominantes anterior et posterior) are developed as ridges which form the cuspis lingualis. This lingual cusp is strongly worn in most teeth, and therefore shaped in a plateau-like manner. Three to five additional striae are developed between the striae dominantes. These additional striae run parallel to one another on their entire length. They end apically before reaching the cuspis lingualis. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits are circular.

Diet:

Due to the uncertain systematic status of BMNH 1946.8.15.48, the feeding habits of this specimen are not properly known.

Sphenomorphus dussumieri (DUMÉRIL & BIBRON, 1839)

(Pl. VII, Fig. 19)

Number of examined specimens: 1 adult

Distribution:

Southwest India, Sri Lanka.

Dental morphology:

Specimen BMNH 1946.8.15.42 bears 29 tooth positions in the right dentary. The teeth of *Sphenomorphus dussumieri* are almost cylindrical with a slight transversal widening of the bases. At least the apical third of the tooth rises above the labial wall of the dentary. The lingual surfaces of the tooth crowns are slightly concave. The tooth crowns are posterolingually oriented. The crista mesialis and the crista distalis are the same length and form a cuspis labialis which in younger teeth appears relatively pointed; in older teeth, the tips are often worn and therefore blunt. A second cusp, the cuspis lingualis, is situated underneath the cuspis labialis. The cuspis lingualis is perfectly blunt in most teeth. Between the two cusps, the antrum intercristatum runs mesially. The antrum forms a wide sulcus in older teeth

whereas it is narrow in younger teeth. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.4:1.0. In specimen BMNH 1946.8.15.42, the resorption pits are covered by mucosa.

Diet:

No data on the diet of *S. dussumieri* are available.

Sphenomorphus indicus (GRAY, 1853)

(Pl. VII, Fig. 20)

Number of examined specimens: 2 adults

Remark:

Specimen AMNH 34884 is cataloged under the synonym *Sphenomorphus formosensis*.

Distribution:

China, Bhutan, Taiwan, Thailand, India east to Indochina and south to western Malaysia.

Dental morphology:

The right dentary of specimen BMNH 1965.1064 bears 29 conical teeth. The tooth crowns are lanceolate and flattened lingually. The teeth are extremely pointed, especially in specimen AMNH 34884. The tooth necks are slender and cylindrical. The tooth crowns of *Sphenomorphus indicus* are characterized by a complex morphology. The crista mesialis and the crista distalis are sinus-like; the former is slightly longer than the later. Both cristae meet at an angle of 70° and form the cuspis labialis. A second, more lingually situated system of cutting edges, comprised of the cristae linguales anterior et posterior, form the cuspis lingualis which is situated in a lower position than the cuspis labialis. Both cusps are recurved posterolingually and are separated from one another by a wide antrum intercristatum. The cristae mesialis et distalis transform into the prominent culmines lateres anterior et posterior basally. A maximum of eight striae are found on the flattened lingual surfaces between the cristae linguales; they are very pronounced and of irregular length. A converging of these striae cannot be observed, but isolated striae bifurcate in basal direction in rare cases. The teeth of the symphyseal region are free of striations up to the sixth tooth position. The ratio tooth length:diameter of tooth neck is 3.9:1.0. The resorption pits are of circular shape.

Diet:

No data about the diet of *S. indicus* are available. This species is probably insectivorous.

Sphenomorphus leptofasciatus GREER & PARKER, 1974

Number of examined specimens: 1 adult

Distribution:

Papua New Guinea.

Dental morphology:

The right mandible of specimen SRK 00.359 bears 24 tooth positions. The teeth of *S. leptofasciatus* are slender and cylindrical. The tooth crowns are conical and unicuspid in younger teeth, and blunt in older teeth as a result of intensive wear. The crista mesialis and the crista distalis are the same length. Apically these cutting edges meet at a 90° angle and form the tip of the cusp. In the basal direction, the two cristae transform into the well developed culmines lateres. Up to three striae are developed on the lingual surfaces of the tooth crowns. The striae converge apically. Older, and therefore worn teeth, show longitudinal scratches in the tooth enamel which extend over the tooth crowns and over the tooth necks as well. In younger teeth, the entire labial surfaces and the lingual surfaces of the tooth necks and tooth bases are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits are circular in shape.

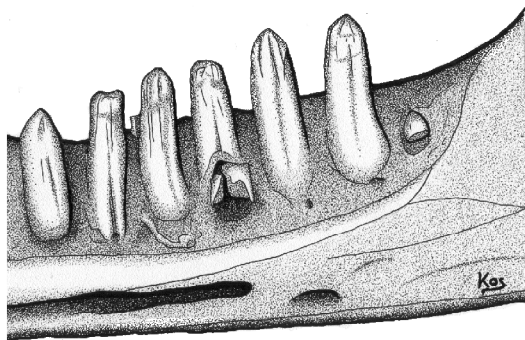


Fig. 89: *Sphenomorphus leptofasciatus* (specimen SRK 00.359) Posterior portion of a right dentary (tooth positions 18-24 from 24); lingual view
Scale bar: 1.0 mm

Diet:

No data about the diet of *S. leptofasciatus* are available.

Sphenomorphus muelleri (SCHLEGEL, 1834) (Pl. VII, Figs. 21-22)

Number of examined specimens: 2 adults

Remark:

Specimen BMNH 88.3.21.-5. was cataloged under the synonym *Lygosoma muelleri*.

Distribution:

Indonesia (Seram, Kai and Aru Islands, Irian Jaya, New Guinea).

Dental morphology:

The dental morphology of *Sphenomorphus muelleri* is unique among extant scincomorphans. Each dentary of this species bears up to 28 tooth positions. The teeth are very long, pointed, and unicuspid. The cross-sections of the teeth are circular at the tooth bases and the tooth necks while the tooth crowns are slightly flattened lingually. The teeth of the posterior third of the tooth row are less pointed than the anterior teeth. All teeth are recurvated in fang-like fashion; especially the apices are extraordinary elongated and curved.

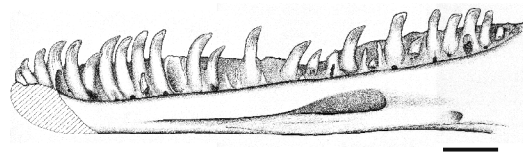


Fig. 90: *Sphenomorphus muelleri* (specimen SRK 00.034) Right dentary; lingual view
Scale bar: 1.0 mm

The cristae mesialis et distalis are the same length and transform over a wide sinus into the culmines lateres. Apically the cristae mesialis et distalis form the very pointed cusp which encloses at an angle of maximum 40°. Parallel to the cristae mesialis et distalis, two lingual cutting edges are found; these are the cristae linguales anterior et posterior. The cristae linguales are separated from the labial cutting edges by a deep antrum intercristatum and converge underneath the cusp without forming a cuspis lingualis. Most of the enamel surfaces are smooth, only very few teeth show fine striations at the lingual surfaces of the tooth crowns. The ratio tooth length:diameter of

tooth neck is 6.0:1.0. The resorption pits of *S. muelleri* are circular at the beginning of replacement and become dorsally elongated during further development.

Diet:

The diet of *S. muelleri* consists of ants, earthworms, and other benthic invertebrates. In captivity, *S. muelleri* accepts *Zophobas* and *Tenebrio* larvae but the skinks refused ants and desiccated coconut in the terrariums of HAUSCHILD & GABNER. *S. muelleri* is able to construct wide burrow-systems.

***Sphenomorphus scutatus* (PETERS, 1867)**

Number of examined specimens: 1 adult

Distribution:

Palau Islands.

Dental morphology:

The teeth of *Sphenomorphus scutatus* are cylindrical with conical tooth crowns. The tooth crowns rise above the labial parapet of the dentary. All teeth are bicuspid with the cusps being situated in a central position. The lingual surfaces of the tooth crowns are only slightly flattened. The crista mesialis and the crista distalis meet at an angle of 90°. The cuspis labialis rises above the cuspis lingualis. The two cusps are separated by the antrum intercristatum which forms a deep mesial sulcus. All enamel surfaces are smooth. The ratio of the tooth length to the diameter of the tooth neck is 3.0:1.0. The resorption pits of specimen USNM 507555 are covered by mucosa.

Diet:

No data on the diet of *S. scutatus* are available.

***Sphenomorphus solomonis* (BOULENGER, 1887)**

Number of examined specimens: 1 adult

Distribution:

Admiralty Islands, northern Moluccas, Solomon Islands, New Guinea, Bismarck Archipelago.

Dental morphology:

The right dentary of specimen SRK 00.357 bears 22 tooth positions. The dentition of *Sphenomorphus solomonis* has a tendency for heterodonty, with short teeth in the anterior portion of the tooth row and larger and more robust teeth in the posterior portion of the tooth

row. The teeth are cylindrical with expanded tooth bases in the enlarged posterior teeth. The tooth crowns are blunt in anterior teeth, while they are pointed in posterior teeth and show flattened lingual surfaces. The crista mesialis is slightly longer than the crista distalis in most teeth. These two cutting edges form the cuspis labialis apically, which shows an apical angle of approximately 130° in anterior and 80° in posterior teeth. In basal the direction, the cristae mesialis et distalis transfer into the prominent culmines lateres. Two lingual cutting edges are developed parallel to the cristae mesialis et distalis. These lingual cutting edges form the cuspis lingualis, which is separated from the main cusp by a well developed antrum intercristatum. In the posterior teeth, the antrum narrows and disappears apically, which leads to a melting of the two cusps so that the posterior teeth are mainly unicuspid. Striations are developed on the flattened surfaces of the anterior tooth crowns. In most teeth, four or five apically converging striae are developed. All labial surfaces and the lingual surfaces of the tooth necks and the tooth bases are unwrinkled. The surfaces of the crowns are almost smooth in posterior teeth. The ratio tooth length:diameter of tooth neck is 4.2:1.0 in the anterior teeth and is 5.0:1.0 in the posterior teeth. The resorption pits of *S. solomonis* are circular but become dorsally elongated during further replacement processes.

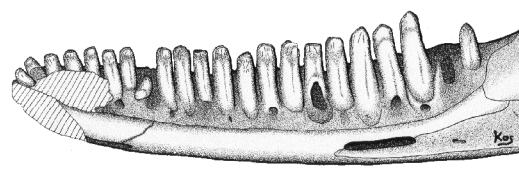


Fig. 91: *Sphenomorphus solomonis* (specimen SRK 00.357)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

S. solomonis feeds on small insects. The skink shows cryptic habits; it dwells within vegetation mats and the litter on the rainforest floor. *S. solomonis* is crepuscular and nocturnal (MCCOY 1980, HUTCHINSON, pers. comm.).

Sphenomorphus striatopunctatus

(BOULENGER, 1907)

(Pl. VIII, Fig. 1)

Number of examined specimens: 1 adult

Distribution:

Sri Lanka.

Dental morphology:

The teeth of *Sphenomorphus striatopunctatus* are slender with slightly transversally expanded cross-sections. Only the apical halves of the tooth crowns rise above the labial parapet of the dentary. The lingual surfaces of the bicuspid tooth crowns are distinctly concave in shape. The tips of the teeth are recurvated and posterolingually oriented. The crista mesialis is longer than the crista distalis and both cristae form the relatively pointed cuspis labialis at their point of intersection. Underneath the main cusp, a second cusp, the cuspis lingualis, is found. The antrum intercratum, which separates the two cusps, is a narrow sulcus running mesially. The cristae mesialis et distalis transform at the lateral sinus into the culmines lateres, which run in the basal direction. A maximum of eight striae are found on the concave lingual surfaces between the culmines lateres. The striae are modestly pronounced and reach the cutting edge associated with the cuspis lingualis. In the basal direction, the striae end at the transition zone between the concave apical surface and the convex lingual surface of the tooth neck. The ratio tooth length to diameter of tooth neck is 3.3:1.0.

Diet:

No data regarding the diet of *S. striatopunctatus* are available.

Sphenomorphus variegatus (PETERS, 1867)

(Pl. VIII, Fig. 2-7)

Number of examined specimens: 1 adult

Distribution:

Malaysia (Borneo), Philippines (Sulu Archipelago, Mindanao, Dinagat, Leyte, Bohol, Camiguin).

Dental morphology:

The teeth of *S. variegatus* are cylindrical and slender. The apical surfaces are lingually curved inwards. The cristae mesialis et distalis are the same length and form the pointed (50-60°) cuspis labialis. The cusp is directed posterolingually as the result of a distinct apical torsion. The cristae mesialis et

distalis transform from the form of a sinus into the culmines lateres, which stretch basally to the surface of the upper tooth neck. Underneath the cuspis labialis, an only slightly prominent cuspis lingualis is developed which is constructed by the short cristae linguales anterior et posterior. Mostly seven to nine prominent parallel striae are present at the concave inner surfaces of the tooth crowns. Hollow structures in the enamel of the labial and therefore oldest tooth row are visible under scanning electron microscopy (magnification: 800). These hollow cavelets are tunnel-like structures within the striae which run through for the entire length of the stria. If the outer enamel layer breaks off, perforations between these micro-tunnels and the outside become visible. These cavities surely represent age-dependent resorption symptoms. All labial surfaces are smooth. The ratio tooth length:diameter of tooth neck is 3.3:1.0. The resorption pits are circular.

Diet:

S. variegatus proved to be an opportunistic feeder in captivity. The species preys on all arthropods it is able to overpower. Adult crickets, *Acheta domestica*, were eaten by lizards with a snout-vent length of 7 cm.

Remarks:

The solely available specimen of *Sphenomorphus variegatus*, SRK 00.297, shows a pathological mode of tooth replacement which was described in this thesis for *Lygosoma afra* as "multiple replacement". The specimen lived in my stock for several years and reached a high individual age which probably is not reached under natural conditions because of the high pressure by predators in the wild. Obviously the parameters of tooth replacement change in very old specimens so that the mechanism of tooth replacement no longer functions. New replacement teeth are steadily developed while the older tooth generations have not fallen out. The result of this malfunction is the development of several parallel tooth rows, as seen in SRK 00.297.

Tiliqua GRAY, 1825

Tiliqua gigas (SCHNEIDER, 1801)
(Pl. VIII, Figs. 8-11)

Number of examined specimens: 5 adults, 1 neonate

Distribution:

New Guinea and surrounding islands (Kei Islands, Trobriand Islands, Admiralty Islands, Karkar Islands).

Dental morphology:

The right dentary of the neonate specimen SRK 00.065 bears 12 tooth positions whereas the right dentary of the adult specimen SRK 00.144 bears 17 tooth positions. Therefore, an ontogenetic increase in the number of tooth positions (including empty loci) in *Tiliqua gigas* must be assumed. The dentition of this species is extraordinarily heterodont. The morphology of the teeth in the neonate specimens (SRK 00.065 and ZFMK 14829) strongly resembles the dental morphology of the related *Hemisphaeriodon gerrardi*. The tooth row is dominated by an extraordinarily large crushing tooth, which is situated in the posterior part of the lower jaw (tooth position 10 in specimen SRK 00.065).

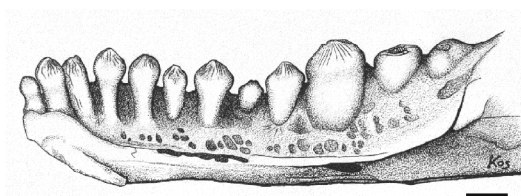


Fig. 92: *Tiliqua gigas*
(specimen SRK 00.065)
Right dentary of a neonate individual; lingual view
Scale bar: 1.0 mm

The more anterior teeth of the neonate specimen are mushroom-shaped with narrow tooth bases and tooth necks and broad tooth crowns. All teeth are circular in occlusal view. The tooth crowns of the neonate specimens are heavily striated with most intense striation in the barrel-shaped molariform tooth. Approximately 24 striae are developed on the lingual and labial surfaces of this crushing tooth. The tips of the anterior teeth of this specimen are rather pointed with an apical angle of 100°. The teeth which are situated posterior of the molariform tooth are cushion-like in shape. These teeth are very broad and short; they appear circular in occlusal view. A

central depression is developed apically. An uplift with a pointed cusp is situated in the center of this depression.

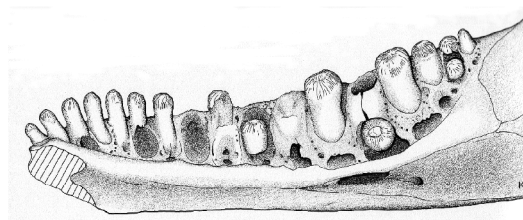


Fig. 93: *Tiliqua gigas*
(specimen SRK 00.144)
Right dentary; lingual view
Scale bar: 1.0 mm

In adult specimens like SRK 00.144, several (four of five) crushing teeth are developed in the posterior parts of the lower jaws. These bulbous barrel-shaped teeth resemble the single crushing tooth of the neonate specimen. The anterior teeth of adult *T. gigas* are robust and cylindrical. The molariform teeth show a depression in their occlusal surface. In the middle of this depression, a shallow uplift is noticeable. This convex structure represents the tooth cusp. Striations are developed on the lingual surfaces of the tooth crowns of anterior teeth and also on the lingual and labial surfaces of the tooth crowns of posterior teeth. These striations are radially arranged in occlusal view. In several teeth, two rudimentary cutting edges are running mesially; these are probably relicts of the cristae mesialis et distalis. Even if they are not pronounced, these striae serve as symmetric elements which separate lingual and labial systems of striations. Predominantly the striae of *T. gigas* do not run straight, but instead they undulate or zigzag. In the basal direction, bifurcations become a common feature, and lead to a branching of the systems of striations. The relationship of the tooth length to the diameter of the tooth neck is 3.8:1.0 in anterior teeth, 1.6:1.0 in crushing teeth, and 0.4:1.0 in the most posterior teeth. The resorption pits are circular in anterior teeth and horizontally elongated in posterior teeth. In the bony material of the interdental spaces, numerous foramina are developed which are arranged in lines and strongly resemble similar structures in the anguimorph *Ophisaurus apodus*. During the research phase of this thesis, comparable structures were observed in the scincid *Egernia kingii* and the cordylid *Cordylus giganteus*. These foramina probably

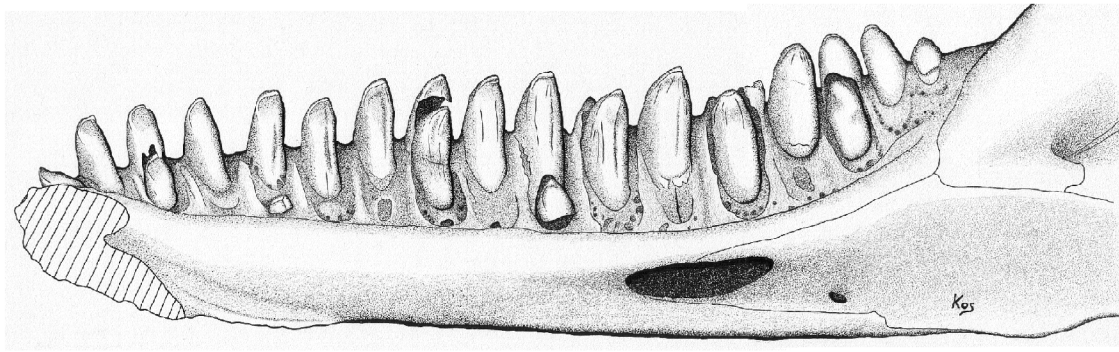


Fig. 94: *Tiliqua nigrolutea*
(specimen SRK 00.177)
Right dentary; lingual view
Scale bar: 1.0 mm

support the innervation and the blood circulation in extraordinarily large teeth.

Diet:

Wild living individuals of *T. gigas* consume large insects, small vertebrates, snails, worms, eggs, and sweet fruits. In captivity, comparable items are accepted; additionally the lizards eat mussels, *Mytilus edulis*, and dog food (HAUSCHILD et al. 2000). Captive specimens of the subspecies *T. gigas evanescens* SHEA, 2000 in both the author's and BROSCINSKI's vivaria consumed a great diversity of food items including raspberries, blueberries, leeches, redcurrant, blackcurrant, blackberries, strawberries, snails, crickets, *Tenebrio molitor* larvae (mealworms), cockroaches, and meat; snails seem to be the preferred food item. The large skinks crush the shells of the snails with their strong jaws and the durophagous posterior teeth. The soft parts of the snail are handled with the tongue and the more pointed anterior teeth, which are also used for grasping insects and berries. An adult male was observed shaking its prey to death (even if it was already immobile) on a regular basis (BROSCINSKI, pers. comm.). This individual even consumed eggs and cheese (which induced indigestion) as well as cookies.

Tiliqua nigrolutea (QUOY & GAIMARD, 1824)

Number of examined specimens: 2 adults

Distribution:

Southeastern Australia, from the Blue Mountains in the West of Sydney to the Snowy

Mountains. The lowland-form inhabits Victoria, Tasmania and South Australia. The western border of the radiation is Port Pirie.

Dental morphology:

The right dentary of specimen SRK 00.177 (Highland-form) bears 17 tooth positions. The dental morphology of *Tiliqua nigrolutea* differs all other examined species of the genus *Tiliqua*. The teeth are of conical shape and show pointed tips. The apical halves or even two-thirds of the teeth rise above the labial wall of the dentary. The lingual surfaces of the tooth crowns are slightly flattened. The tooth crowns are oriented posterolingually. The crista mesialis is longer than the crista distalis and together these two cutting edges enclose at an apical angle of 80° at the cuspis labialis. Underneath the cuspis labialis the cuspis lingualis is developed, separated from the former by the very narrow sulcus of the antrum intercristatum. The posterior teeth appear more robust than the anterior teeth, but no durophagous adaptations, as found in other *Tiliqua* species, are developed in *T. nigrolutea*. The enamel surfaces are unwrinkled, and isolated striae are only rarely found. The ratio tooth length:diameter of tooth neck is 3.3:1.0. The resorption pits are circular. Numerous minute foramina are situated in the bony material around the resorption pits.

Diet:

T. nigrolutea is the only montanous species of the genus *Tiliqua*. These unusual bluetongue skinks are well adapted to montanous habitats characterized by low temperatures and humid climatic conditions.

The food spectrum of *T. nigrolutea* is also adapted to this extraordinary alpine habitat and consists of snails, slugs, insects (predominantly beetles, cicadas, and caterpillars), spiders, leaves, flowers, and fruits. Small-sized vertebrates like smaller skinks are also preyed on (HAUSCHILD et al. 2000). In addition to the former mentioned items, stomach content analyses of fresh road kills of this species also found mushrooms, grass, and seeds (WEBB & SIMPSON 1985). In the summer, *T. nigrolutea* consumes vast numbers of christmas beetles, *Anaplognathus*. By examining the stomach contents of a specimen of *T. nigrolutea* in 1836, Charles DARWIN was one of the first biologists to note that blue-tongue skinks are partly herbivorous (SHINE & HUTCHINSON 1991). A diet consisting of soft items like slugs and plant matter is well compatible with the unique dental morphology of *T. nigrolutea* from a functional morphological point of view. The pointed teeth are very useful in grasping and penetrating the soft bodies of slugs or caterpillars which are living in the cool and often humid habitat of this skink, whereas a durophagous dentition, which is important for the shell-crushing *Tiliqua* species of arid habitats, is not needed by the alpine *T. nigrolutea*.

***Tiliqua occipitalis* (PETERS, 1864)**

Number of examined specimens: 1 adult

Distribution:

Arid areas of South Australia, southern part of Western Australia to Carnarvon, southern part of the Northern Territory, western part of New South Wales, and the northwestern part of Victoria.

Dental morphology:

The right dentary of specimen SRK 00.248 bears 18 tooth positions. *Tiliqua occipitalis* shows a durophagous dentition. The teeth are very robust and barrel-shaped. The tooth crowns rise above the labial wall of the dentary. The cross-sections of the teeth are circular. The adaptational degree to durophagy is comparable to most other examined species of this genus (e.g. *Tiliqua gigas*, *Tiliqua rugosa*, *Tiliqua scincoides*). The crushing teeth are situated in posterior positions, while the anterior teeth are more slender and cylindrical. The tooth crowns are blunt in posterior teeth. In the anterior teeth, a centrally situated cuspis labialis is prominent, and is separated from a

low cuspis lingualis by a rudimentary mesial antrum intercristatum. Striations are developed on the lingual surfaces of the tooth crowns in anterior teeth. In the tooth crowns of posterior teeth, all enamel surfaces are wrinkled so that more than 50 prominent striae can be developed together on lingual and labial surfaces. These striae are radially orientated and meet at the tip of the tooth. The tooth necks are unwrinkled. In older teeth, the wrinkled enamel layer is badly worn, leading to a smooth appearance of their surfaces. Striations are already developed in replacement teeth which have not yet been used. The ratio tooth length:diameter of tooth neck is 1.9:1.0. The resorption pits are circularly shaped. As in *Tiliqua gigas*, numerous minute foramina are situated in the bony material around the resorption pits.

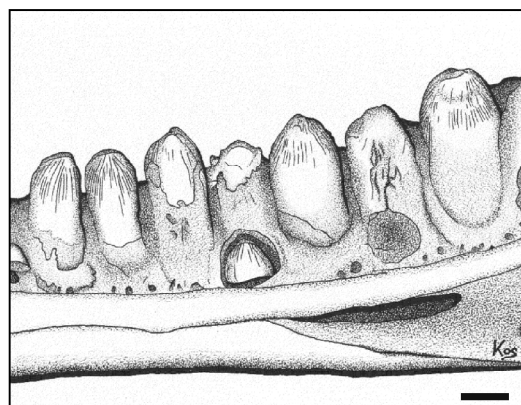


Fig. 95: *Tiliqua occipitalis* (specimen SRK 00.248) Central portion of a right dentary (tooth positions 9-15 from 18); lingual view Scale bar: 1.0 mm

Diet:

Captive specimens of *T. occipitalis* consume large cockroaches, locusts, snails, pinky mice, and sweet fruits (HAUSCHILD & GABNER 1995); green vegetables are neglected.

***Tiliqua rugosa* (GRAY, 1825)**

(Pl. VIII, Figs. 12-15)

Number of examined specimens: 10 adults, 1 embryo

Remark:

Most of the examined specimens are cataloged under the older synonym *Trachydosaurus rugosus*. Four subspecies are known.

Distribution:

The four subspecies are spread over southern Australia and Rottcnst Island.

Dental morphology:

The tooth number of the jaw rami is very low in the sleepy lizard, *Tiliqua rugosa*. The right dentary of the adult specimen SRK 00.232 bears 13 tooth positions. The durophagous dentition of *T. rugosa* corresponds to the generalized *Tiliqua* bauplan. As a result of the heterodonty, the anterior teeth are cylindrical with lingually slightly flattened tooth crowns whereas the posterior teeth are barrel-shaped molariforms. The apical angle of the conical tooth crowns is 80°, but often the teeth are blunt as a result of intensive wear. Especially in anterior teeth, a complex tooth crown morphology is common. In this case, the prominent cristae mesialis et distalis form the cuspis labialis, which is recurved in the lingual direction. Underneath the cuspis labialis and separated from it by the sulcus of the antrum intercristatum, a cuspis lingualis is developed in several anterior teeth. This second cusp is lower than the cuspis labialis and the corresponding cutting edges are shorter than the cristae mesialis et distalis. Striations are developed on lingual surfaces as well as on labial surfaces throughout all teeth of the tooth row. The striations are restricted to the tooth crowns and are radially oriented to the main cusp. The majority of the striae is very pronounced and develop a tendency for bifurcation in the basal direction. More than 80 striae per tooth can be counted. None of these striae cross the transition zone between tooth crown and tooth bases. The ratio tooth length:diameter of tooth neck is 1.8:1.0 in the posterior crushing teeth. The resorption pits are circular in shape. A large number of minute foramina are situated in the dentary close to the tooth bases; due to their irregular arrangement, these structures are probably the results of reabsorption processes here.

The patterns of striations are already fully developed in specimen SDS 68064, which is an embryo of the examined specimen SDS 68063 from San Diego Zoo. The posterior teeth of the embryo are very pointed with apical angles of 70° since they were never worn. For the same reason, the striations are also distinctly pronounced in the embryonal specimen.

The observation that the successive tooth arises behind the predecessor (VOROBYEVA & CHUGUNOVA 1991) cannot be corroborated here. The examined specimen show the typical

iguanid pattern of replacement with the replacement pits being situated directly underneath the tooth bases.

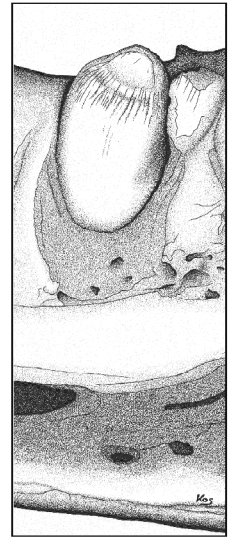


Fig. 96: *Tiliqua rugosa* (specimen SRK 00.232) Crushing tooth from the posterior portion of a right dentary (tooth position 11 from 13); lingual view
Scale bar: 1.0 mm

Diet:

T. rugosa is predominantly herbivorous. The diet consists of flowers, berries, seedlings, and fruits. Additionally these skinks prey on insects, snails (*Theba pisana*), and small vertebrates (small skinks of other genera and juvenile birds). Fecal pellets of wild specimens showed 92 % plant matter (HAUSCHILD & GABNER 1995). A great percentage of the consumed plant matter is made up by the yellow and green berries of *Enchylaena tomentosa* and *Brassica tournefortii*. Diverse herbs like the poisonous *Solanum nigrum* are also accepted by *T. rugosa* (HAUSCHILD et al. 2000). Occasional sleepy lizards consume carrion (e.g. road kills). The percentage of plant matter in the diet of *T. rugosa* increases with increasing individual age.

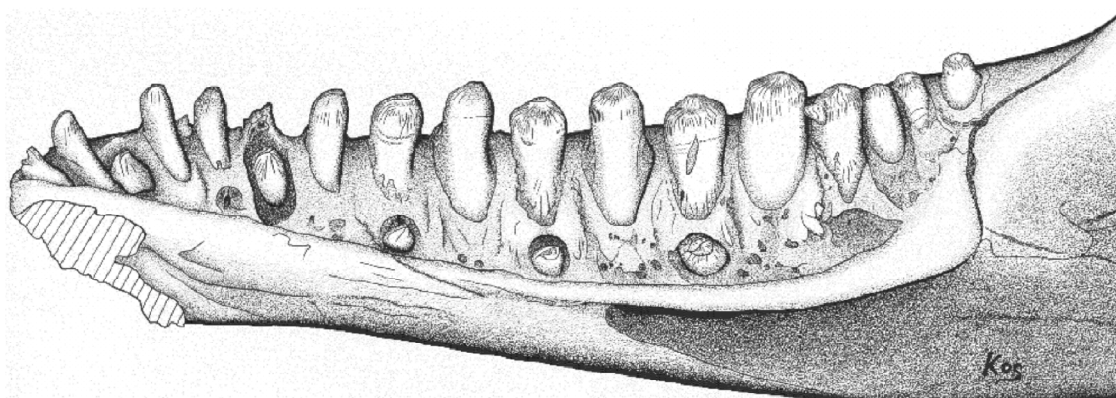


Fig. 97: *Tiliqua s. scincoides*
(specimen SRK 00.231)
Right dentary; lingual view
Scale bar: 1.0 mm

Tiliqua scincoides (WHITE, 1790)
(Pl. VIII, Fig. 16; Pl. IX, Figs. 1-2)

Number of examined specimens: 3 adults

Distribution:

The three subspecies of *Tiliqua scincoides* are spread over eastern (*T. s. scincoides*) and northern Australia (*T. s. intermedia*) and the Tanimbar Islands (*T. s. chimaerea*).

Dental morphology:

The dentition of *Tiliqua scincoides* strongly resembles the dentition of *Tiliqua rugosa*. This is not surprising since the two species are able to interbreed in captivity (the hybrids are reproductive; however, the following generation is hardly capable of surviving). The right dentary of specimen SRK 00.231 bears 17 tooth positions. The dentition is heterodont with more slender cylindrical teeth in the symphyseal region and molariform crushing teeth in the posterior portion of the tooth row.

The cross-sections of the anterior teeth are transversally broadened. The teeth of tooth positions 1 to 7 show lingually flattened or concave apical surfaces. The tips of these teeth are recurved in the posterolingual direction and are bicuspid with a relatively pointed cuspis labialis and a lower cuspis lingualis; both are separated by the very narrow sulcus of the antrum intercristatum. Pronounced striations of the anterior teeth are restricted to the concave lingual surfaces of the tooth crowns. The isolated striae run to the cuspis lingualis. All

labial surfaces of the anterior teeth show very weak striae or are unwrinkled.

The posterior teeth of *T. scincoides* are modified as crushing teeth and therefore differ from the anterior teeth in terms of size, shape, and enamel striations. The habitus of the very large crushing teeth is quite robust and bulbous. The tooth crowns are mushroom-shaped with very blunt cusps. Often an occlusal depression with a central uplift of the cusp is developed. Striations are found on lingual surfaces as well as on labial surfaces, but are restricted to the tooth crowns. More than 40 prominent striae per tooth are developed. The striae are oriented radially with the cusp being the central point. In the basal direction, the majority of the striae bifurcate, but they end abruptly at the transition zone between the tooth crown and the tooth neck. The ratio tooth length:diameter of tooth neck is 2.0:1.0 in posterior teeth and 3.7:1.0 in anterior teeth. The resorption pits are circular and surrounded by foramina which are situated in the dentary bone close to the tooth bases.

Diet:

The natural diet of *T. scincoides* consists of berries, snails, flowers, fruits, large insects, small vertebrates, and carrion (HAUSCHILD & GABNER 1995).

Tribolonotus DUMERIL & BIBRON, 1839

Tribolonotus gracilis DE ROOIJ, 1909

Number of examined specimens: 1 adult

Distribution:

Papua New Guinea, Admiralty Islands.

Dental morphology:

The right dentary of specimen SRK 00.139 bears 21 tooth positions. The teeth are robust and chisel-shaped. More than the apical halves of the teeth rise above the labial wall of the dentary. In lingual view, the outlines of the teeth appear rectangular since the angulus mesialis and the angulus distalis are very pronounced. In cross-sections, the transversal widening of the teeth is visible. The lingual surfaces of the tooth crowns are slightly concave in anterior teeth. The flanks are inwardly curved. The occlusal cutting edges run horizontally. A labial cutting edge runs straight from the angulus mesialis to the angulus distalis and is accompanied by a lingual cutting edge situated parallel and in a lower position. The two cutting edges are separated by the narrow sulcus of the antrum intercristatum. Pointed cusps are not developed in *Tribolonotus gracilis*. Isolated striae are developed on the flattened lingual surfaces of the tooth crowns in several anterior teeth. All other enamel surfaces are smooth. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits are circular or slightly elongated dorsally.

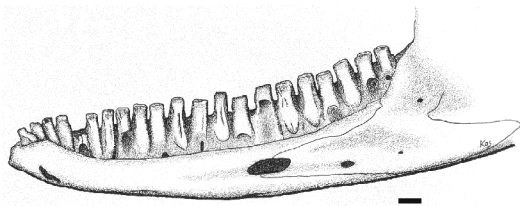


Fig. 98: *Tribolonotus gracilis*
(specimen SRK 00.139)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

In captivity, individuals of this species consume locusts, house crickets, slugs, and earthworms (CHARLIER 1999). Since *T. gracilis* is dwelling preferentially in moist rain forests, a diet consisting of soft-bodied invertebrates like insect larvae, slugs, and worms is plausible.

Tribolonotus novaeguineae (SCHLEGEL, 1834)
(Pl. IX, Fig. 3)

Number of examined specimens: 2 adults

Distribution:

Indonesia (Irian Jaya).

Dental morphology:

The right dentary of specimen BMNH 1905.11.29.10 bears 21 tooth positions. The dental morphology of *Tribolonotus novaeguineae* strongly resembles the dental morphology of *Tribolonotus gracilis*, described above. Likewise, no striations are found in this species. The occlusal cutting edges of tooth number 19 in specimen BMNH 1905.11.29.10 do not run horizontally, but rather concave in their central portion.

Diet:

Captive specimens consume crickets. The diet of wild living individuals is not known.

Tropidophorus DUMÉRIL & BIBRON, 1839

Tropidophorus beccarii PETERS, 1871
(Pl. IX, Figs. 4-5)

Number of examined specimens: 1 adult

Distribution:

Borneo.

Dental morphology:

The slender teeth of the semiaquatic water skink *Tropidophorus beccarii* are transversally broadened in their basal portions. The lingual surfaces of the tooth crowns are concave shaped whereas all labial surfaces are convex. The tooth tips are narrow and posterolingually oriented. The crista mesialis is longer than the crista distalis. These two cutting edges form a relatively pointed cuspis labialis. Underneath this labial cusp, a lower plateau-like cuspis lingualis is situated. The antrum intercristatum is well developed. The cristae mesialis et distalis transform into the short but prominent culmines lateres in the basal direction. The cusps of several teeth are worn so that the line between dentine and tooth enamel becomes visible. The tooth enamel is the same thickness lingually and labially. Striations are not to be found in *T. beccarii*. The ratio tooth length:diameter of tooth neck is 2.8:1.0. The resorption pits are circular and contain extremely pointed replacement teeth.

Diet:

T. beccarii inhabits the banks of forest creeks. These skinks often escape into the water. Presumably, *T. beccarii* preys on water insects and their larvae. Adult individuals show cannibalistic tendencies towards juveniles (MANTHEY & GROSSMANN 1997).

***Tropidophorus brookei* (GRAY, 1845)**

Number of examined specimens: 1 adult

Distribution:

Borneo.

Dental morphology:

The right dentary of specimen BMNH 1900.1.23.15 bears 30 tooth positions. The tooth morphology of *Tropidophorus brookei* is similar to the tooth morphology of the closely related *Tropidophorus beccarii* (above described) in all aspects.

Diet:

The dietary spectrum of *T. brookei* is assumed to be comparable to the dietary spectrum of *T. beccarii*.

***Tropidophorus grayi* GÜNTHER, 1861**

Number of examined specimens: 2 adults

Distribution:

Philippines, excluding the Palawan and Sulawesi regions.

Dental morphology:

The right dentary of specimen SRK 00.052 bears 26 tooth positions. The teeth strongly resemble the teeth of other examined *Tropidophorus* species under the aspects of general tooth morphology. A light heterodonty is developed in *Tropidophorus grayi* with the anterior teeth being more slender than the posterior teeth. The apical third of the tooth rises above the labial wall of the dentary. The tooth bases and the tooth necks are slightly broadened transversally. Therefore the teeth are flattened. The lingual surfaces of the tooth crowns are concave especially in the anterior teeth. The tooth crowns are oriented in the posterolingual direction. The crista mesialis is little longer than the crista distalis. These two cutting edges form a moderately pointed cuspis labialis. Underneath this labial cusp and separated from it by a narrow antrum intercrisatum, the less pronounced cuspis lingualis is situated. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of

tooth neck is 6.0:1.0. Resorption pits are developed at the tooth bases of the majority of teeth. This feature leads to the assumption that tooth replacement takes place very frequently. The resorption pits are circular or dorsally elongated.

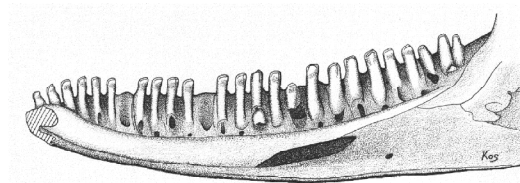


Fig. 99: *Tropidophorus grayi* (specimen SRK 00.052)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

T. grayi is bound to a humid environment. These skinks dwell in the immediate vicinity of the banks of rainforest creeks and their habitat is comparable to a moist salamander habitat. Water is absorbed through the skin (e.g. of a leg or the tail) which makes active drinking unnecessary. *T. grayi* is assumed to consume beetle larvae, earthworms, minute freshwater crustaceans, small snails, insects, and spiders (HAUSCHILD & GABNER 1995). Captive specimens accept *Zophobas* larvae, *Tenebrio* larvae, crickets, earthworms, and tadpoles. Additionally isopods are also accepted (EGGERS 1999).

***Tropidophorus herdmorei* (BLYTH, 1853)**
(Pl. IX, Figs. 6-7)

Number of examined specimens: 1 adult

Remark:

Specimen BMNH 1964.964 is cataloged under the older synonym *Tropidophorus yunnanensis*.

Distribution:

China (Yunnan), Burma, Thailand, Vietnam.

Dental morphology:

The teeth of *Tropidophorus herdmorei* strongly resemble the teeth of other examined *Tropidophorus* species. The teeth are slender and show slightly transversally broadened tooth bases. The tooth crowns are posterolingually oriented. The lingual surfaces of the tooth crowns are inwardly curved. The crista mesialis is longer than the crista distalis and together,

these two cutting edges form the moderately pointed cuspis labialis. In the basal direction, the cristae mesialis et distalis transform into the sinus-shaped culmines lateres anterior et posterior. A lingual system of cutting edges runs parallel to the cristae mesialis et distalis and forms the low cuspis lingualis which is situated underneath the cuspis labialis. Between these two cusps, the relatively wide sulcus of the antrum intercristatum is found. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 5.0:1.0. The resorption pits are circular and like in *T. grayi*, replacement processes can be observed at nearly all teeth within the entire tooth row. Several replacement teeth which are still situated within the resorption pits and therefore are non functional already show minute replacement teeth of the next generation at their bases.

Diet:

No data concerning the feeding behavior of *T. herdmorei* are available.

Tropidophorus robinsoni SMITH, 1919
(Pl. IX, Fig. 8)

Number of examined specimens: 1 adult

Distribution:

Burma and Thailand.

Dental morphology:

The right dentary of specimen BMNH 1933.5.13.27 bears 31 tooth positions. The dental morphology of *Tropidophorus robinsoni* strongly resembles the dental morphology of other examined species of this genus. The teeth are slender and almost cylindrical. The tooth bases are only slightly broadened in the transversal direction. The tooth crowns are posterolingually oriented. The lingual surfaces of the tooth crowns are concave. The crista mesialis and the crista distalis are of equal length. In their point of intersection, these two cutting edges form the moderately pointed cuspis labialis. A lingual system of cutting edges is running parallel to the cristae mesialis et distalis and forms the low plateau-shaped cuspis lingualis which is situated underneath the cuspis labialis. The two cusps are separated from each other by the wide sulcus of the antrum intercristatum. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.5:1.0. The resorption pits are circular and replacement processes take place at almost all tooth bases.

Diet:

No data on the prey spectrum of *T. robinsoni* are available. Probably the diet of this species is comparable to the above described diet of *Tropidophorus grayi* since the ecology, as well as the dental morphology, of both species are almost identical.

4.1.4.4 Subfamily Scincinae Gray, 1825

(Diagnosis: see GREER 1970)

Brachymeles DUMÉRIL & BIBRON, 1839

Brachymeles boulengeri TAYLOR, 1922

(Pl. IX, Fig. 9)

Number of examined specimens: 2 adults
(*Brachymeles boulengeri taylori*)

Distribution:

Philippine islands (Panay, Visayas).

Dental morphology:

The numerous teeth of *Brachymeles boulengeri* are cylindrical and show subrectangular tooth crowns in lingual view. The lingual surfaces of the tooth crowns are concave. The tooth crowns are lingually oriented. The crista mesialis and the crista distalis are the same length. Both cutting edges run horizontally, which makes the cuspis labialis appear less pointed. However, the angulus mesialis and the angulus distalis are well developed. Underneath the cuspis labialis, a second cusp (the cuspis lingualis) is found. The associated lingual cutting edges run parallel to the labial cutting edges. The two cusps are separated from each other by a relatively wide antrum intercristatum. In the basal direction, the labial cutting edges transfer into the prominent culmines lateres anterior et posterior. All enamel surfaces are unwrinkled. The ratio tooth length to diameter of tooth neck is 3.1:1.0. The resorption pits of the investigated specimens are covered by mucosa.

Diet:

The trophic structures of the worm skinks, genus *Brachymeles*, whose limbs are gradually reduced, is dependent on the burrowing habits of the members of this group. The diet of *B. boulengeri* presumably consists of insects including their larvae and earthworms, as recorded for *Brachymeles apus* (MANTHEY & GROSSMANN 1997).

Brachymeles tridactylus BROWN, 1956
(Pl. IX, Fig. 10)

Number of examined specimens: 1 adult

Distribution:

Philippine islands (Negros, Panay, Carabao, Boracay, Inampulugan, W-Visayas).

Dental morphology:

The teeth of the solely available specimen of *Brachymeles tridactylus* are cylindrical and show pointed bicuspid cusps. The lingual surfaces of the tooth crowns are concave. The tips of the teeth are posterolingually orientated. The crista mesialis meets the crista distalis apically at a 60° angle. The cuspis labialis is therefore distinctly pointed as is the more lower situated cuspis lingualis. The labial and also the lingual cutting edges diverge in the basal direction. Therefore, the apically narrow antrum intercristatum becomes expanded in its basal portions. The enamel surfaces of all teeth are unwrinkled in *B. tridactylus*. The ratio tooth length:diameter of tooth neck as well as the habitus of the resorption pits cannot be determined since the tooth bases are covered by mucosa.

Diet:

The feeding ecology of *B. tridactylus* is probably comparable to the feeding ecology of *Brachymeles boulengeri*.

Chalcides LAURENTI, 1768

Chalcides bedriagai (BOSCA, 1880)
(Pl. IX, Fig. 11)

Number of examined specimens: 1 adult

Distribution:

Spain, Portugal.

Dental morphology:

The right dentary of the investigated specimen bears 15 tooth positions. The teeth of *Chalcides bedriagai* are cylindrical with flattened lingual surfaces of the tooth crowns. The apices are oriented in the lingual direction. The cristae distalis et mesialis are the same length and are bow-shaped. Both cristae transfer into the prominent culmines lateres in the basal direction. Underneath the cuspis labialis, the moderately pointed cuspis lingualis is found. The two cusps are connected over the transversal running carina intercuspidalis, which is formed as an extraordinary broad ridge. Approximately seven striae are situated on the flattened lingual surfaces of the tooth

crowns. The striae are very pronounced and run parallel to one another. The ratio tooth length to diameter of tooth neck is 3.0:1.0.

Diet:

Stomach contents of *C. bedriagai* showed a diet consisting of spiders, beetles, *Tipula* species, ants, isopoda, locusts, insect eggs, and sandy particles (ROGNER 1994). The majority of the prey items consists of minute invertebrates, which inhabit the intersticium between rocks or roots. *C. bedriagai* was described as euryphageous (MELLADO et al. 1975).

Remarks:

Limb reduction in various degrees is common in the genus *Chalcides*.

Chalcides chalcides (LINNAEUS, 1758)
(Pl. IX, Fig. 12)

Number of examined specimens: 2 adults

Distribution:

Spain, Portugal, South France, Italy (Sardinia), North Morocco, North Algeria, North Tunisia.

Dental morphology:

The right dentaries of the investigated specimens bear 18 (specimen SRK 00.277) or 20 (specimen SRK 00.278) tooth positions. The teeth of *Chalcides chalcides* are cylindrical with lingually flattened tooth crowns. The apices are orientated in the posterolingual direction. The cristae distalis et mesialis are the same length and bow-shaped as in *Chalcides bedriagai*. Both cristae transform into the prominent culmines lateres in the basal direction. The cuspis lingualis is extremely pronounced; it is formed by the cristae linguales anterior et posterior and the apical portions are often intensively worn. In several teeth, the line between dentine and tooth enamel is visible as a result of wear. The enamel of *C. chalcides* is very thick. The antrum intercristatum is distinctly broad and deep. Prominent striae are situated on the lingual surfaces of the tooth crowns in the anterior teeth. The numbers of these striae reach from two striae in the anteriormost tooth to approximately eight striae in the teeth of the central section of the tooth row. The striae are not arranged in parallel patterns; instead, they converge or diverge apically as well as basally. All striae are restricted to the concave portions of the lingual surfaces. Hence, the tooth necks and bases and all labial surfaces as well are

unwrinkled. The tooth crowns of the posterior teeth are blunt and lack the complex tooth crown morphology of the anterior and central teeth. The ratio tooth length to diameter of tooth neck is 4.0:1.0. The resorption pits are circular or dorsally elongated.

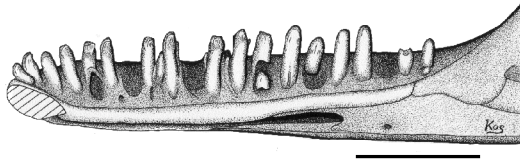


Fig. 100: *Chalcides chalcides*
(specimen SRK 00.278)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

Spiders are shown to be the main prey item of *C. chalcides* in various populations (CAPIZZI et al. 1998). The main secondary prey category was constituted by terrestrial Coleoptera larvae. In addition, Isopoda are consumed regularly. Hence, over 90 % of the total diet of this three-toed skink is made up by arthropods. Pulmonata are consumed rather seldomly. Stomach contents analyses made by MELLADO et al. (1975) on 22 stomachs of *C. chalcides* showed a diet composition that strongly contrasts the aforementioned results. Here, the diet consists of 10.3 % Isopoda, 2.0 % Myriapoda, 18.6 % spiders, 6.2 % Orthoptera, 8.3 % cockroaches, 3.1 % Hemiptera, 1.0 % ants (Formicidae), 4.1 % Diptera, 24.7 % Coleoptera, 10.3 % Lepidoptera larvae, 7.2 % other larvae and 3.1 % indeterminable remains.

Chalcides mionecton (BÖTTGER, 1874)

Number of examined specimens: 1 neonate

Distribution:

Morocco (W lowlands/ Atlantic coast).

Dental morphology:

The right dentary of specimen SRK 00.360 bears 14 tooth positions. However, since this specimen is a neonate, the tooth number of adult individuals of this species is probably higher. The teeth are cylindrical and relatively short. The posterior teeth are conical whereas the anterior teeth show lingually concave surfaces of the posterolingually oriented tooth crowns. The cristae mesialis et

distalis are the same length and form the moderately pointed cuspis labialis. Underneath the cuspis labialis, the cuspis lingualis is situated. The associated cutting edges of the cuspis lingualis run parallel to the cristae mesialis et distalis. The posterior teeth of *Chalcides mionecton* are unicuspid. Striations are restricted to the anterior and central teeth of the tooth row. The striae are short and faint. The maximal number of striae per tooth is five. The ratio tooth length to diameter of tooth neck is 2.7:1.0. The resorption pits are circular in shape.

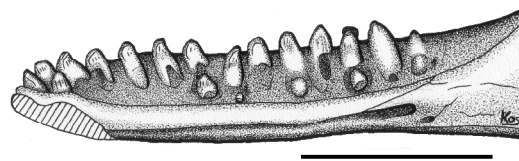


Fig. 101: *Chalcides mionecton*
(specimen SRK 00.337)
Right dentary of a juvenile individual; lingual view
Scale bar: 1.0 mm

Diet:

The diet of *C. mionecton* is probably dominated by arthropods.

Chalcides ocellatus (FORSKAL, 1775)
(Pl. IX, Fig. 13)

Number of examined specimens: 10 adults

Distribution:

Italy, Malta, Greece, Cyprus, Turkey, Turkmenistan, Saudi Arabia, Iraq, Morocco, Algeria, Tunisia, Libya, Egypt, Niger, Israel, Kenya, Somalia, Ethiopia, Eritrea, Sudan, Chad, Yemen, Iran, Pakistan.

Dental morphology:

The right mandible of specimen SRK 00.104 bears 17 tooth positions. The teeth of all investigated *Chalcides ocellatus* specimens differ from the teeth of their cogenetics since the tooth crowns strongly contrast with the tooth necks. The tooth bases and tooth necks are very slender and extremely expanded transversally. The flanks are concave. The blunt tooth crowns are mesially expanded and robust; they have concave lingual surfaces. The tooth morphology is perfectly adapted for durophagy, especially the cupola-shaped tooth crowns are advanced crushing tools. The cristae mesialis et distalis form a plateau-like cuspis labialis at their occlusal ends. The lower

positioned cuspis lingualis is formed by two prominent ridges. These main striae represent the striae dominantes anterior et posterior which are surrounded by numerous less pronounced striae. All striations are restricted to the concave lingual surfaces of the tooth crowns. Approximately 10 striae can be found between the striae dominantes, with one or two additional striae situated between the stria dominans anterior and the culmen lateris anterior on the one hand and one or two striae situated between the stria dominans posterior and the culmen lateris posterior on the other (e.g., specimens BMNH 63.2.21.29 and BMNH 1920.1.20.784). In other specimens, the striae dominantes are not clearly identifiable and the corresponding structures more likely resemble cutting edges. In specimen USNM 313453, the striae bifurcate in the basal direction and therefore show a branch-like appearance. The posterior teeth of most individuals are unicuspid. In other specimens, all striae converge in a more or less pronounced cuspis lingualis without developing any main striae (e.g., specimens ZFMK 7850, ZFMK 9199, ZFMK 9200). The labial surfaces of all investigated specimens are unwrinkled and convex. The ratio tooth length:diameter of tooth neck is 5.2:1.0. The resorption pits are of circular shape. The patterns of striations are already fully developed in replacement teeth which are still situated inside the resorption pits.

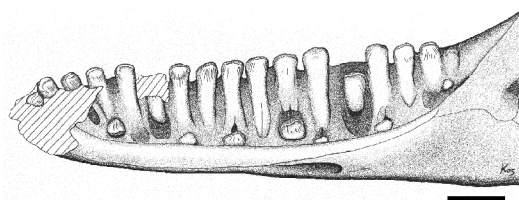


Fig. 102: *Chalcides ocellatus*
(specimen SRK 00.104)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

C. ocellatus preys on various insects, spiders, and consumes a relatively high percentage (30 %) of plant matter. In captivity these skinks also consume small snails, meat, grasshoppers, moths, apples, bananas, cherries, strawberries, and juveniles of their own species. Even large lizards like adult male

Podarcis tiliguerta are overpowered and eaten (BÖHME 1981).

***Chalcides sexlineatus* STEINDACHNER, 1891**

Number of examined specimens: 3 adults
(*Chalcides s. sexlineatus*)

Distribution:

Canary Islands (Gran Canaria).

Dental morphology:

The right dentary of specimen SRK 00.125 bears 16 tooth positions; 8 of these are represented as empty loci occupied by minute replacement teeth. The dentition is heterodont with slender cylindrical anterior teeth and robust, rather bulbous teeth in the posterior section of the tooth row. The tooth crowns are lingually oriented and their lingual surfaces are flattened. The cristae mesialis et distalis are the same length and form a relatively blunt cuspis labialis which is situated in a central position. Underneath the cuspis labialis, the prominent cuspis lingualis is found. The antrum intercratum is deep and narrow; it often appears widened as a result of intensive wear. A maximum of eight fine striae are situated on the flattened lingual surfaces of the apices in several teeth. These striae run parallel to each other. Many teeth completely lack striations. The ratio tooth length:diameter of tooth neck amounts to 3.8:1.0 in anterior teeth and is 2.2:1.0 in posterior teeth. The resorption pits are dorsally elongated.

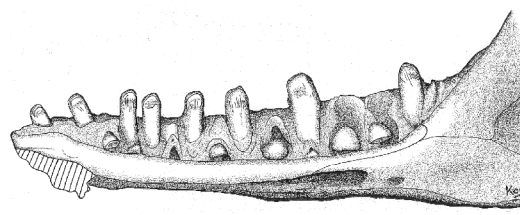


Fig. 103: *Chalcides sexlineatus*
(specimen SRK 00.125)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The longitudinally striped Canary Islands skink consumes small insects, crustaceans, snails, spiders, earthworms, and the occasional sweet soft fruits. Stomach contents show Diptera, beetles, and Heteroptera (BISCHOFF 1998). BISCHOFF also observed

Chalcides sexlineatus consuming flowers of *Launaea arborescens* in the natural habitat.

Chalcides viridanus (GRAVENHORST, 1851)
(Pl. IX, Fig. 14)

Number of examined specimens: 2 adults

Distribution:

Canary Islands (El Hierro and La Gomera), Madeira.

Dental morphology:

The dentary of specimen SRK 00.126 bears 16 tooth positions. The dentition shows a high degree of heterodonty with slender cylindrical teeth in tooth positions 1 to 9 contrasted by distinctly robust teeth in tooth positions 10 to 16. In the anterior teeth, the apical thirds of the teeth rise above the labial parapet of the dentary whereas in the posterior teeth the apical halves rise above the labial parapet of the dentary. The lingual surfaces of the apices are concave in anterior teeth; they are only slightly flattened in posterior teeth. The anterior tooth crowns are slightly posterolingually orientated. The cristae mesialis et distalis are the same length. Together these two cutting edges form the inwardly curved and relatively blunt cuspis labialis. Underneath the cuspis labialis, the plateau-shaped cuspis lingualis is situated. The antrum intercristatum is shallow and in the majority of the teeth, it is rather wide. Striations are only found in the anterior teeth. The striae are fine and restricted to the lingual surfaces of the tooth crowns. In several teeth, more than ten striae are found. The ratio tooth length:diameter of tooth neck amounts to 3.7:1.0 in anterior teeth and is 2.2:1.0 in posterior teeth. The resorption pits are of circular shape or dorsally elongated.

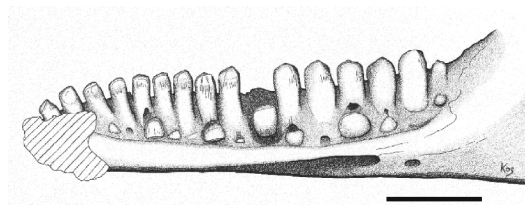


Fig. 104: *Chalcides viridanus*
(specimen SRK 00.126)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

Chalcides viridanus preys on arthropods and terrestrial snails. In captivity, sweet fruits are also accepted (BISCHOFF 1985). Fecal pellets of *Chalcides viridanus coeruleopunctatus* specimens captured in the Valle Gran Rey on La Gomera contained large fragments of chitinous cuticula (own observation), which suggest that prey items occasionally are very large compared to the small size of these skinks.

Eumeces WIEGMANN, 1834

Eumeces fasciatus (LINNAEUS, 1758)
(Pl. IX, Fig. 15)

Number of examined specimens: 3 adults

Distribution:

Southern and Eastern USA, SE Canada.

Dental morphology:

Eumeces fasciatus bears approximately 25 tooth positions in each jaw ramus. The teeth are slender and have transversally expanded bases whereas the apical portions of the teeth are cylindrical. The lingual surfaces of the tooth crowns are intensively inwardly curved. The tooth crowns are posterolingually oriented. The cristae mesialis et distalis are the same length and form a relatively pointed cuspis labialis. The lower positioned cuspis lingualis as well is acute and prominent. The antrum intercristatum is rather wide but narrows in the apical direction, which results in an immediate association of the two cusps. The two pronounced cutting edges which form the cuspis lingualis run across the concave apical surface and frame a heavily striated area. In the majority of teeth, four or five striae are found in the spaces between these cristae linguales. These striae are arranged in parallel and are distinctly pronounced. In rare cases, one or two isolated striae are situated between the crista lingualis anterior and the culmen lateris anterior or are found between the crista lingualis posterior and the culmen lateris posterior. The number of striae is highest in the central section of the tooth row whereas less striae are found in the anterior teeth and in the posterior teeth as well. All labial surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.7:1.0. The resorption pits are circular in shape.

Diet:

E. fasciatus prefers large moving prey items. The skinks use their well developed Jacobson's organ and nasal structures for locating the prey (BURGHARDT 1964). During several experiments, BURGHARDT observed *E. fasciatus* attacking crickets and spiders too large to be swallowed. Under captive conditions, the skinks consistently chose the largest available food items. In their natural habitat, these skinks prey on small vertebrates, cockroaches, beetles, crickets, locusts, spiders, terrestrial snails, and small crustaceans (HAUSCHILD & GÄBNER 1995). In captivity, the skinks consume insects, insect larvae, and occasionally ripe soft fruits.

Eumeces gilberti VAN DENBURGH, 1896
(Pl. IX, Fig. 16-17)

Number of examined specimens: 4 adults (one of these belongs to the subspecies *Eumeces gilberti rubricaudatus*)

Distribution:

USA (California, Nevada, Arizona), Mexico (N Baja California).

Dental morphology:

The teeth of *Eumeces gilberti* are rather narrowly spaced, robust, and blunt. The tooth crowns contrast with the tooth necks since the tooth crowns appear cylindrical whereas the tooth necks and bases are strongly expanded transversally. The flanks are concave. The tooth crowns alone rise above the labial parapet of the dentary. The lingual surfaces of the tooth crowns are concave and the tooth crowns are posterolingually orientated. The crista mesialis is slightly longer than the crista distalis. Apically, both cristae form the blunt cuspis labialis. Laterally, they construct the pronounced anguli mesialis et distalis. The culmines lateres are pronounced. Separated from the cuspis labialis by a wide antrum intercratum and situated in a lower position, the prominent cuspis lingualis is found. The two cristae forming the cuspis lingualis are distinctly pronounced and frame a heavily striated area. Four to six prominent and parallel striae are situated between the cristae linguales. Some additional striae are occasionally found outside the area framed by the cristae linguales. This pattern of striations is already completed in replacement teeth which are not in function. The dental morphologies of all investigated individuals are rather similar. The ratio tooth

length:diameter of tooth neck is 3.6:1.0. The resorption pits are circular.

Diet:

E. gilberti consumes insects and spiders in the wild (STEBBINS 1985).

Eumeces inexpectatus TAYLOR, 1932
(Pl. IX, Fig. 18)

Number of examined specimens: 1 adult

Distribution:

USA (Louisiana, Mississippi, Tennessee, Alabama, Georgia, Florida, South Carolina, North Carolina, Virginia, Maryland).

Dental morphology:

The teeth of *Eumeces inexpectatus* are slender and cylindrical. The tooth crowns are relatively pointed and show concave lingual surfaces. The cusps are lingually oriented. The cristae mesialis et distalis are equal in length; these cutting edges transfer in the basal direction into the moderately pronounced culmines lateres. The prominent cuspis lingualis is formed by the well developed cristae linguales anterior et posterior. The wide antrum intercratum narrows apically; it is formed as a deep but extremely narrow sulcus situated between the two cusps. Striations are weak or absent in the majority of teeth. The ratio tooth length:diameter of tooth neck is 3.5:1.0. The resorption pits are circular in shape.

Diet:

E. inexpectatus consumes insects and diverse other arthropods. Occasionally, terrestrial snails are eaten in the natural habitat (ROGNER 1994).

Eumeces laticeps (SCHNEIDER, 1801)
(Pl. IX, Fig. 19-20)

Number of examined specimens: 3 adults

Distribution:

USA (Southern States).

Dental morphology:

The right dentary of the male specimen USNM 525729 bears 30 tooth positions. The teeth of *Eumeces laticeps* appear very slender in lingual view. The tooth bases and tooth necks are extremely broadened transversally and the flanks are flattened or concave. The tooth crowns are posterolingually directed and strongly contrast with the tooth necks. The tooth crowns emerge from the labial margin of

the dentary. The lingual surfaces of the tooth crowns are distinctly concave. The cristae mesialis et distalis are of equal length. The recurved tooth tips are only moderately pointed. The labial cutting edges slope gradually in the basal direction and transfer into the prominent and long culmines lateres. The cuspis lingualis and the antrum intercristatum are less pronounced. A maximum of seven striae are found on the concave lingual surfaces of the apices. The striae are distinctly pronounced and form straight ridges, which run parallel to the longitudinal axes of the teeth. In their apical portions, the striae often converge. The tooth necks, the tooth bases, and the labial surfaces of the tooth crowns are unwrinkled. Specimen USNM 9242 completely lacks striations. The ratio tooth length:diameter of tooth neck is 5.0:1.0. The resorption pits are circular.

Diet:

E. laticeps inhabits moist forests and grasslands. It preys on insects and their larvae, snails, isopods, spiders, and lizards (e.g. *Anolis carolinensis* and juveniles of other *Eumeces* species). *E. laticeps* is specialized in rousing prey animals; this behavior strongly contrasts the sit-and-wait hunting technique of other skinks (HAUSCHILD & GÄBNER 1995). This species, like other skinks, uses prey odor discrimination for detecting hidden prey. Location of prey items takes place inside and under rotting logs as well as beneath surface litter (COOPER 1989).

Remarks:

This species is known for its intensive care during breeding. For example, *Eumeces obsoletus* females defend the egg nests and collect scattered eggs.

Eumeces longirostris (COPE, 1861)

(Pl. IX, Fig. 21)

Number of examined specimens: 1 adult

Distribution:

Bermuda Islands.

Dental morphology:

The teeth of specimen USNM 217505 are slender and cylindrical. The lingual surfaces of the tooth crowns are flattened or lightly concave. The tooth crowns are posterolingually orientated. The crista mesialis is as long as the crista distalis; both cristae form a moderately pointed cuspis labialis. In the basal direction, these cutting edges

transform into the short but prominent culmines lateres. The cuspis lingualis and the antrum intercristatum are only rudimentary developed. The striations of the tooth enamel are subordinated in *Eumeces longirostris*. Maximally 16 fine striae run parallel to the longitudinal axes of the teeth across the central portions of the flattened lingual surfaces of the tooth crowns. The labial surfaces of the teeth are smooth. The ratio tooth length:diameter of tooth neck is 3.3:1.0.

Diet:

E. longirostris is probably insectivorous.

Eumeces marginatus (HALLOWELL, 1861)

(Pl. IX, Fig. 22)

Number of examined specimens: 2 adults

Distribution:

Japan (Riu Kiu Islands).

Dental morphology:

The teeth of *Eumeces marginatus* strongly resemble the teeth of *Eumeces longirostris*. All teeth are slender and cylindrical. The lingual surfaces of the tooth crowns are slightly concave. The tooth crowns are oriented in the posterolingual direction. The cristae mesialis et distalis are the same length. Together, these labial cutting edges form a moderately pointed cuspis labialis. In the basal direction, these cutting edges transfer into the short, but prominent culmines lateres. The cuspis lingualis and the antrum intercristatum are developed more distinctly than in *Eumeces longirostris*. The cuspis lingualis often forms an apical plateau, which is labially bordered by the shallow antrum intercristatum. Striations are extremely weak in *E. marginatus*; in most teeth, they are even absent. If present at all, the striae are restricted to the concave lingual surfaces of the tooth crowns. The labial surfaces of the teeth are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits are of circular shape.

Diet:

E. marginatus is probably an insectivorous species.

Eumeces obsoletus (BAIRD & GIRARD, 1852)
(Pl. X, Fig. 1)

Number of examined specimens: 1 adult

Distribution:

USA (Wyoming, Iowa, from the Midwest to Colorado, Arizona, New Mexico, and Texas), Mexico.

Dental morphology:

The teeth of *Eumeces obsoletus* are very robust and slightly expanded in the transversal direction. The apical portions of the tooth crowns rise above the labial parapet of the dentary. The tooth crowns are oriented posterolingually and they strongly contrast with the tooth necks. The lingual surfaces of the tooth crowns are concave. The crista mesialis is little longer than the crista distalis. The cristae mesialis et distalis form the moderately pointed cuspis labialis. Underneath this main cusp, the cuspis lingualis is situated. The cuspis lingualis is extensively worn in most teeth. The two cusps are separated by the deep sulcus of the antrum intercratum. The cristae mesialis et distalis transform into the distinctly pronounced culmines lateres in basal the direction. These culmines frame the concave surfaces of the tooth crowns, where approximately eight prominent striae are situated. In many teeth, these striae alternate in length; a short stria is often positioned between two long striae. The striae are arranged parallel; several striae stretch to the lingual surfaces of the tooth necks. In the apical direction, the striae converge toward the cuspis lingualis. All labial tooth surfaces are unwrinkled. The ratio tooth length to diameter of tooth neck is 3.1:1.0.

Diet:

E. obsoletus consumes various insects (beetles, crickets, locusts), insect larvae, spiders, snails, and insect eggs. Even smaller congenetics belong to the prey spectrum of this species. *E. obsoletus* shows a sit-and-wait foraging behavior (HAUSCHILD & GÄBNER 1995).

Remarks:

The Golden Great Plain skinks are known for their intensive breeding care. The female defends the egg nest, rolls itself around the clutch for protection, occasionally turns around the eggs, keeps them moist, and cares for the neonates for several days after hatching.

Eumeces skiltonianus (BAIRD & GIRARD, 1852)
(Pl. X, Fig. 3)

Number of examined specimens: 5 adults

Distribution:

Canada, USA (west), Mexico.

Dental morphology:

The teeth of *Eumeces skiltonianus* are relatively slender and cylindrical. The pointed tooth crowns are lingually flattened or slightly concave. The tips of the apices are directed lingually (e.g. specimen SDS 63107) or posterolingually (e.g. specimen SDS 68049). The crista mesialis and the crista distalis show the same length. Both cristae are sloping steeply in a labially directed sinus without forming an angulus. The cuspis labialis appears extremely pointed. In several teeth, a low cuspis lingualis is situated underneath the cuspis labialis. However, many teeth lack this second cusps as a result of intensive wear. The antrum intercratum is narrow and only slightly concave in *E. skiltonianus*. The cristae mesialis et distalis transform into the prominent culmines lateres in the basal direction. Some three to five striae are found on the concave surfaces between the culmines lateres. These striae run parallel to the longitudinal axes of the teeth and are moderately pronounced. The ratio tooth length to diameter of tooth neck is 3.3:1.0. The resorption pits of the investigated specimen are covered by mucosa.

Diet:

E. skiltonianus consumes insects, spiders, and sowbugs (STEBBINS 1985).

Eumeces tunganus STEJNEGER, 1924
(Pl. X, Fig. 4)

Number of examined specimens: 1 adult

Distribution:

China (W Sichuan).

Dental morphology:

The teeth of *Eumeces tunganus* are robust and show transversally expanded tooth bases and tooth necks. The flanks are flattened or slightly concave. The lingual surfaces of the tooth crowns are flattened. The cristae mesialis et distalis are the same length. At their apical ends, these two cutting edges form the lingually directed cuspis labialis. Laterally, the cristae mesialis et distalis form the elaborated sinus-shaped anguli mesialis et distalis, from which the short but prominent culmines lateres are

sloping in the basal direction. The lingual surfaces of the anguli are strongly curved inward. Underneath the cuspis labialis sits the pronounced cuspis lingualis. This secondary cusp shows an occlusal plateau-like surface between its tip and the shallow antrum intercristatum. In many teeth, the cusps are extensively worn. Up to seven faint striae are situated on the lingual surfaces of the tooth crowns. These striae converge apically and stretch almost up to the cuspis lingualis. All striations are restricted to the lingual surfaces of the tooth crowns whereas the remaining tooth surfaces are unwrinkled in *E. tunganus*. The ratio tooth length:diameter of tooth neck is 3.4:1.0. The resorption pits are shaped circularly.

Diet:

No data about the prey spectrum of *E. tunganus* are available.

***Eurylepis* BLYTH, 1854**

***Eurylepis taeniolatus* BLYTH, 1854**
(Pl. X, Fig. 5)

Number of examined specimens: 1 adult

Remark:

Specimen AMNH 110170 is cataloged under the synonym *Eumeces taeniolatus*.

Distribution:

Saudi Arabia, Yemen, Iran, Iraq, Afghanistan, Pakistan, India (Kashmir), Turkmenistan.

Dental morphology:

The teeth of *Eurylepis taeniolatus* are slender and show transversally broadened tooth bases and tooth necks. The robust tooth crowns strongly contrast with the tooth necks. The lingual surfaces of the tooth crowns are concave. The tooth crowns are slightly orientated posterolingually. The crista mesialis is longer than the crista distalis, which leads to a shifting of the cuspis labialis from a central position to a more posterior position. The crista mesialis slopes shallowly to the sinus-shaped angulus mesialis, whereas the crista distalis slopes steeply and transfers directly into the culmen lateris posterior. Apically, the two cristae meet at an angle of 110 degrees and form the cuspis labialis. Underneath this main cusp, the pronounced cuspis lingualis is found. The cuspis lingualis is formed by its accompanying cutting edges, the crista lingualis anterior and the crista lingualis

posterior. The crista lingualis anterior in the basal direction converges with the crista mesialis, while the crista lingualis posterior converges with the crista distalis. Hence, the antrum intercristatum, which is distinctly wide between the two cusps, narrows in the anterior as well as in the posterior direction. The antrum intercristatum is only slightly concave and often extensively worn. The lingual surfaces of the tooth crowns are heavily striated in *Eurylepis taeniolatus*. A maximum of 12 striae are found on each tooth. The striae are very prominent and orientated parallel to the longitudinal axes of the teeth. The majority of striae are extremely short and are restricted to the central area of the concave apical surface. However, several striae are more dominant and stretch from the transition zone between the tooth crown and the tooth neck immediately to the cristae linguales. The ratio tooth length:diameter of tooth neck is 3.6:1.0. The resorption pits are circular in shape.

Diet:

E. taeniolatus is probably an insectivorous species.

***Janetaescincus* GREER, 1970**

***Janetaescincus braueri* (BOETTGER, 1896)**
(Pl. X, Fig. 6)

Number of examined specimens: 1 adult

Remark:

Specimen BMNH 1910.3.18.33 is cataloged under the synonym *Scelotes braueri*.

Distribution:

Seychelles.

Dental morphology:

The dentition of *Janetaescincus braueri* strongly resembles the dentition of *Scelotes bipes*. The right dentary of specimen BMNH 1910.3.18.33 bears 33 tooth positions. The teeth are pointed, cylindrical, and their apical portions are strongly recurved in the posterolingual direction. The tooth necks and tooth bases are slightly expanded transversally. The tooth crowns rise above the labial parapet of the dentary. The lingual surfaces of the conical tooth crowns are flattened or concave. The crista mesialis is slightly longer than the crista distalis. Underneath the relatively pointed cuspis labialis, the rudimentary cuspis lingualis is situated; it is formed as an inconspicuous ledge. The antrum intercristatum is only weakly developed. The culmines lateres are

short and not prominent. Striations are absent. The ratio tooth length:diameter of tooth neck is 4.5:1.0. The resorption pits are of circular shape in *J. braueri*.

Diet:

A diet consisting mainly of termites and beetle larvae can be assumed for *J. braueri*.

Melanoseps BOULENGER, 1887

Melanoseps occidentalis (PETERS, 1877)
(Pl. X, Fig. 7)

Number of examined specimens: 1 adult

Distribution:

Cameroon, Equatorial Guinea, Gabon, Democratic Republic of the Congo (Zaire), Angola.

Dental morphology:

The right dentary of specimen BMNH 1907.5.22.6A bears 13 tooth positions. The teeth of the burrowing skink *Melanoseps occidentalis* are distinctly pointed, long, and cylindrical. The apical halves of the teeth, which bend in a hook-like fashion posterolingually, rise above the labial parapet of the dentary. The longest teeth of the tooth row are situated in the anterior portion of the dentary, while the lengths of the teeth decrease in the posterior section of the mandible. The lingual surfaces of the conical tooth crowns are concave. The cristae mesialis et distalis are the same length. Underneath the extremely pointed cuspis labialis, a low but pointed cuspis lingualis is developed with a narrow and deep antrum intercratum separating the two cusps. Most teeth completely lack any culmines lateres. However, in some teeth weakly developed culmines are found. All tooth surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 5.0:1.0. The resorption pits of *M. occidentalis* are of circular shape.

Diet:

The diet of *M. occidentalis* probably consists of soft bodied larvae.

Neoseps STEJNEGER, 1910

Neoseps reynoldsi STEJNEGER, 1910
(Pl. X, Fig. 8)

Number of examined specimens: 1 adult

Distribution:

USA (Central Florida).

Dental morphology:

The teeth of the burrowing skink *Neoseps reynoldsi* are of simple conical habitus. The lingual surfaces of the tooth crowns are only slightly flattened and are directed posterolingually. The teeth are very straight. The cuspis labialis is pointed and encloses an apical angle of 50 degrees. Undeneath the cuspis labialis, a less prominent cuspis lingualis is found. The antrum intercratum appears only slightly concave and is extremely narrow. Most teeth lack the culmines lateres. However, if they are present, they are formed as subordinate ridges. All tooth surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 3.5:1.0. The resorption pits of the investigated specimen are covered by mucosa.

Diet:

The diet of the sand skink *N. reynoldsi*, whose limbs are strongly reduced, consists mainly of termites and beetle larvae; these prey items are predominantly caught and eaten while burrowing (CONAN & COLLINS 1998).

Novoeumeces GRIFFITH, NGO & MURPHY, 2000

Novoeumeces algeriensis (PETERS, 1864)

Number of examined specimens: 1 adult

Remark:

Until recently, this species was treated as a subspecies of *Eumeces schneideri* and is hence better known as *Eumeces schneideri algeriensis*.

Distribution:

NW Africa.

Dental morphology:

The dentition of specimen SRK 00.136 is similar to the dentition of *Eumeces schneideri*.

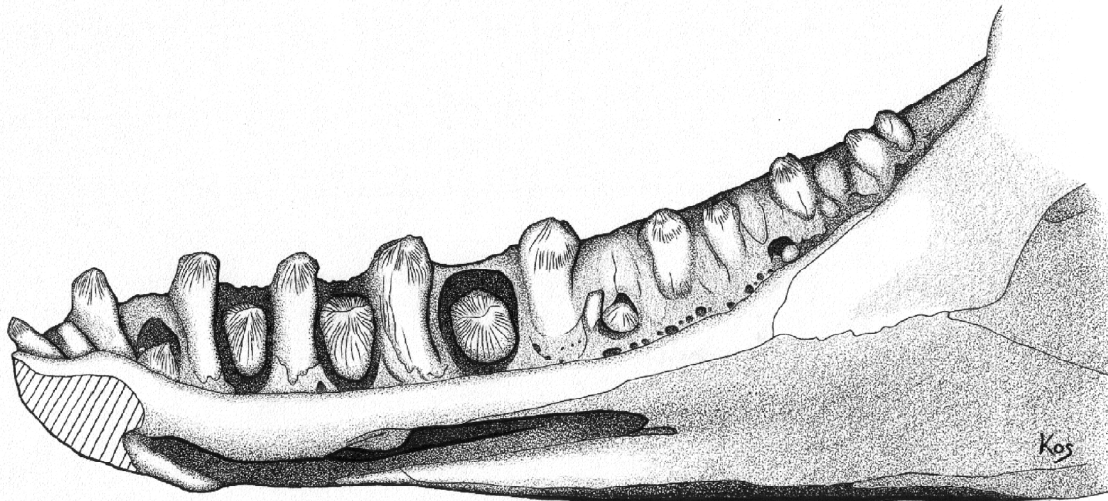


Fig. 105: *Novoeumeces schneideri*
(specimen SRK 00.083)
Right dentary; lingual view
Scale bar: 1.0 mm

Novoeumeces schneideri (DAUDIN, 1802)

Number of examined specimens: 3 adults

Remark:

The investigated specimens are cataloged under the more popular synonym *Eumeces schneideri*.

Distribution:

From NW Africa to W Asia.

Dental morphology:

The right dentary of specimen SRK 00.083 bears 19 tooth positions. The dentition of *Novoeumeces schneideri* shows a durophagous morphology and is conspicuously heterodont with large anterior crushing teeth and minute posterior teeth; this condition was found in the genus *Novoeumeces* alone. In other durophagous scincomorphans (e.g., *Tiliqua*, *Hemisphaeriodon*, *Tupinambis*), the crushing teeth are always situated in the posterior portions of the dentaries. All teeth of *N. schneideri* are stocky and the apical portions of the tooth crowns hardly rise above the labial parapet of the dentary. The transition zone between the two morphotypes of teeth is extremely short; the changes of tooth sizes within the tooth row take place abruptly.

The anterior teeth of *N. schneideri* are exceptionally large and show conspicuous adaptations for a durophagous diet. The lingually concave tooth crowns contrast with the transversally broadened tooth necks. The interdental spaces are very narrow between

the tooth crowns. The tooth crowns are lingually oriented. The cristae mesialis et distalis are the same length and form a relatively blunt cusp. This cusp cannot be referred to as the “*cuspis labialis sensu stricto*” (even if the position of the cusp corresponds to the position of the *cuspis labialis* in other taxa) since a *cuspis lingualis* is not present. In several teeth, the crista distalis runs concave and forms a cusp-like protruding angulus distalis. The lingual surface of this lateral cusp is strongly curved inward. The culmines lateres are extremely short and extend only across the apical halves of the tooth crowns. The apical portions of the lingual surfaces of the tooth crowns are concave, whereas the basal portions of the tooth crowns are convex and appear inflated. The entire lingual surfaces of the tooth crowns are heavily striated. More than 26 striae (most of which are distinctly pronounced) are found in each tooth. Bifurcations of the striae in the basal direction are common in *N. schneideri*. The striae converge apically at the main cusp. In several teeth, additional striations are situated at the labial surfaces; however, these striae are less numerous than the lingual striations and are less pronounced. The enamel surfaces of the tooth necks and tooth bases are unwrinkled. Non functional replacement teeth show extensive wrinkling of their enamel surfaces since they are not exposed to wear. The ratio tooth length:diameter of tooth neck is

3.0:1.0 in anterior teeth. The resorption pits are circular in shape.

In contrast to the anterior teeth, the posterior teeth of *N. schneideri* are small sized and almost globular or egg-shaped. The cupola-shaped tooth crowns of the posterior teeth show an intensive wrinkling. The striations converge at the centrally positioned cusp. The striae are short. Their total number can exceed twenty striae (most of these are situated lingually). The ratio tooth length:diameter of tooth neck is 1.6:1.0 in these posterior teeth. The resorption pits are of circular shape.

Numerous foramina are found in the bony material at the bases of the teeth; these foramina are arranged in a line parallel to the dentary shelf. These structures are obviously a result of resorbing processes.

Diet:

Captive specimens of *N. schneideri* accept various arthropods, snails, pinky mice and meat, freshwater fishes, liver, fruits, and flowers (ROGNER 1994). The skinks show a strong preference for terrestrial snails. Even poisonous scorpions are preyed upon (ZIEGLER & BÖHME 1996). The inverted durophageous dentition with large anterior and small posterior teeth is interpreted as an adaptation to this partly durophageous diet accompanied by a specialized feeding behavior.

Remarks:

A great diversity of subspecies is known in this wide ranging species; the subspecies gradually change geographically and often intermingle (MERTENS 1946); this leads to a uncertain status of several populations within this group.

Scelotes FITZINGER, 1826

Scelotes bipes (LINNAEUS, 1766)

Number of examined specimens: 1 adult

Distribution:

Republic of South Africa.

Dental morphology:

The teeth of the dwarf burrowing skink *Scelotes bipes* are pointed, cylindrical, and their apical portions are strongly recurved in the posterolingual direction whereas the tooth necks as well as the tooth bases both are straight. The tooth crowns rise above the labial parapet of the dentary. The lingual surfaces of the conical tooth crowns are concave. The crista mesialis is slightly longer than the crista

distalis. Underneath the pointed cuspis labialis, the blunt cuspis lingualis is found. The antrum intercristatum is only weakly developed. The culmines lateres are not prominent. All surfaces of the teeth are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.5:1.0. The resorption pits of the two-toed *S. bipes* are circular. Tooth replacement processes are visible at the bases of almost all teeth in the jaw ramus. The replacement teeth are extremely pointed, whereas older functional teeth are often extensively worn.

Diet:

S. bipes has stump-like hindlimbs with two toes and inhabits coastal beaches where it hides under rocks or burrows in the sand. The diet consists mainly of various insects, spiders, worms, and other invertebrates (ROGNER 1994). The consumption of marine arthropods cannot be excluded due to the habitats of these minute skinks.

Scelotes gronovii (DAUDIN, 1802)

(Pl. X, Fig. 11)

Number of examined specimens: 1 adult

Distribution:

Republic of South Africa.

Dental morphology:

The teeth of the single-toed dwarf burrowing skink *Scelotes gronovii* are moderately pointed, cylindrical and compared to *Scelotes bipes*, appear rather straight. Because of the lack of available individuals, it cannot be determined whether the rectilinear habitus of the teeth of *S. gronovii* is a character of this species or if the dental morphology underlies a great variability within the genus *Scelotes*. The tooth crowns rise above the labial parapet of the dentary. The lingual surfaces of the conical tooth crowns are flattened or slightly concave. The cristae mesialis et distalis are the same length. The cristae linguales anterior et posterior run parallel to the cristae mesialis et distalis and form the pronounced cuspis lingualis. The antrum intercristatum is the same width throughout its entire length and is hardly curved inward. The culmines lateres are short and inconspicuous. The ratio tooth length:diameter of tooth neck is 3.2:1.0. The resorption pits of *S. gronovii* are circular in shape.

Diet:

A diet consisting mainly of termites and insect larvae can be assumed for *S. gronovii*.

Scincopus PETERS, 1864

Scincopus fasciatus PETERS, 1864
(Pl. X, Fig. 12)

Number of examined specimens: 1 adult

Remark:

Specimen BMNH 1906.5.7.5 is cataloged under the synonym *Scincopus (Scincopus) fasciatus*.

Distribution:

Algeria, Tunisia, Mauritania, Mali, Niger, Chad, Sudan, Libya, and the Sahara.

Dental morphology:

The teeth of *Scincopus fasciatus* are robust and unicuspid. The tooth necks and the tooth bases are cylindrical whereas the tooth crowns are lingually slightly concave or at least flattened. The cristae mesialis et distalis are of equal length and they form the blunt cusp. The angulus mesialis and the angulus distalis are pronounced. The prominent and long culmines lateres run relatively straight from the anguli in the basal direction. A belt of approximately 20 striations is situated on the concave surface between the culmines lateres. The striae are orientated parallel to the longitudinal axes of the teeth. Since the striae are rather short, none reaches the cusp. The distances between the striae and their prominences vary greatly. All labial surfaces and the lingual surfaces of the tooth necks and the tooth bases are smooth. The ratio tooth length:diameter of tooth neck is 2.4:1.0 in *S. fasciatus*. The resorption pits are of circular shape.

Diet:

Captive specimens of this nocturnal desert dwelling species accept various large insects, earthworms, pinky mice, smaller lizards (e.g. *Scincus scincus*), melons, and bananas. Lettuce and seeds are refused by *S. fasciatus* (HAUSCHILD & GÄBNER 1995).

Scincus GRONOVIVS, 1763

Scincus mitranus ANDERSON, 1871
(Pl. X, Fig. 13)

Number of examined specimens: 1 adult

Distribution:

Arabian Peninsula east of the Asir and Yemen highlands, and north to Kuwait.

Dental morphology:

The teeth of *Scincus mitranus* are slender and show cylindrical shafts. The tooth crowns are mesially expanded and strongly concave lingually. The cristae mesialis et distalis are the same length and form a blunt and lingually recurved cuspis labialis. The sinus-shaped anguli mesialis et distalis are distinctly prominent. From here, the pronounced and long culmines lateres slope in the basal direction. Underneath the cuspis labialis, the protruding cuspis lingualis is found. The cutting edges, which form the cuspis lingualis, run parallel to the cristae mesialis et distalis. The antrum intercratum is extremely wide and notch-like in *S. mitranus*. Two striae are found on the concave lingual surfaces of several teeth; one of these striae is situated in the immediate vicinity of the culmen lateris anterior whereas the other stria is situated in the immediate vicinity of the culmen lateris posterior. Apically, both striae end abruptly at the lingual cutting edges. All other enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck amounts to 4.8:1.0. The resorption pits are of circular shape.

Diet:

No data on the diet of *S. mitranus* are available.

Scincus scincus (LINNAEUS, 1758)

(Pl. X, Figs. 14-15)

Number of examined specimens: 7 adults (one of these belongs to the subspecies *Scincus s. cucullatus*)

Distribution:

Morocco, Tunisia, Algeria, Libya, Egypt, Sinai, Israel, Jordan, Yemen, United Arab Emirates, Bahrain, Kuwait, Iraq, Iran, Senegal, Mali, Niger, Nigeria, and Saudi Arabia.

Dental morphology:

The right dentary of specimen SRK 00.069 bears 17 tooth positions. The teeth are narrowly spaced, relatively short, and robust. The tooth necks and tooth bases are transversally expanded whereas the tooth crowns appear conical. The teeth of *S. scincus* show belt-like horizontal constrictions at the lingual surfaces of their tooth crowns; aside

from these slightly concave structures, which strongly contrast other scincomorphans, the teeth are convex shaped. The crista mesialis is slightly longer than the crista distalis; together these cutting edges, at their apical ends, form the moderately pointed cuspis labialis. In the basal direction, the cristae mesialis et distalis transform gradually into the prominent culmines lateres. Underneath the cuspis labialis, the cuspis lingualis is situated. Both cusps are separated by a deep antrum intercrisatum whose degree of expansion varies in different teeth. The antrum narrows mesially as well as distally. In several teeth, the cusps and the associated antrum intercrisatum are extensively worn. Striations are arranged garland-like and are restricted to the constrictions of the lingual surfaces of the tooth crowns. The striae are extremely short in some specimens (e.g., specimen BMNH 1909.7.28.34, specimen IFSZ 19107), but the striae can be longer in other individuals (e.g., specimen SDS 65230) or they are more or less absent in others (e.g., specimen SRK 00.069). The labial surfaces as well as the lingual surfaces of the tooth necks and the tooth bases are unwrinkled in *S. scincus*. The ratio tooth length:diameter of tooth neck is 3.8:1.0 on average. The resorption pits are circular in shape.

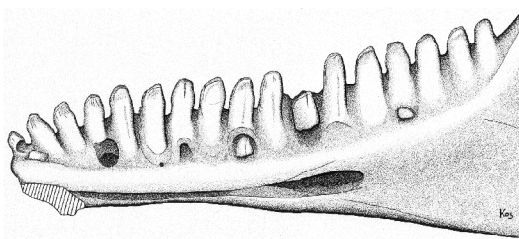


Fig. 106: *Scincus scincus*
(specimen SRK 00.069)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The feeding behavior of the sand-swimming *S. scincus* is well known. These highly specialized heliophile desert skinks consume plant matter as well as animal matter. Stomach contents analyses showed seeds of *Aristida pungens*, *Retama raetam*, *Cyperus conglomeratus*, occasionally flowers of *Genista saharae*, Coleoptera (genera *Phyllognathus*, *Pentodon*, *Pimelia*, *Erodium*, *Leptonychus*, *Scarites*) and their larvae, scorpions, and

juvenile lacertids (*Acanthodactylus* sp.). The skinks strongly prefer larvae and pupae of the aforementioned Coleoptera. Juveniles show a more larvae-dominated diet than adults (HARTMANN 1989a). Foraging techniques are based on visual as well as olfactory senses. Hence, even if the lizards are hidden underneath the sand surface, they are able to locate moving prey with a sensitive sense for vibrations, which allows an exact location of the prey item. Various prey animals can be differentiated with this seismic sense (HAUSCHILD & GABNER 1995). Captive specimens of *S. scincus* accept locusts, crickets, beetle larvae, small cockroaches, seeds of *Phalaris canariensis*, grass seeds, semi-ripe grains, and seeds of *Stellaria media*. Occasionally, sand particles are swallowed.

Sphenops WAGLER, 1830

Sphenops sepsoides (AUDOUIN, 1829)

Number of examined specimens: 3 adults

Distribution:

Libya, Egypt, Sinai, Israel.

Dental morphology:

The right jaw ramus of specimen SRK 00.077 bears 17 tooth positions. The short and robust teeth of *Sphenops sepsoides* are relatively widely spaced. The teeth are of almost cylindrical habitus and they have slightly transversally expanded bases and lingually inwardly curved tooth crowns. The tips of the teeth are distinctly pointed and recurved in the posterolingual direction. The crista mesialis is little longer than the crista distalis and together these two cutting edges form the cuspis labialis. A second cusp, the cuspis lingualis, is situated directly underneath the cuspis labialis. The cuspis lingualis shows a narrow plateau-like occlusal surface which is bordered labially by the narrow antrum intercrisatum. The posteriormost teeth of *S. sepsoides* are unicuspid. The cristae mesialis et distalis steeply slope downward and transform gradually into the prominent but short culmines lateres. The concave surfaces between the sinus-shaped culmines lateres are heavily striated. On each tooth, up to seven prominent short striae run parallel to the longitudinal tooth axes. The striae do not show the tendency for an apical convergence which is found in many other scincomorphans; instead, they run perfectly parallel their entire lengths. The

spaces between the striae are relatively homogeneous. All labial surfaces and the lingual surfaces of the tooth necks and tooth bases are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits of *S. sepsoides* are circular or horizontally elongated.

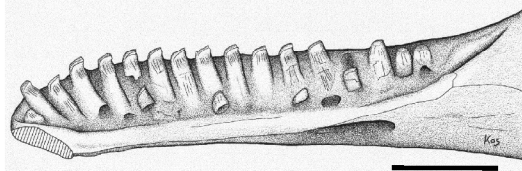


Fig. 107: *Sphenops sepsoides*
(specimen SRK 00.077)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The snout of the desert dwelling *S. sepsoides*, shows several adaptations to a burrowing lifestyle; it hence resembles the snout of *Scincus scincus* (HARTMANN 1989). Accordingly, a comparable diet of the two taxa can be assumed. This diet consists of seeds of *Aristida pungens*, *Retama raetam*, *Cyperus conglomeratus*, occasionally flowers of *Genista saharae*, Coleoptera (genera *Phyllognathus*, *Pentodon*, *Pimelia*, *Erodius*, *Leptonychus*, *Scarites*) and their larvae, scorpions, and juvenile lacertids (*Acanthodactylus* sp.).

Typhlacontias BOCAGE, 1873

Typhlacontias gracilis ROUX, 1907
(Pl. X, Fig. 16)

Number of examined specimens: 1 adult

Distribution:

Namibia, Zimbabwe, Botswana, Angola, Zambia.

Dental morphology:

The right dentary of specimen USNM 159338 bears 13 tooth positions. The fang-like unicuspid teeth of this minute legless burrowing skink are strongly recurved. The teeth are simple conical, pointed, and show circular cross-sections. The apical halves of the teeth of *Typhlacontias gracilis* rise above the labial parapet of the dentary. The largest teeth are situated in the central section of the tooth row. All surfaces are convex and smooth. The ratio tooth length:diameter of tooth neck is

3.6:1.0. The resorption pits are covered by mucosa.

Diet:

The diet of the related *Typhlacontias brevipes* consists of termites, ants, beetles, and ant-lions. The diet of *Typhlacontias gracilis* is probably comparable.

4.1.5 Family Teiidae GRAY, 1827

(Diagnosis: see ESTES 1983)

Remark:

After HARRIS et al. (2001), who analysed the squamate relationships on the basis of *C-mos* nuclear DNA sequences, the Teiidae are no longer included within the Scincomorpha but are an outgroup of all other Squamata (including Serpentes).

4.1.5.1 Subfamily Teiinae MACLEAN, 1974

(Diagnosis: see ESTES 1983)

Traditionally, this group is referred to as the macroteiids.

After SINITSIN (1928) the skulls of this subfamily belong to the catarrhine type.

This subfamily is often treated as a family (Teiidae) opposing the Gymnophthalmidae, but the conclusive taxonomic status is still unsolved.

Ameiva MEYER, 1795

Ameiva ameiva (LINNAEUS, 1758)

Number of examined specimens: 10 adults

Distribution:

Panama, Trinidad, Tobago, Brazil, Colombia, Suriname, French Guiana, Guyana, Venezuela, Bolivia, Ecuador, Peru, Argentina, Lesser Antilles.

Dental morphology:

The right dentary of specimen SRK 00.057 bears 28 tooth positions. The dentition of *Ameiva ameiva* is distinctly heterodont. The anterior portion of the tooth row bears ten to twelve minute and short unicuspid teeth whereas the teeth of the central portion gradually become larger in the caudal direction and show mesial side cusps. These bicuspid teeth are situated approximately between tooth positions 10/11/12 and tooth positions 19/20.

The posterior teeth are tricuspid with an additional distal side cusp which is mostly little smaller than the mesial side cusp. The teeth of *A. ameiva* show cylindrical shafts and lingually compressed tooth crowns. All teeth are pointed except some older teeth that are intensively worn. The tips of the anterior teeth are recurved whereas the central and posterior teeth are straight and almost symmetrical in lingual view. The occlusal cutting edges between the main cusps and the lateral cusps are cut by a deep V-shaped notch. Hence, the lateral cusps are clearly devided from the main cusps. The cristae mesiales and the cristae distales of the main cusps have the same length. This tooth crown morphology is already found in some replacemt teeth which are situated within the resorption pits. All enamel surfaces lack striations. The ratio tooth length:diameter of tooth neck is 3.0:1.0. The resorption pits of *A. ameiva* are of perfectly circular shape.

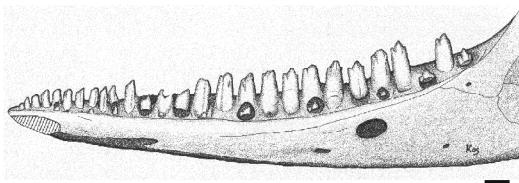


Fig. 108: *Ameiva ameiva*
(specimen SRK 00.057)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

A. ameiva as an active hunter preys on various arthropods and young mice. However, occasionally these lizards consume ripe and sweet fruits (ROGNER 1994).

Ameiva auberi COCTEAU, 1838

(Pl. X, Fig. 17)

Number of examined specimens: 3 adults (including two specimens of *Ameiva auberi sabulicolor* SCHWARTZ, 1970)

Distribution:

Cuba, Isla de la Juventud, Cat Island, Grand Bahama Bank.

Dental morphology:

The right dentary of specimen USNM 220669 (*A. auberi sabulicolor*) bears 20 tooth positions. The tooth morphology is similar to the tooth morphology of *Ameiva ameiva* in all aspects.

Diet:

The diet of *A. auberi* is probably comparable to the dict of *A. ameiva*.

Ameiva bifrontata COPE, 1862

(Pl. X, Fig. 18)

Number of examined specimens: 1 adult

Distribution:

Peru, Colombia, Venezuela, Testigo Island, Dutch Leeward Island, Margarita Island, Aruba Island.

Dental morphology:

The right dentary of specimen ZFMK 21640 bears 29 tooth positions. The dentition of *Ameiva bifrontata* resembles the dentition of *Ameiva ameiva*. In contrast to *A. ameiva*, the posterior teeth of *A. bifrontata* are bicuspid with solely mesial side cusps being developed. The occlusal cutting edges of the investigated specimen are extremely sharp.

Diet:

The diet of *A. bifrontata* is probably comparable to the diet of *A. ameiva*.

Ameiva chrysoleama COPE, 1868

(Pl. X, Figs. 19-21)

Number of examined specimens: 7 adults (including one specimen of *Ameiva chrysoleama boekeri* MERTENS, 1938, two specimens of *Ameiva chrysoleama parvoris* SCHWARTZ & KLINIKOWSKI, 1966, one specimen of *Ameiva chrysoleama regularis* FISCHER, 1838, and two additional specimens of *Ameiva chrysoleama umbratilis* SCHWARTZ & KLINIKOWSKI, 1966)

Distribution:

Hispaniola, Isla Beata, Isla Saona, Isla Catalina, Cayos Siete Hermanos, Isla Cabras, Ile de la Gonave, Ile de la Tortue, Ile a Cabrit, Grosse Caye.

Dental morphology:

The numbers of tooth positions in the various subspecies of *Ameiva chrysoleama* are almost constant: 23 tooth positions are found in specimen USNM 225056 (*A. chrysoleama regularis*), in the male specimen USNM 259527 (*A. chrysoleama boekeri*), and in the female specimen USNM 259532 (*A. chrysoleama parvoris*). The right dentary of specimen USNM 225053 (*A. chrysoleama umbratilis*) bears 21 tooth positions. Sexual dimorphisms in terms of dental morphology

can be excluded at least for this species, in which the sexes of several individuals are known. The highest tooth number among the investigated specimens of *A. chrysolema* is reached by specimen SDS 64800 with 27 tooth positions represented in its right dentary. The tooth morphology of *A. chrysolema* strongly resembles the tooth morphology of *Ameiva ameiva*. However, in contrast to *A. ameiva*, the posterior teeth of *A. chrysolema* are bicuspid with solely mesial side cusps being developed.

Diet:

The diet of *A. chrysolema* is assumed to be comparable to the diet of *A. ameiva*.

Ameiva corax CENSKY & PAULSON, 1992
(Pl. X, Fig. 22)

Number of examined specimens: 4 adults

Distribution:

Lesser Antilles.

Dental morphology:

The right dentary of the female specimen USNM 236388 bears 23 tooth positions. However, only 19 tooth positions are found in another female specimen (USNM 236392). Apart from a slightly more conical tooth habitus and the absence of tricuspid teeth, the teeth of *Ameiva corax* strongly resemble the teeth of *Ameiva ameiva*.

Diet:

The diet of *A. corax* is probably comparable to the diet of *A. ameiva*.

Ameiva dorsalis GRAY, 1838

Number of examined specimens: 2 adults

Distribution:

Jamaica.

Dental morphology:

The right dentary of specimen SDS 63967 bears 23 tooth positions. Apart from a lack of tricuspid teeth, the tooth morphology of *Ameiva dorsalis* is identical with the tooth morphology of *Ameiva ameiva*.

Diet:

The diet of *A. dorsalis* is assumed to be comparable to the diet of *A. ameiva*.

Ameiva erythrocephala DAUDIN, 1802

Number of examined specimens: 1 juvenile, 2 adults

Distribution:

Lesser Antilles (St. Eustatius, St. Christopher, Nevis).

Dental morphology:

The dental morphology of *Ameiva erythrocephala* strongly resembles the dental morphology of *Ameiva ameiva*. The tricuspid teeth in the posterior portion of the tooth row are already found in juveniles.

Diet:

The diet of *A. erythrocephala* is probably comparable to the diet of *A. ameiva*.

Ameiva exsul (COPE, 1862)
(Pl. X, Fig. 23, Pl. XI, Fig. 1)

Number of examined specimens: 1 juvenile, 2 adults

Remark:

Specimen USNM 221745 (*Ameiva exsul desecheensis* HEATWOLE & TORRES, 1967) is cataloged under the synonym *Ameiva desecheensis*.

Distribution:

Puerto Rico (including offshore islands), Vieques, Culebra, Virgin Islands, Mona, Desecheo.

Dental morphology:

The right dentary of the female specimen USNM 221745 (*Ameiva exsul desecheensis*) bears 20 tooth positions. The posteriormost teeth of this specimen are tricuspid. Several teeth show a prominent ridge running from the tip of the main cusp across the lingual surface of the tooth crown to the transition zone between the tooth crown and the tooth neck. The right dentary of the juvenile specimen USNM 314244 bears 23 tooth positions, most of which are occupied by bicuspid teeth whereas tricuspid teeth are not found. In general, the dental morphology of *A. exsul* resembles the dental morphology of *Ameiva ameiva*.

A specimen of *A. exsul alboguttata* illustrated by ESTES (1984) shows bulbous and hypertrophied bicuspid teeth in tooth positions 15 to 18 of the left dentary which are opposed by durophagous teeth in the posterior portion of the maxillary.

Diet:

Data concerning the diet of *A. exsul* are not available.

Remarks:

Fossils of *A. exsul* are known from Late Pleistocene outcrops in Puerto Rico (PREGILL 1981).

Ameiva festiva (LICHTENSTEIN, 1856)
(Pl. XI, Fig. 2)

Number of examined specimens: 3 adults

Distribution:

Mexico, Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panama, Colombia.

Dental morphology:

The dentaries of the investigated specimens of *Ameiva festiva* bear 22 or 23 tooth positions. Several tricuspid teeth are found in the posterior portions of the tooth rows and the dental morphology strongly resembles the dental morphology of *Ameiva ameiva*.

Diet:

The diet of *A. festiva* is probably comparable to the diet of *A. ameiva*.

Ameiva fuscata GARMAN, 1887
(Pl. XI, Fig. 3)

Number of examined specimens: 1 adult

Distribution:

Dominica (Lesser Antilles).

Dental morphology:

The right dentary of specimen USNM 158908 bears 29 tooth positions. The dental morphology of the anterior and central portions of the tooth row strongly resemble the dental morphology of *Ameiva ameiva*. However, the posterior teeth of *Ameiva fuscata* dramatically differ from the posterior teeth of *A. ameiva* since they are of almost globular shape. These crushing teeth are blunt, bulbous, and all enamel surfaces are unwrinkled.

Diet:

The highly modified crushing teeth of *A. fuscata* probably indicate an adaptation for a durophagous diet.

Remarks:

Crushing teeth in *Ameiva fuscata*, *Ameiva griswoldi*, *Ameiva plei*, and in *Ameiva pluvianotata* are already recorded in PREGILL (1984).

Ameiva griswoldi BARBOUR, 1916
(Pl. XI, Fig. 4)

Number of examined specimens: 3 adults

Distribution:

Antigua (Lesser Antilles).

Dental morphology:

The dental morphology of the investigated specimens of *Ameiva griswoldi* strongly resemble the dental morphology of *Ameiva ameiva*. Some tricuspid teeth with minute distal side cusps are situated in the posterior portion of the tooth row in the female specimen USNM 218353. Crushing teeth in *A. griswoldi* were recorded by PREGILL (1984) but were not observed in the investigated specimens here.

Diet:

The diet of *A. griswoldi* is probably comparable to the diet of *A. ameiva*.

Ameiva lineolata DUMÉRIL & BIBRON, 1839

Number of examined specimens: 2 adults (including one specimen of *Ameiva lineolata privigna* SCHWARTZ, 1966)

Distribution:

Hispaniola, Isla Beata, Isla Cabras, Isla Catalina, Isla Cabritos.

Dental morphology:

The teeth of specimen SDS 64832 (*A. lineolata privigna*) are lingually compressed and reach their greatest widths at their bases. The posterior teeth of *A. lineolata* are tricuspid with well developed lateral cusps and pointed tips. Generally, the dental morphology of *A. lineolata* strongly resembles the dental morphology of *Ameiva ameiva*.

Diet:

The diet of *A. lineolata* is probably comparable to the diet of *A. ameiva*.

Ameiva plei (DUMÉRIL & BIBRON, 1839)
(Pl. XI, Figs. 5-8)

Number of examined specimens: 2 juveniles, 6 adults

Distribution:

Lesser Antilles.

Dental morphology:

The numbers of tooth positions in the dentaries of the investigated *Ameiva plei* individuals reach from 17 to 21. The dentition of the juvenile female specimen USNM 236379

strongly resembles the dentition of *Ameiva ameiva*. The posterior teeth are tricuspid with well developed mesial and distal side cusps and pointed central main cusps. This tooth morphology is strongly contrasted by the tooth morphology in individuals of higher individual age. In these older individuals, the five to seven posteriormost teeth are perfectly globular. Interestingly, the last tooth of the tooth row in specimen USNM 236394 again shows a pointed cusp and a conical habitus. Probably the globular shape of the posterior teeth is a result of intensive wear. Hence, the primarily pointed teeth probably become rounded after a certain time of being in function. In this case, the pointed posterior tooth of specimen USNM 236394 belongs to a younger tooth generation than its neighbors, what is also confirmed by the small size of the resorption pit at the basis of this tooth. Another interesting observation is the presence of tricuspid embryonal teeth in the resorption pits at the bases of the crushing teeth. The tricuspidity of the non functional replacement teeth presumes a secondary reconfiguration of the globular shape of the posterior teeth during their erecting as a result of abrasion. The mesolingual and distolingual surfaces of the embryonal teeth are sometimes heavily striated. However, no trace of these striations is found in fully erected teeth, which also suggests an intensive abrasion as a result of wearing processes. The ratio tooth length:diameter of tooth neck is 1.2:1.0 in the hardest worn teeth. The resorption pits of *A. plei* are perfectly circular.

Diet:

The highly modified crushing teeth of *A. plei* probably indicate an adaptation to a durophagous diet.

***Ameiva pluvianotata* GARMAN, 1887**

(Pl. XI, Figs. 9-10)

Number of examined specimens: 5 adults

Distribution:

Lesser Antilles (Montserrat, Redonda Island).

Dental morphology:

The right dentary of specimen SDS 64011 bears 20 tooth positions. Apart from being even more pointed, the teeth of *Ameiva pluvianotata* strongly resemble the tooth morphology observed in *Ameiva ameiva*. PREGILL (1984) observed crushing teeth in *A. pluvianotata*, but the posterior teeth of the

specimens investigated here are typically tricuspid.

Diet:

The diet of *A. pluvianotata* is probably comparable to the diet of *A. ameiva*.

***Ameiva quadrilineata* (HALLOWELL, 1861)**

(Pl. XI, Fig. 11)

Number of examined specimens: 3 adults

Distribution:

Panama, Costa Rica, Nicaragua.

Dental morphology:

The teeth of *Ameiva quadrilineata* are very robust and show slightly bulbous tooth bases. The lateral cusps of the tricuspid posterior teeth are very prominent and large. A deep occlusal notch is found between the main cusp and each of its lateral cusps. Apart from these features, the dentition of *A. quadrilineata* is almost similar to the dentition of *Ameiva ameiva*.

Diet:

The diet of *A. pluvianotata* is probably comparable to the diet of *A. ameiva*.

***Ameiva taeniura* COPE, 1862**

(Pl. XI, Fig. 12)

Number of examined specimens: 1 adult

Distribution:

Hispaniola.

Dental morphology:

The right dentary of specimen USNM 55053 bears 24 tooth positions. The dentition of *Ameiva taeniura* strongly resembles the dentition observed in *Ameiva ameiva*. However, several minor differences between the two taxa were recognized:

- The teeth of *A. taeniura* are maximally bicuspid, tricuspid teeth (which are present in *A. ameiva*) are absent.
- Most teeth are recurved to a certain extent in *A. taeniura* whereas the teeth of *A. ameiva* are straight (except the anteriormost teeth).

Whether these different character states are of taxonomic value or rather individual abnormalities cannot be determined here because of a lack of additional *A. taeniura* specimens.

Diet:

Stomach contents analyses on seven specimens of *A. taeniura* proved a diet consisting predominantly of Dictyoptera and

Diptera (larvae). Smaller percentages of Homoptera, Lepidoptera (larvae), and Orthoptera were also consumed. The ingestion of plant matter presumably happened adventitiously (POWELL 1989).

Ameiva undulata (WIEGMANN, 1834)

Number of examined specimens: 1 adult

Distribution:

Costa Rica, Nicaragua, Honduras, El Salvador, Guatemala, Belize, Mexico.

Dental morphology:

The dentition of *Ameiva undulata* strongly resembles the dentition of *Ameiva ameiva* in all aspects.

Diet:

The diet of *A. undulata* is probably comparable to the diet of *A. ameiva*.

Ameiva wetmorei STEJNEGER, 1913
(Pl. XI, Fig. 13)

Number of examined specimens: 2 juveniles

Distribution:

Puerto Rico.

Dental morphology:

Due to the small size of the specimens, the posterior portions of the casts of the lower jaws stuck to the mould and could not be removed. Therefore the crushing teeth recorded by PREGILL (1984) cannot be described here. The dentition of the anterior portions of the minute dentaries of *Ameiva wetmorei* consists mainly of moderately pointed unicuspid teeth. These teeth show cylindrical shafts and linguallly concave tooth crowns. In several teeth, a prominent ridge runs across the lingual surfaces of the tooth crowns from the tips to the tooth necks. The apices are slightly recurved in the posterolingual direction.

Diet:

The diet of *A. wetmorei* is probably comparable to the diet of *A. ameiva*.

Callopiestes GRAVENHORST, 1838

Callopiestes flavipunctatus (DUMÉRIL & BIBRON, 1839)
(Pl. XI, Fig. 14)

Number of examined specimens: 1 adult

Distribution:

Peru, Ecuador (interandean valleys).

Dental morphology:

The right dentary of specimen BMNH 1900.2.26.11 bears 21 tooth positions. The teeth show cylindrical shafts. The tooth crowns of *Callopiestes flavipunctatus* are linguallly and labially compressed and slightly recurved. The anterior teeth are unicuspid whereas the central and posterior teeth are bicuspid with pointed main cusps and small mesial side cusps. Between the two cusps, the occlusal cutting edges are cut by a deep V-shaped notch. All enamel surfaces are free of striations. The ratio tooth length:diameter of tooth neck is 2.3:1.0. The resorption pits are perfectly circular. The absence of tricuspid teeth in the investigated specimen of *C. flavipunctatus* is less of taxonomic value and more interpreted as an individual character of the solely available specimen since tricuspid teeth were observed in this species by PRESCH (1974).

Diet:

The diet of *C. flavipunctatus* is assumed to be comparable to the diet of *Callopiestes maculatus*.

Remarks:

Fossils of this genus are known from the Pliocene (ALBINO 1996). GORMAN (1970) assumed *Callopiestes* to be closely related to the basis of primitive members of the genus *Dracaena*. This author further assumed that a teiid ancestor moved from America to Asia and gave rise to the lacertids.

Callopiestes maculatus GRAVENHORST, 1838
(Pl. XI, Fig. 15)

Number of examined specimens: 7 adults

Distribution:

Chile.

Dental morphology:

The right dentary of specimen ZFMK 7828 bears 21 tooth positions. However, only 17 tooth positions are found in specimen ZFMK 7858. Despite the presence of tricuspid teeth in the posterior portions of the tooth rows in *Callopiestes maculatus*, the teeth of *C.*

maculatus are almost similar to the teeth of *Callopiastes flavipunctatus*. The distal side cusps are always smaller and situated in a lower position than the mesial side cusps.

Diet:

GREENE (1982) observed a tendency for eating other lizards in *C. maculatus*. Usually, these lizards consume large arthropods and juvenile mice (ROGNER 1994). In the wild, probably other small mammals are consumed in addition to the aforementioned food items.

***Cnemidophorus* WAGLER, 1830**

***Cnemidophorus communis* COPE, 1878**

Number of examined specimens: 1 adult

Distribution:

Mexico.

Dental morphology:

The tooth morphology of *Cnemidophorus communis* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

The only significant dietary differences in sympatric *Cnemidophorus* species are associated with body size; smaller species tend to eat smaller prey items (WRIGHT & VITT 1993). Most species of this genus are generalized, opportunistic insectivores.

***Cnemidophorus exsanguis* LOWE, 1956**
(Pl. XI, Fig. 16)

Number of examined specimens: 4 adults

Remark:

The specimens SDS 63187 and SDS 63254 are cataloged under the synonym *Cnemidophorus exsanguis*.

Distribution:

USA (Arizona, Texas), Mexico.

Dental morphology:

The right dentary of specimen SDS 64562 bears 18 tooth positions. The tooth morphology of *Cnemidophorus exsanguis* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

The food of this parthenogenetic species consists of insects and spiders (ROGNER 1984). Generally, the diet of whiptail lizards is composed of relatively sedentary prey (particularly termites) that are simply picked up upon encounter; these lizards appear to have

difficulties in successfully pursuing evasive prey such as grasshoppers and flying insects (EIFLER & PASSEK 2000). A detailed analysis of stomach contents from *C. exsanguis* proved a diet composition (percent volume) consisting of 37.5 % Lepidoptera (mainly moths and their larvae), 19.7 % Coleoptera, 9.6 % Hymenoptera, 9.3 % Araneida, 8.1 % Orthoptera, 5.6 % unidentified larvae, 2.9 % Hemiptera, 2.5 % Neuroptera, 2.4 % Diptera, and 2.4 % other prey items (MEDICA 1967). STEBBINS (1985) records scorpions as part of the diet of *C. exsanguis*.

***Cnemidophorus gularis* BAIRD & GIRARD, 1852**

Number of examined specimens: 6 adults

Distribution:

USA (Texas, Oklahoma), Mexico.

Dental morphology:

The dentaries of the investigated specimens of *Cnemidophorus gularis* bear 20 to 21 tooth positions on average. The two anteriormost teeth are unicuspid, conical, and slightly recurved; the teeth in tooth positions 3 to 16 or 17 are bicuspid with a small but clearly separated mesial side cusp. The four or three posteriormost teeth are tricuspid with an additional minute distal side cusp.

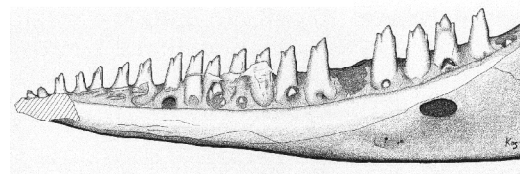


Fig. 109: *Cnemidophorus gularis*
(specimen SRK 00.064)
Right dentary; lingual view
Scale bar: 1.0 mm

In specimen SRK 00.064, the posteriormost tooth again is bicuspid. The main cusps of the slender teeth in the central portion of the tooth row are slightly recurved whereas the more robust posterior teeth are perfectly straight. The cristae mesiales et distales are formed as sharp ridges. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits are of perfectly circular shape.

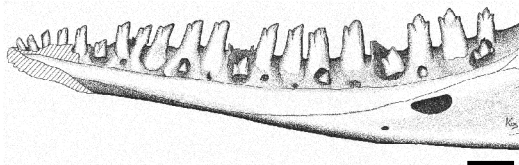


Fig. 110: *Cnemidophorus gularis* (specimen SRK 00.102)
Right dentary, demonstrating the intraspecific similarities in jaw morphology; lingual view
Scale bar: 1.0 mm

Diet:

C. gularis consumes predominantly termites and locusts. However, other insects and spiders are also preyed on in minor percentages (ROGNER 1994). The volume of termites in the diet of *C. gularis* is 32.3 % (MEDICA 1967).

***Cnemidophorus guttatus* WIEGMANN, 1834**

Number of examined specimens: 1 adult

Remark:

The solely available specimen belongs to the subspecies *Cnemidophorus guttatus immutabilis* COPE, 1878.

Distribution:

Mexico.

Dental morphology:

The tooth morphology of *Cnemidophorus guttatus* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

C. guttatus is assumed to be a generalized, opportunistic insectivore like most species in the genus *Cnemidophorus*.

***Cnemidophorus hyperythrus* COPE, 1864**
(Pl. XI, Fig. 17)

Number of examined specimens: 3 adults

Remark:

Specimen SDS 64563 belongs to the subspecies *Cnemidophorus hyperythrus beldingi* (STEJNEGER, 1894).

Distribution:

USA (California, New Mexico), Mexico.

Dental morphology:

The teeth of *Cnemidophorus hyperythrus* are perfectly conical with circular cross-sections and pointed tips. The tooth crowns are not or only slightly compressed. The approximately three anterior teeth are

unicuspid whereas all following teeth are bicuspid with slightly recurved main cusps and minute mesial side cusps. These lateral cusps are strongly connected to the main cusps. All enamel surfaces lack striations. The ratio tooth length:diameter of tooth neck is 2.8:1.0. The resorption pits are of perfectly circular shape.

Diet:

The diet of *C. hyperythrus* consists mainly (85.05 %) of termites (MEDICA 1967). This termite-dominated diet corresponds well with the extremely pointed tooth tips and the mainly insular distribution of this species on Baja California. In addition, beetles and spiders are consumed by this whiptail lizard (STEBBINS 1985).

***Cnemidophorus lemniscatus* (LINNAEUS, 1758)**

(Pl. XI, Fig. 18)

Number of examined specimens: 6 adults

Distribution:

Guatemala, Belize, Honduras, Nicaragua, Panama, Colombia, Venezuela, Brazil, Trinidad, Tobago, Pato, Margarita, Coche, Cubagua, Aruba, St. Thomas, Swan, Milford, Isla San Andres, Isla de Providencia, Isla St. Catalina.

Dental morphology:

The majority of the investigated dentaries of *Cnemidophorus lemniscatus* bear 19 or 20 tooth positions. Some six unicuspid anterior teeth are followed by two or three bicuspid teeth; the first tricuspid tooth appears already in tooth position 9. Accordingly, the majority of the teeth are tricuspid in *C. lemniscatus*. The tooth crowns are lingually and labially compressed. In contrast to the slender anterior and central teeth, the posterior teeth are rather robust and enlarged. The occlusal notches between the main cusps and the lateral cusps are cut deeper than in any other investigated *Cnemidophorus* species. The lateral cusps are relatively large and the distal side cusps are the same size as the mesial side cusps. In specimen USNM 313933, the lateral cusps are extremely long and sometimes slightly recurved in the downward direction. The cristae mesiales et distales are extremely sharp. The tips of the main apices are slightly bend in the lingual direction. All enamel surfaces are free of striations. The ratio tooth length:diameter of tooth neck is 3.5:1.0 in

central teeth. The resorption pits are perfectly circular.

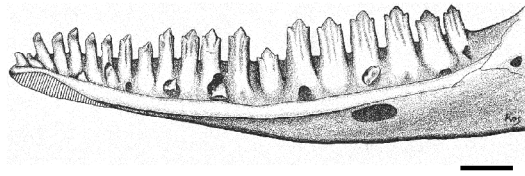


Fig. 111: *Cnemidophorus lemniscatus*
(specimen SRK 00.023)
Right dentary; lingual view
Scale bar: 1.0 mm

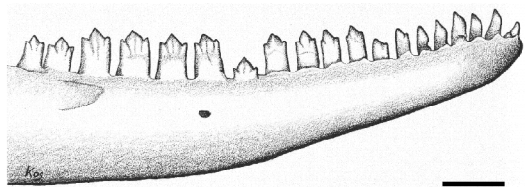


Fig. 112: *Cnemidophorus lemniscatus*
(specimen SRK 00.023)
Right dentary; labial view
Scale bar: 1.0 mm

Diet:

C. lemniscatus consumed various semiadult crickets (*Acheta domestica*, *Gryllus* sp.) in my terrarium (pers. observation).

Cnemidophorus murinus (LAURENTI, 1768)
(Pl. XI, Fig. 19)

Number of examined specimens: 1 adult

Distribution:

Curacao, Bonaire Islands.

Dental morphology:

The right dentary of specimen BMNH 91.11.4.-16. bears 21 tooth positions. The posterior tricuspid teeth are barrel-shaped in the solely available specimen of *Cnemidophorus murinus*. The lateral cusps are strongly connected to the blunt main cusp and the distances between the tip of the main cusp and the tips of the lateral cusps are unusually short. The anterior and central teeth are slender; they show cylindrical shafts and pointed bicuspid tooth crowns. The lingual surfaces of these tooth crowns are concave and the tips of the main cusps are posterolingually directed. Maximally four striae are situated at the distal

sections of these concave surfaces. The striae are formed as prominent parallel running ridges that stretch in the apical direction from the transition zone between the tooth neck and the tooth crown to the vicinity of the tip of the main cusp where they gradually decrease. *C. murinus* is the only species of the genus in which striations of the tooth enamel are found.

Diet:

No data concerning the diet of *C. murinus* were available.

Remarks:

As a member of the *lemniscatus* species group, *C. murinus* was assumed to be "primitive" since it retained some *Ameiva*-like features. The North American species groups sequentially derived from this root (WRIGHT & VITT 1993).

Cnemidophorus sackii WIEGMANN, 1834
(Pl. XI, Fig. 20)

Number of examined specimens: 2 adults

Distribution:

Mexico.

Dental morphology:

The right dentary of specimen USNM 165690 bears 18 tooth positions. The tooth morphology of *Cnemidophorus sackii* is similar to the tooth morphology of *Cnemidophorus gularis*. Opposing the observations of PRESCH (1974), who stated the teeth of *C. sackii* as being "biconodont" (bicuspid), distinctly tricuspid teeth are found in specimen USNM 165690.

Diet:

Data concerning the diet of *C. sackii* were not available.

Remarks:

A left dentary of *C. sackii* illustrated in OLSON (1986) bears 21 tooth positions. This author stated that variations in the dentitions of the genus *Cnemidophorus* do exist equally among the groups: "The number of teeth and this ratio overlap extensively, making it extremely impractical to attempt to use these characters in classification of species" (OLSON 1986).

Cnemidophorus sexlineatus (LINNAEUS, 1766)
(Pl. XI, Fig. 21)

Number of examined specimens: 4 adults

Distribution:

Texas, New Mexico, Colorado, Wyoming, South Dakota, Nebraska, Kansas, Oklahoma, Missouri, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Florida, South Carolina, North Carolina, Tennessee, Kentucky, Virginia, Maryland, Illinois, Iowa, Wisconsin, Michigan, Minnesota), Mexico.

Dental morphology:

The left dentary of specimen USNM 220273 bears 21 tooth positions. The tooth morphology of *Cnemidophorus sexlineatus* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

C. sexlineatus consumes insects, spiders, and snails (STEBBINS 1985). Detailed studies of the diet of *C. sexlineatus* were made by PAULISSEN (1987) who observed different prey preferences among various age groups. PAULISSEN states that grasshopper-like insects are the most valuable prey for adults, whereas plant and ground arthropods are the most valuable prey for juveniles. Each age-class adopts foraging tactics which increase the chances to find the most valuable prey.

Cnemidophorus sonorae LOWE & WRIGHT, 1964
(Pl. XI, Fig. 22)

Number of examined specimens: 4 adults

Distribution:

USA (Utah, Colorado, Arizona, New Mexico), Mexico.

Dental morphology:

The right dentary of specimen SDS 64564 bears 21 tooth positions. The tooth morphology of the parthenogenetic *Cnemidophorus sonorae* is almost similar to the tooth morphology of *Cnemidophorus gularis*. In the posterior tricuspid teeth, the occlusal notches which are situated between the main cusp and the lateral cusps are cut deeper in *C. sonorae* than they are in *C. gularis*.

Diet:

C. sonorae consumes grasshoppers (Acrididae) and termites (EIFLER & PASSEK 2000).

Cnemidophorus tessellatus (SAY, 1823)
(Pl. XI, Fig. 23)

Number of examined specimens: 4 adults

Distribution:

USA (Colorado, New Mexico, Texas), Mexico.

Dental morphology:

Aside from the complete lack of tricuspid teeth, the tooth morphology of *Cnemidophorus tessellatus* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

The parthenogenetic *C. tessellatus* was observed preying upon a wide variety of food items in the studies of WRIGHT & VITT (1993). STEBBINS (1985) mentions insects, spiders, and centipedes as prey items of *C. tessellatus*.

Cnemidophorus tigris BAIRD & GIRARD, 1852
(Pl. XII, Fig. 1)

Number of examined specimens: 7 adults

Distribution:

USA (Idaho, Oregon, Utah, California), Mexico.

Dental morphology:

The right dentary of specimen USNM 229863 bears 21 tooth positions and there are even 23 tooth positions found in specimen USNM 292549. Aside from the absence of tricuspid teeth, the tooth morphology of *Cnemidophorus tigris* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

C. tigris was observed preying upon a wide variety of food items (WRIGHT & VITT 1993). The diet of this species consists of insects, spiders, scorpions, and lizards (STEBBINS 1985). According to a more detailed analysis, the diet of *C. tigris* consists of 38 % Lepidoptera (mainly moths and their larvae), 18.6 % Coleoptera, 9.7 % unidentified larvae, 8.6 % Araneida, 7.9 % unidentified parts, 7.8 % others, 6.0 % Diptera, 5 % Orthoptera, and 4.6 % Hymenoptera (MEDICA 1967).

Cnemidophorus uniparens WRIGHT & LOWE, 1965
(Pl. XII, Fig. 2)

Number of examined specimens: 4 adults

Distribution:

USA (Arizona, New Mexico), Mexico.

Dental morphology:

The right dentary of specimen SDS 66596 bears 19 tooth positions. The tooth morphology of *Cnemidophorus uniparens* is similar to the tooth morphology of *Cnemidophorus gularis*.

Diet:

C. uniparens consumes insects (STEBBINS 1985). In experimental studies, the observed specimens of *C. uniparens* preyed upon grasshoppers (Acrididae) and termites (EIFLER 2000).

Remarks:

C. uniparens is a parthenogenetic triploid species.

Cnemidophorus vanzoi (BASKIN & WILLIAMS, 1966)
(Pl. XII, Fig. 3)

Number of examined specimens: 4 adults

Distribution:

Maria Island (off SE coast of St. Lucia).

Dental morphology:

The dentaries of *Cnemidophorus vanzoi* bear 18 (SDS 65759) to 21 (SRK 00.101) tooth positions. Compared to *Cnemidophorus gularis*, the number of tricuspid teeth is higher in *C. vanzoi*. The three or four most anterior teeth are unicuspid. These are followed by several bicuspid teeth which again are followed by numerous tricuspid teeth. In specimen SRK 00.101, tooth position 9 already bears a tricuspid teeth and a total of 13 tricuspid teeth is found throughout the entire tooth row. The anterior teeth are slender and cylindrical whereas the posterior teeth are enlarged and robust. The tooth crowns are lingually and labially compressed and appear symmetrical in lingual view since the cristae mesiales et distales are the same lengths. The mesial side cusps and the distal side cusps are of equal size. The lateral cusps are almost as pointed as the main cusps. The lateral cusps are separated from the main cusps by deep occlusal notches. All enamel surfaces lack striations. The ratio tooth length:diameter of tooth neck is

4.0:1.0 in central teeth. The resorption pits are of perfectly circular shape.

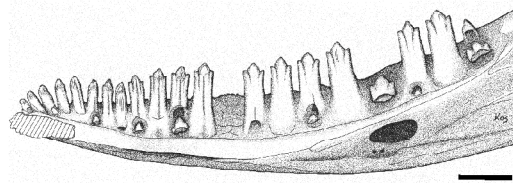


Fig. 113: *Cnemidophorus vanzoi*
(specimen SRK 00.101)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

Data on the diet of *C. vanzoi* were not available.

Crocodilurus SPIX, 1825

Crocodilurus lacertinus (DAUDIN, 1802)
(Pl. XII, Fig. 4)

Number of examined specimens: 1 adult

Distribution:

French Guiana, Brazil, Colombia, Venezuela, Peru.

Dental morphology:

The right dentary of the solely available specimen bears 17 tooth positions. The dentition of *Crocodilurus lacertinus* is heterodont and rather particular. The seven anterior teeth are unicuspid, pointed, and slightly recurved. The shafts of these teeth are cylindrical and the enamel surfaces are perfectly unwrinkled. These teeth gradually transform into tricuspid teeth in the posterior section of the tooth row. These posterior teeth are highly modified. The tooth bases, the tooth necks, and the tooth crowns are extremely compressed lingually and labially. The widths of the tooth bases are larger than the widths of the tooth crowns. The lateral cusps appear miniaturized. However, they are clearly separated from the main cusp by deep occlusal notches. The lateral cusps are of equal size. The main cusps are pointed and show sharp occlusal cutting edges (cristae mesiales et distales) which are the same length and enclose an apical angle of approximately 100°. The lingual surfaces of the tooth crowns are distinctly striated. Some 20 striae are found in the tooth occupying tooth position 15. The

striae are fine, but at least the striae which are situated in the center of the field of striations are sometimes distinctly prominent. The striae converge apically and end at the tip of the main cusp. The labial surfaces of the tooth crowns are striated as well. However, the striations are weaker here than at the lingual surfaces. This tooth morphology is rather unusual among teiids. The tooth bases of *C. lacertinus* are partly covered by cementum. The ratio tooth length:diameter of tooth neck is 2.8:1.0 in anterior and is 1.1:1.0 in posterior teeth. The resorption pits are not preserved in this cast.

Diet:

No data concerning the diet of *C. lacertinus* were available. However, the trophic structure of this taxon is especially interesting because of its exceptional dentition.

Remarks:

ESTES (1964) records "slight wrinkling of the crown surface" in the closely related and probably ancestral *Chamops segnisi* from the Cretaceous Lance formation. *Crocodylus* is probably the most primitive of all tupinambid genera (RIEPEL 1980).

Crocodylus lacertinus is able to walk bipedally over water surfaces like some *Basiliscus* species (VANZOLINI & VALENCIA 1965).

Dicrodon DUMERIL & BIBRON, 1839

Dicrodon guttulatum DUMERIL & BIBRON, 1839

(Pl. XII, Figs. 5-8)

Number of examined specimens: 3 adults

Remark:

The female specimen SDS 30842 was cataloged under the synonym *Dicrodon lentiginosus*.

Distribution:

Ecuador, Peru.

Dental morphology:

The right dentary of specimen BMNH 1932.9.7.-8 bears 20 tooth positions whereas only 15 tooth positions are found in the right dentary of specimen SDS 30842. The dentition of *Dicrodon guttulatum* is unique among scincomorphans since it is heterodont to the highest degree. The anterior portion of the dentary bears approximately 6 unicuspid teeth. The shafts of these teeth are conical and the tooth crowns are pointed and slightly recurved. The lingual surfaces of the tooth crowns are

flattened or concave. The cristae mesiales are little longer than the cristae distales. All enamel surfaces are unwrinkled in the anterior teeth. In the central portion of the tooth row, the teeth gradually transform into the multicuspid molariforms which are situated in the posterior portion of the tooth row. These molariforms are highly derived and point out that *D. guttulatum* is a specialized feeder. In occlusal view, these teeth are transversally expanded and appear oval. The tooth necks are short, massive, and robust. The tooth crown morphology is dominated by two pyramid-shaped main cusps. The lingual main cusp is distinctly shorter than the lingual main cusp. Both main cusps are pointed and show an apical angle of 70°. The central surface of the tooth which is situated between the main cusps is formed as a deep depression. The posterior margin of this central hollow is framed by three or four lateral cusps. These lateral cusps are moderately pointed and they increase in the lingual direction, so that the largest lateral cusp is situated in the immediate vicinity of the lingual main cusp. The anterior margin of the central depression is marked by a ridge from which the surface of the anterior flank drops steeply. The enamel surfaces of the two dominating cusps are heavily striated lingually as well as labially. About fifty striae are found at each of the labial cusps in specimen SDS 30842. The spaces between the striae are almost constant and the striae converge apically directly at the tips of the main cusps. The intensity of the striations varies among various teeth and also between different individuals. In specimen BMNH 1932.9.7.-8, the striae are less pronounced than in specimen SDS 30842. The ratio tooth length:diameter of tooth neck is 4.3:1.0 in anterior teeth and is 1.9:1.0 in posterior teeth. The resorption pits are of perfectly circular shape.

Diet:

The herbivorous *D. guttulatum* consumes fruits and leaves of *Prosopis* trees (GREENE 1982) and is hence considered as being predominantly phytophagous. The related *Dicrodon heterolepis* is strictly vegetarian (PRESCH 1974).

Remarks:

The complex molariforms of *D. guttulatum* strongly resemble the cheek teeth of the Cretaceous *Peneteius aquilonius* (ESTES 1969). These teeth perfectly occlude with the corresponding teeth of the upper jaw (MACLEAN 1974). The later author illustrated a

Dicrodon specimen (AMNH 21871) that bears 12 unicuspid teeth in the anterior portion of the dentary. The herbivorous and comparably small sized *Dicrodon guttulatum* is an exception of the rule that only a large body size provides the physical strength necessary for an adequate reduction of vegetation (SOKOL 1967).

Dracaena DAUDIN, 1802

Dracaena guianensis (LACÉPÈDE, 1788)
(Pl. XII, Figs. 9-10)

Number of examined specimens: 2 adults

Distribution:

Brazil, Colombia, Ecuador, Peru, French Guiana.

Dental morphology:

The right dentary of specimen USNM 71729 bears 12 tooth positions. All teeth of *Dracaena guianensis* are unicuspid. However, a heterodonty concerning the sizes and the shapes of the teeth does exist. The anterior teeth of this highly specialized molluscivorous species are small and conical and show inwardly curvatures of the lingual surfaces of the tooth crowns. The tips of the anterior teeth are pointed. In strong contrast to this condition, the posterior teeth are represented as large globular crushing teeth. The apical surfaces of the anterior teeth are heavily striated lingually as well as labially. Some 40 striae are found in the first tooth. The apical surfaces of the mushroom-shaped crushing teeth show a unique pattern of striations. Bulge-like structures ("Dentinzylinder" *sensu* PEYER (1929)) are arranged radially around the rounded apex. These swollen bulges have relatively constant diameters of about 0.1 mm and stretch continuously from the highest point of the tooth to the tooth neck. SANDER (1999) describes "radial wrinkles that meet apically in an elongate crest zone". In the specimens investigated in this work, the wrinkles meet in one point at the apex, and an elongate crest zone is not developed. The bulges are separated by deep notches ("Konturlinien" and "Vertikalfurchung" *sensu* PEYER (1929)). The pattern of striations dissolves into fragmentation in several basal areas. The result of this transformation of the enamel surface morphology is the presence of crater-like depressions that are irregularly arranged. The ultrastructures observed in *D. guianensis* can best be compared to ultrastructures found in the

teeth of several species of the scincid genus *Tiliqua*. The ratio tooth length:diameter of tooth neck is 1.6:1.0 in anterior teeth and is 0.6:1.0 in posterior teeth. The resorption pits are circular or laterally extended.



Fig. 114: *Dracaena guianensis*
Outline drawing after PEYER (1929).
Right mandible; labial view
Without scale

Extensively striated posterior teeth in *D. guianensis* are already recorded by ESTES & WILLIAMS (1984). These authors stated two parallel tooth generations for this species, which are not fused.

The teeth of the upper and lower jaws of *D. guianensis* do not meet in occlusion (DALRYMPLE 1979); this strongly contrasts the chewing mechanisms of *Dicrodon guttulatum*.

Diet:

D. guianensis is a durophagous species that predominantly consumes water snails (ROGNER 1994), but also feeds on terrestrial gastropods. RAND (1964) observed *D. guianensis* foraging underwater. The lizards were completely submerged in approximately 30 cm deep water and hunted for snails which were brought to the surface and swallowed there. In addition, mussels are consumed by *D. guianensis* (CONANT 1955).

Remarks:

Fossil representatives of this group, e.g., *Paradracaena colombiana*, are known from the Miocene of South America (ALBINO 1996, SULLIVAN & ESTES 1997). The subacrodont dentition of this fossil species already presented finely striated molariforms (ESTES 1961).

The evolutionary history of this taxon was worked out by GORMAN (1970), who stated that Gerrhosauridae and Lacertidae are the closest relatives of the Teiidae. GORMAN further stated that *Callopietes* is close to the basis of the primitive *Dracaena*. PRESCH (1974) stated *Dracaena* as the "most derived genus" of the Teiidae.

The more primitive recent sister taxon *Dracaena paraguayensis* is also a shell crusher (VANZOLINI & VALENCIA 1965). These

authors describe an extreme tendency for acrodoncy in *Dracaena*, leading to the formation of pseudo-alveoli which give the molariforms the needed support for their shell-crushing function. The correlation between the dental structure and the diet in *D. guianensis* was already recognized by VOROBYEVA & CHUGUNOVA (1991), who stated that any adaptation for herbivory involves solely the crown apex. The crushing teeth are found even in juvenile individuals of *D. guianensis* and hence are not the result of ontogenetic alteration. A trend for the reduction in tooth numbers during the evolution of the genus *Dracaena* does exist (DAIRYMPLE 1979).

***Kentropyx* SPIX, 1825**

***Kentropyx calcarata* (SPIX, 1825)**
(Pl. XII, Figs. 11-13)

Number of examined specimens: 1 adult

Distribution:

Brazil, Bolivia, Guyana, French Guiana, Suriname, Venezuela.

Dental morphology:

The right dentary of specimen BMNH 1902.5.29.91 bears 22 tooth positions. The dental morphology of *Kentropyx calcarata* strongly resembles the dental morphology of *Ameiva ameiva*. However, in contrast to the unwrinkled enamel surfaces of *A. ameiva* some distinct striations are found in *K. calcarata*. The striations are restricted to the lingual surfaces of the tooth crowns and are best developed in the teeth between tooth position 3 and tooth position 15. These tooth positions include unicuspid, bicuspid, and tricuspid teeth. Some ten striae can be found in a solely tooth. The striae are pronounced and they are best developed in the centers of the concave inner surfaces of the tooth crowns. The striae converge apically, and several striae show a bifurcation in the basal direction. The posterior teeth are completely unwrinkled. The ratio tooth length:diameter of tooth neck is 2.5:1.0 in central teeth. The resorption pits are of circular shape.

Diet:

No data on the diet of *K. calcarata* are available.

***Teius* MERREM, 1820**

***Teius teyou* (DAUDIN, 1802)**
(Pl. XII, Figs. 14-18)

Number of examined specimens: 5 adults

Distribution:

Brazil, Bolivia, Uruguay, Argentina, Paraguay.

Dental morphology:

The dentaries of the investigated specimens bear 14 (specimen IFSZ 25471) to 16 (specimen BMNH 1910.12.16.4.-12.) tooth positions. The dentitions represent two extremely different morphotypes what leads to the conclusion that specimen IFSZ 25471 was probably wrongly determined and actually belongs to the genus *Tubinambis*. The dentition of *Teius teyou* consists of unicuspid anterior teeth with cylindrical shafts and pointed recurved apices, and molariform posterior teeth. The molariforms of *T. teyou* resemble the molariforms of *Dicrodon guttulatum* since they are transversally expanded and are dominated by two pyramid-shaped main cusps. The lingual main cusp is situated in a slightly more anterior position and distinctly shorter than the lingual main cusp. Both main cusps are pointed and show an apical angle of 50° (cuspis labialis) or 60° (cuspis lingualis). The main cusps are linked by an flange-like occlusal ridge that drops at the labial surface of the lingual cusp into a central depression and rises again at the lingual surface of the labial cusp. The labial cusp is more than double as long as the lingual cusp. Additional lateral cusps which are present in *Dicrodon*, are not found in *T. teyou*. The tooth necks are short, massive, and robust. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 2.0:1.0 in the molariform teeth. The resorption pits are of circular shape. The dentition of specimen IFSZ 25471 is adapted to a durophagous trophic structure and shows enlarged globular posterior teeth which are heavily radially striated. Accordingly, I assume that this specimen was determined as *T. teyou* accidentally.

Diet:

T. teyou is probably a herbivorous species. However, data on the diet of this species are not available.

Remarks:

Like in *Dicrodon guttulatum*, the posterior molariform teeth in the dentary of *T.*

teyou perfectly occlude with the corresponding teeth of the maxilla (MACLEAN 1974).

Tupinambis DAUDIN, 1802

Tupinambis merianae (DUMÉRIL & BIBRON, 1839)

(Pl. XIII, Figs. 1-4)

Number of examined specimens: 8 adults

Remark:

All specimens were cataloged under the synonym *Tupinambis teguixin*. This species was renamed after AVILA-PIRES in 1995 proved that the lectotype of *T. teguixin* actually was a *T. nigropunctatus* specimen (KÖHLER & LANGERWERF 2000).

Distribution:

Brazil, Argentina, Uruguay, Bolivia.

Dental morphology:

The right dentaries of *Tupinambis merianae* bear 15 (specimen ZFMK 21638) to 18 (specimen ZFMK 53532) tooth positions. Most teeth are unicuspid, but the outer shape and the size of the teeth greatly vary:

- The anterior teeth are conical, unicuspid, and recurved. Their pointed tooth crowns are lingually concave. The cristae mesialis et distalis are well developed and are the same length. The concave lingual surfaces of the tooth crowns are covered by extremely fine striations. The ratio tooth length:diameter of tooth neck is 2.0:1.0 in the anterior teeth.

- The central teeth of the tooth row are bicuspid. They show minute mesial side cusps and large blunt main cusps. The lateral cusp in most central teeth is separated from the main cusp by a deep occlusal notch. The entire apical surfaces of the teeth are heavily crenulated. These striae are formed as sharp prominent ridges which are separated by deep furrows. Some 60 to 70 striae can be found in a single tooth. These striae are arranged radially around the apex. The striae are not restricted to the main cusps but are present in several lateral cusps as well. The intensity of the striations is higher at the lingual surfaces of the teeth than it is at the labial surfaces. The ratio tooth length:diameter of tooth neck is 1.5:1.0 in the central teeth.

- The posterior teeth are highly derived crushing teeth with a complex tooth crown morphology. These crushing teeth are mesially expanded (in occlusal view, the longitudinal widths of these molariforms are 2.5 times

larger than the transversal widths) and of globular or flattened habitus. The occlusal surfaces of the teeth are often concave and show small central uplifts with pointed apices. In several crushing teeth, an elongated apical crest which is mesially orientated is found. The prominent striae which are found at the apical surfaces of the crushing teeth converge at this crest. In the largest crushing teeth which are usually situated in tooth positions 12 to 15, the surfaces of the anterior and posterior flanks appear as bulge-like processes. These processes almost overlap the mesial and distal portions of the teeth and sometimes rise above the central apex. Interestingly, the surfaces of these processes are unwrinkled whereas the lingual and labial surfaces of the tooth crowns are heavily crenulated. The ratio tooth length:diameter of tooth neck is 0.5:1.0 in the molariform teeth. The resorption pits are laterally expanded. ESTES (1961) describes resorption pits (replacement crypts) in interdental positions; a slightly shifting of the large resorption pits in the caudal direction is also visible in the individuals investigated for this thesis.

Diet:

T. merianae is a voracious omnivor. An adult female in my terrarium consumes chicken legs, eggs, large insects (Blattaria, *Grillus* sp., *Anacridium aegypticum*), and occasionally soft sweet fruits as grapes, bananas, pears, and cherries. This large tegu shows a strong preference for terrestrial Gastropoda (*Cepaea* sp., *Achatina* sp.), which are easily crushed between the strong jaws. The crushed snails are put down, investigated with the tongue, and are then once again crushed between the jaws. This procedure is repeated several times. Most shell fragments are flicked away by the tongue before the soft parts of the snails are swallowed. MERCOLLI & YANOSKY (1994) proved complete snail shells with operculae in the digestive tracts of *T. merianae* and assumed an ingesting of snails without chewing. Egg shells are crushed by flinging the eggs to the ground (KÖHLER & LANGERWERF 2000). However, the lizards often puncture the egg shells with the help of their crushing teeth and lick the contents of the eggs through a minute hole with their long tongue until the egg is emptied (pers. observation). Stomach contents analyses of wild *T. merianae* individuals proved a predominantly vegetarian diet (66.8 % plant matter) and a lower percentage of animal food (12.9 % invertebrates (molluscs, insects)

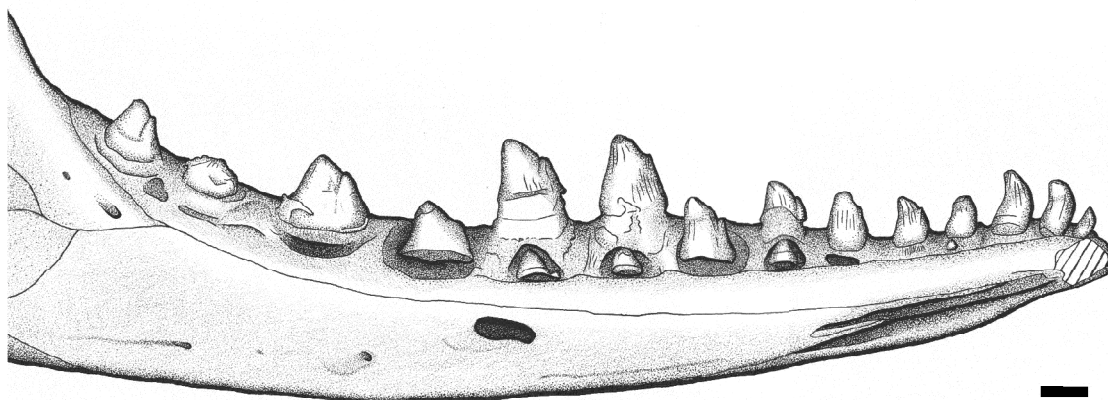


Fig. 115: *Tupinambis teguixin*
(specimen SRK 00.195)
Left dentary; lingual view
Scale bar: 1.0 mm

and 20.3 % vertebrates (bird eggs, fish, amphibians, snakes, and small mammals)) (KÖHLER & LANGERWERF 2000, LANGERWERF 1995). Detailed stomach contents analyses on 70 individuals of *T. merianae* (the formerly *Tupinambis teguixin*) were published by MERCOLLI & YANOSKY (1994). The dominating food types in this study are the plants Pindó (25.40 Vol. %), Palma (11.43 Vol. %), Mora (7.85 Vol. %), Coquito (7.12 Vol. %), Higuerón (1.90 Vol. %), and Congorosa (1.81 Vol. %), the invertebrate groups Gastropoda (6.94 Vol. %), Lepidoptera (larvae) (1.87 Vol. %), and Crustacea (0.99 Vol. %), the vertebrate groups Amphibia (Anura) (10.44 Vol. %), Mammalia (Rodentia) (3.20 Vol. %), Pisces (1.87 Vol. %), Serpentes (1.44 Vol. %), Aves (eggs) (1.42 Vol. %), and adult Aves (1.17 Vol. %).

Remarks:

T. merianae is known from the late Miocene and early Pliocene of South America. *Tupinambis huilensis* from the Miocene of South America is the oldest representative of this group (ALBINO 1996). Presch (1974) described an ontogenetic change in the tooth structure. The dentitions of juvenile individuals show homodont and sharply pointed anterior teeth which grade into a tricuspid condition caudally. Unfortunately, juvenile specimens were not available for the present study.

Tupinambis teguixin (LINNAEUS, 1758)
(Pl. XIII, Fig. 7)

Number of examined specimens: 2 semiadults,
1 adult

Remark:

Specimens SDS 64932 and SDS 67087 were cataloged under the synonym *Tupinambis nigropunctatus*.

Distribution:

Brazil, Peru, Colombia, Venezuela, Ecuador, Trinidad, Argentina, Uruguay, Bolivia, Guyana, Suriname, French Guiana.

Dental morphology:

DESSEM (1985) described identical dentitions of *Tupinambis merianae* (formerly *Tupinambis teguixin*) and *Tupinambis teguixin* (formerly *Tupinambis nigropunctatus*). However, the dentitions of these two taxa show extremely different morphologies. The left dentary of specimen SRK 00.195 bears 14 tooth positions. The dentition of *T. teguixin* is heterodont with 7 or 8 small recurved anterior teeth and large bicuspid or tricuspid teeth in the central and posterior portions of the tooth row. The anterior teeth are fang-like and show unicuspid tooth crowns with concave lingual surfaces. Approximately at tooth position 5 the teeth develop minute mesial side cusps which gradually become more pronounced in the caudal direction. The concave lingual tooth surfaces show maximally seven or eight fine striae which converge apically. The ratio tooth length:diameter of tooth neck is 2.5:1.0 in the anterior teeth. The resorption pits are laterally

expanded and are situated at the bases of the teeth.

The posterior teeth of the adult *T. teguixin* individual (SRK 00.195) are of almost pyramidal habitus with a mesial expansion of the tooth bases and of the tooth necks. The mesial side cusps are closely linked to the main cusps. In central teeth, the crista mesialis is slightly longer than the crista distalis. However, both cutting edges are the same length in the posteriormost teeth. Faint striations are found in the anterior teeth. The enamel surfaces of the posteriormost teeth are unwrinkled. The ratio tooth length:diameter of tooth neck is 1.0:1.0 in the posterior teeth. The resorption pits are laterally expanded and situated at the bases of the teeth. The posterior teeth of the semiadult female SDS 64932 are tricuspid and perfectly unwrinkled. These teeth resemble the posterior teeth of *Ameiva ameiva* in their general shape. Accordingly, an ontogenetic change in the dentition of *T. teguixin* from an *Ameiva*-like condition in juveniles to a more durophagous condition in the adults can be assumed.

Diet:

The diet of *T. teguixin* consists of plant matter, earthworms, snails, arthropods, frogs, lizards, small mammals, and eggs of the large Amazonian river-turtle *Podocnemis unifilis* (KÖHLER & LANGERWERF 2000).

Remarks:

Illustrated dentaries of this species documentate a more abrupt change between the unicuspid anterior and the tricuspid posterior teeth (ESTES et al. 1988, RIEPPEL 1980). The size-dependent heterodonty is less evolved in these formerly studied individuals.

4.1.5.2 Subfamily *Gymnophthalminae*

MACLEAN, 1974

(Diagnosis: see ESTES 1983)

Tendency for limb reduction. Approximately 40 gymnophthalmine genera are known at present.

Traditionally this group is referred to as the microteiids.

After SINITSIN (1928), the skulls of this subfamily belong to the platyrrhine type.

This subfamily is often treated as a family (Gymnophthalmidae) (ALBINO 1996, COLLI et al. 1998, ESTES 1983, KIZIRIAN & MCDIARMID 1998, PRESCH 1983). However, the taxonomic status is still unsolved. Among others, a subfamilial status of this group is assumed by

FOX & GAO (1991), GAO & FOX (1996), MACLEAN (1974), and PRESCH (1980).

Neusticurus DUMERIL & BIBRON, 1839

Neusticurus ecpleopus COPE, 1876
(Pl. XIII, Fig. 8)

Number of examined specimens: 1 adult

Distribution:

Colombia, Ecuador, Bolivia, Brazil, Peru.

Dental morphology:

The right dentary of specimen SDS 46994 bears 21 tooth positions. The anterior teeth (tooth positions 1 to 8) are unicuspid whereas all following teeth are bicuspid. The teeth of *Neusticurus ecpleopus* are narrow spaced, relatively long, and of bottle-shaped appearance. The tooth bases are slightly bulbous, showing a slight transversal expansion whereas the widths of the tooth crowns are minor.

The anterior teeth show pointed and slightly recurved cusps. The lingual surfaces of the tooth crowns are concave in the anterior teeth. The cusps are divided into a cuspis labialis and a lower cuspis lingualis, they hence appear bicuspid *sensu stricto*. The cuspis labialis is formed by the cristae mesialis et distalis whereas the cuspis lingualis is formed by two dominating striae, the striae dominantes anterior et posterior. The two cusps are linked by the sharp-ridged carina intercuspidalis. The enamel surface between the stria dominans anterior and the crista mesialis as well as the surface between the stria dominans posterior and the crista distalis are concave (this depression is comparable to the antrum intercristatum which was found in many scincid taxa), whereas the lingual surface between the two dominant striae is elevated plateau-like. Some 2 to 5 parallel striae are situated between the striae dominantes. The apical angle of the anterior teeth encompasses 60°.

The posterior teeth of *N. ecpleopus* differ from the anterior teeth in the following characters:

Presence of mesial side cusps which are separated from the larger main cusps by deep occlusal notches; apical angle encompasses 80°; well developed culmines lateres; striations absent.

The ratio tooth length:diameter of tooth neck is 4.0:1.0 in *N. ecpleopus*. The resorption pits are of circular shape.

Diet:

The aquatic *Neusticurus* often forages at the water surface. Stomach contents analyses and observations of *Neusticurus rudis* proved a diet consisting of tadpoles, fishes, water beetles, horseflies, dragonflies, larvae of freshwater crabs, and snails. Captive kept *Neusticurus* individuals additionally consumed earthworms, crickets, moths, cockroaches, and Amphipoda (*Gammarus* sp.) (MÄGDEFRAU & MÄGDEFRAU 1994). Many prey items are caught when the lizards are swimming. UZZELL (1966) records a piscivorous trophic structure of this genus.

Remarks:

The genus *Neusticurus* is the ancestral form of the genus *Echinosaura* (FRITTS & SMITH 1969).

***Pholidobolus* PETERS, 1862**

***Pholidobolus montium* (PETERS, 1863)**
(Pl. XIII, Figs. 9-10)

Number of examined specimens: 2 adults

Distribution:

Colombia, Ecuador.

Dental morphology:

The right dentary of specimen SRK 00.323 bears 18 tooth positions. The tooth bases and tooth shafts are mesially expanded in *Pholidobolus montium*. The lingual surfaces of the tooth crowns are flattened or concave. The seven anterior teeth are unicuspid and show recurved apices and cylindrical shafts. The teeth numbers 8 to 17 are bicuspid with pointed but robust main cusps and small mesial side cusps. A shift toward more robust posterior teeth is recognizable among these tooth positions. The posteriormost tooth of specimen SRK 00.323 is unicuspid again, but in contrast to the anterior teeth it is of conical habitus. The main cusps show complex tooth crown morphologies. A lanceolate or leaf-shaped uplift is situated within the concave lingual surface of the tooth crown. This elevated section of the lingual surface is framed by the striae dominantes anterior et posterior. The protruding plateau-like structure strongly resembles comparable structures in the tooth crowns of *Neusticurus ecpleopus* and hence may be an autapomorphic character of the

Gymnophthalmidae. The main cusp is divided into a cuspis labialis and a lower cuspis lingualis which are linked by the sharp edged carina intercuspidalis. The cuspis lingualis is formed by the striae dominantes and it therefore represents the apical portion of the elevated leaf-shaped surface dominating the tooth crown morphology of *P. montium*. Several posterior teeth of specimen BMNH 1986-278-286 show a tendency for tricuspidity since the angulus distalis is modified as an "embryonal" additional side cusp. Some seven striae are situated at the lingual surfaces of the tooth crowns in *P. montium*. Most of these striae are restricted to the elevated surfaces between the striae dominantes. However, isolated striae can additionally be found at the lingual surfaces of the mesial side cusps. The striae are arranged parallel but converge apically. The ratio tooth length:diameter of tooth neck is 2.4:1.0. The resorption pits are circular or slightly elongated in the apical direction.

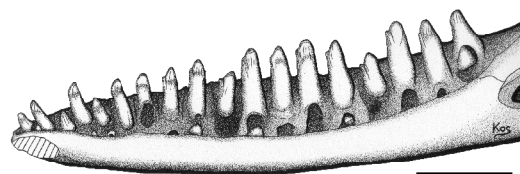


Fig. 116: *Pholidobolus montium*
(specimen SRK 00.323)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

The diet of *P. montium* consists of various arthropods (ROGNER 1994).

Remarks:

A right dentary of *P. montium* illustrated by PRESCH (1980) shows 16 tooth positions and exceptionless unicuspid teeth, most of which are recurved and fang-like. The complex tooth crown morphology was not illustrated in detail. This specimen is probably a juvenile or belongs to another species. Even if the Gymnophthalminae are not represented in the fossil documentation (ESTES 1983), the discovery of fossil remains of this group is a question of time since the major diversification of *Pholidobolus* is believed to have occurred during the Pleistocene (MONTANUCCI 1973). *Pholidobolus affinis* as being the most primitive member of the genus gave rise to a generalized-derived *P. montium*-like stock which in turn underwent

evolutionary radiation and produced highly derived species like *Pholidobolus annectens*.

4.1.6 Family Xantusiidae BAIRD, 1859

(Diagnosis: see ESTES 1983)

Many authors exclude the Xantusiidae (night lizards) from the Scincomorpha and transfer them to the Gekkota since they share several affinities with this group, while others cling to the historical classification which includes the Xantusiidae within the Scincomorpha (GAO & FOX 1996, GAO & DASHZEVEG 1999, SCHATZINGER 1980). Since the taxonomic position of the family is still unclear, the Xantusiidae are tentatively placed within the Scincomorpha in this study.

The fossil record of the Xantusiidae extends to the Middle Paleocene of Montana and the Middle Eocene of Wyoming with *Palaeoxantusia fera* HECHT, 1956 or even into the Late Cretaceous, if *Contogenys* (formerly classified as Scincidae) proves to be related to the Xantusiidae (GAO & FOX 1996, GAO & DASHZEVEG 1999). *Paracontogenys estesi* was also classified as a xantusiid (SULLIVAN & LUCAS 1996).

Cricosaura GRUNDLACH & PETERS, 1863

Cricosaura typica GRUNDLACH & PETERS, 1863

(Pl. XIII, Fig. 11)

Number of examined specimens: 1 adult

Distribution:

Cuba.

Dental morphology:

The right dentary of specimen ZFMK 54260 bears 19 tooth positions. The dentition of the small sized night lizard *Cricosaura typica* is homodont with little alteration between anterior and posterior teeth. The teeth are of almost conical shape; only the lingual surfaces of the tooth crowns are flattened or slightly concave. All teeth are unicuspid with blunt apices. The culmines lateres are developed as moderately pronounced ridges which frame the concave inner surfaces of the tooth crowns. The teeth gradually increase in size caudally. The tips of the four anteriormost teeth are recurved and the tips of several central teeth show wear facets. All enamel surfaces are unwrinkled. The ratio tooth length:diameter of

tooth neck is 3.5:1.0. The resorption pits are laterally expanded and situated at the bases of the teeth.

Diet:

C. typica inhabits a small area (200 km²) in the hinterland of the southwestern Cape of the Cuban province Oriente and hence is almost unknown to science. A captive specimen consumed small house crickets and field crickets, minute cockroaches, and a variety of other arthropods (ROGNER 1994).

Remarks:

Recently, *C. typica* is often stated as the only representative of an own subfamily, the Cricosaurinae (CROTHER et al. 1986). It differs from other xantusiids in the following characters: two frontonasal scales present; one frontal scale; parietal scale absent; fourth finger with four phalanges.

Lepidophyma DUMÉRIL, 1851

Lepidophyma flavimaculatum DUMÉRIL, 1851

Number of examined specimens: 3 juveniles, 1 adult

Distribution:

Mexico, Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, Panama.

Dental morphology:

The right dentary of the adult specimen SRK 00.068 bears 16 tooth positions (this tooth number perfectly agrees with WALKER (1955) who stated 16 teeth per dentary in *Lepidophyma flavimaculatum* and 17 teeth in the dentary of *Lepidophyma micropholis*). The sutures between the bones of the lower jaw are blurred by synostosis. The teeth of *Lepidophyma flavimaculatum* are relatively large and very long (the apical halves rise above the labial parapet of the dentary). The dentition is almost homodont. The apices of all teeth reach the same altitudes. The posterior teeth gradually become slightly more robust than the anterior teeth. The tooth crown morphology of *L. flavimaculatum* is unusual. The blunt apices of the five anteriormost teeth are divided into a cuspis lingualis and a cuspis labialis. Both cusps are of crest-like shape and separated from each other by a deep antrum intercratum. All following teeth show a flat apical plateau with a minute central uplift. A furrow runs from this plateau across the lingual surface of the tooth crown into the basal direction. Among all taxa investigated in this

study, this feature is only found in *L. flavimaculatum* and the lacertid *Ichnotropis squamulosa*. In *L. flavimaculatum* (specimen SRK 00.068), this groove is already developed in non functional replacement teeth; a wear implied origin of this groove can hence be excluded. Aside from these furrows, the tooth surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.9:1.0. The resorption pits are of circular shape.

The tooth numbers increase ontogenetically in *L. flavimaculatum*. In juvenile (neonate) individuals only 14 or 15 tooth positions are found in each dentary.

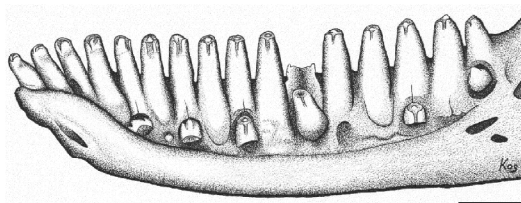


Fig. 117: *Lepidophyma flavimaculatum* (specimen SRK 00.068)
Right dentary; lingual view
Scale bar: 1.0 mm

Diet:

Captive specimens of *L. flavimaculatum* at San Antonio Zoo, Texas, were fed with adult crickets (HOLMBACK 1984). Two adult *L. flavimaculatum* in my terrarium do well and reproduce on a diet consisting of crickets (*Gryllus* sp.), house crickets (*Acheta domestica*), *Tenebrio* larvae, and earthworms (*Lumbricus rubellus*). The night lizards are able to overpower and swallow comparably large prey animals.

Several *Lepidophyma* populations are cavernicolous (BEZY 1984, GUZMAN-VILLA et al. 1998). At least one of these species is predominantly herbivorous. The diet of *Lepidophyma smithii* consists mainly (91 %) of fig fruits which drop into the caves inhabited by the lizards (MAUTZ & LOPEZ-FORMENT 1978). But even these lizards that superficially appear highly specialized, switch to an opportunistic diet in captivity. Unfortunately no specimens of *L. smithii* were available for this study, hence the information about possible dental adaptations to this frugivorous diet can only be taken from literature: a left dentary of *L. smithii* illustrated by HECHT (1956) shows 17 teeth, most of which are tricuspid with minute mesial and distal side cusps.

Remarks:

The division of *Lepidophyma* into subgenera was proven to be invalid by BEZY & CAMARILLO (1992). Several *Lepidophyma* species often sympatrically inhabit the same area (CORTÉS et al. 1990) whereas others are allopatric (BEZY & CAMARILLO 1997). Interestingly, the presence of scale sense organs in *Lepidophyma* is a character shared solely with the teiid *Dracaena paraguayensis* (VANZOLINI & VALENCIA 1965).

Xantusia BAIRD, 1859

Xantusia henshawi STEJNEGER, 1893
(Pl. XIII, Fig. 12)

Number of examined specimens: 12 adults

Distribution:

Mexico, USA (California).

Dental morphology:

The dentaries of *Xantusia henshawi* bear approximately 16 tooth positions on average. The dentition is homodont and consists of slender, conical teeth with lingually slightly flattened tooth crowns. The apical halves of the teeth rise above the labial parapet of the dentary. The tooth crowns are moderately pointed and unicuspid. The tips of the cusps are slightly concave lingually. The enamel surfaces are unwrinkled in *X. henshawi*. The ratio tooth length:diameter of tooth neck is 4.0:1.0. The resorption pits are of circular shape.

NORELL (1989) describes enamel striations in *X. henshawi* (in contrast to the unwrinkled teeth of the Cenozoic *Xantusia downsi*). Contrary to this observation, the *X. henshawi* specimens investigated here completely lack striations.

Diet:

Stomach contents analyses of 252 *X. henshawi* individuals proved a diet consisting predominantly of Formicidae, unidentified insects, unidentified spiders, and Coleoptera (Carabidae and Tenebrionidae). A minor percentage of the diet was made up by Argiopidae, Lycosidae, Agelenidae, Thomisidae, scorpions, centipedes, ticks (Ixodidae), Isopoda, Thysanura, Locustidae, Blattidae, Odonata, Aphidae, Membracidae, Miridae, Lygaeidae, Coreidae, Lepidoptera (mainly larvae), Sarcophagidae, Phoridae, Buprestidae, Scarabacidae, Chrysomelidae, Curculionidae, Apidae, insect eggs, and plants (BRATTSTROM 1952).

Remarks:

A left dentary with 15 teeth is illustrated in labial view in ESTES, R., DE QUEIROZ, K. & GAUTHIER, J. (1988); another left dentary shows 16 tooth positions (HECHT 1956).

Xantusia riversiana (COPE, 1884)
(Pl. XIII, Figs. 13-14)

Number of examined specimens: 3 adults

Distribution:

USA (San Clemente, Santa Barbara, San Nicolas Islands (California)).

Dental morphology:

The right dentary of specimen USNM 220288 bears 13 tooth positions. The tooth number of *Xantusia riversiana* is reduced relative to other species of the Xantusiidae (except *Xantusia vigilis*). The tooth shafts are long and columnar whereas the tooth crowns are mesially expanded. The tooth crowns tower above the labial parapet of the dentary. In occlusal view, the teeth resemble the teeth of the herbivore scincid *Corucia zebrata*. *X. riversiana* is the only taxon investigated that shows tricuspid teeth throughout the entire tooth row; the first tooth already shows the tricuspid condition. The teeth appear distinctly symmetrical since the mesial and the distal side cusps are of almost equal size. Compared to tricuspid teeth in other taxa, the lateral cusps of *X. riversiana* appear rather large. The lateral cusps are distinctly separated from the central main cusps by deep occlusal notches. The lingual surfaces of the tooth crowns are concave and the inwardly curvatures are best developed in the immediate vicinity of the lateral cusps. The cristae mesiales et distales are formed as extraordinary sharp edges. The enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.7:1.0. The resorption pits are circular or elongated in the apical direction.

Diet:

X. riversiana is a specialized island species (BEZY & FLORES-VILLELA 1999). Stomach contents of 91 individuals of this species proved a diet consisting almost entirely of plant matter (leaves, seeds, stems, and bits of other tissue). Especially the subspecies from Santa Barbara Island, *X. riversiana reticulata*, is almost 100 % vegetarian. Individuals of other subspecies consume at least occasionally insects, preferably ants. On very rare occasions, spiders or beetles (Coleoptera) are eaten by *X.*

riversiana (BRATTSTROM 1952). This predominantly vegetarian trophic structure corresponds well with the highly specialized dentition of the island night lizard and proves a high adaptational degree of lizard dentitions.

BRATTSTROM (1952) assumes that "The presence of small bits of marine snail shells in stomachs of *X. r. riversiana* from San Nicolas Island suggests occasional foraging about the beach for marine isopods and amphipods.". Another explanation for the presence of shell fragments is the voluntary ingestion of these fragments for calcium support. A comparable behavior was observed in two species of the agamid genus *Uromastix* in the indoor vivaria of the author. Several *Uromastix* individuals which are usually vegetarian, ingested shell fragments of terrestrial snails (*Cepaea* sp.).

Remarks:

The dentition of *X. riversiana* was formerly illustrated by HECHT (1956) and MCDOWELL & BOGERT (1954).

Xantusia vigilis BAIRD, 1859
(Pl. XIII, Figs. 15-16)

Number of examined specimens: 4 adults

Distribution:

USA (California, Nevada, Utah, Arizona), Mexico.

Dental morphology:

As in *Xantusia riversiana*, the tooth number of *Xantusia vigilis* is reduced. The majority of the investigated dentaries bear 13 tooth positions. The narrow spaced dentition of *X. vigilis* is strictly homodont. All teeth are unicuspid and are of conical habitus. The tooth shafts are slender and long. The tooth crowns are lingually flattened. In the anterior teeth, the lingual surfaces of the tooth crowns are concave. The apices are recurved in the anteriormost teeth. The cristae mesiales et distales are developed as sharp edges. The enamel surfaces are unwrinkled. The ratio tooth length:diameter of tooth neck is 4.8:1.0. The resorption pits are circular or apically expanded.

Diet:

The crepuscular desert night lizard, *X. vigilis*, is an insectivorous species. Stomach contents analyses on 291 individuals proved that the dominating prey items are ants. However, these night lizards additionally consume beetles, bugs, termites, Lepidoptera larvae, and flies in great numbers.

Occasionally, tails of other *X. vigilis* individuals are eaten. This observation proves certain cannibalistic tendencies in *X. vigilis* (BRATTSTROM 1952). The prey items are chewed relatively long before they are swallowed (ROGNER 1994).

Remarks:

NORELL (1989) observed enamel striations in *X. vigilis*. However, the tooth enamel surfaces of the specimens investigated in this study were perfectly smooth.

4.1.7 Discussion

4.1.7.1 Discussion on particular feeding habits

Many recent lizards are generalized opportunistic feeders lacking any morphological adaptations for a special trophic structure. However, others show some conspicuously or unusually feeding habits that require to be analysed in detail. For example, saurophagy occurs in several scincomorphan taxa. The transitions between true or habitual saurophagy (better known from serpentes and performed by lizards only to a lesser degree) and accidental saurophagy appear to show no clear dividing line. The consumption of juvenile burrowing skinks (*Typhlosaurus* sp.) by the cordylid *Platysaurus intermedius* recorded by BROADLEY (1978) seems to represent accidental saurophagy since the worm skinks occupy the target niche of earthworms and can easily be confused with worms by a predator. However, saurophagy seems to be rather common among recent scincomorphans (e.g., *Cordylus cataphractus* (consumes lacertids), *Gallotia stehlini* (consumes geckos, skinks, and juvenile conspecifics), *Podarcis melisellensis* (consumes juvenile conspecifics), *Acontias meleagris* (consumes juvenile conspecifics), *Acontias plumbeus* (consumes other burrowing skinks), *Egernia inornata* (consumes smaller lizards), *Eremiascincus richardsonii* (consumes *Lerista* sp., and small *Ctenotus* sp.), *Eumeces obsoletus* (consumes juvenile congenetics), *Eugongylus albifasciolatus* (consumes smaller lizards), *Mabuya multifasciata* (consumes smaller lizards), *Mabuya quinquetaeniata*

(consumes smaller skinks), *Scincopus fasciatus* (consumes juveniles of *Scincus scincus*), *Tiliqua nigrolutea* (consumes smaller skinks), and *Callopiastes maculatus* (shows a tendency for eating other lizards)). The widely distributed scincine *Chalcides ocellatus* is able to overpower and consume even large lizards (adult male *Podarcis tiliguerta*). An interesting behavior is the consumption of smaller congenetics by the scincine *Eumeces obsoletus*: The female cares for the neonates for several days after hatching; however, these skinks prey on juveniles of other *Eumeces* species. This behavior indicates an ability to recognize the own offspring. Although the bodies of the scincids are protected by strong dermal armour, these osteoscutes do not prevent the animals completely from being eaten by other lizards. However, the teeth of the predators do not always have to break through the dermal armour of their victims since the prey is often swallowed in a single piece.

Many scincomorphans, especially scincids, are able to consume extraordinarily large prey items. Fecal pellets of *Chalcides viridanus coeruleopunctatus*-specimens captured in the Valle Gran Rey on La Gomera contained large fragments of chitinous cuticula (own observation), which suggest the consumption of extremely large prey items compared to the small size of these skinks. The bulbous posterior teeth of *Chalcides viridanus* are ideal for crushing the cuticula of large arthropods.

In experimental studies, BURGHARDT (1964) observed *Eumeces fasciatus* attacking crickets and spiders too large to be swallowed. Under captive conditions, these skinks consistently chose the largest available food items. The consumption of large prey items makes a chopping or chewing of the prey necessary. The striations observed in the tooth enamel of most scincids enables the lizard to withhold the struggling prey.

Herbivory is common among the Scincomorpha and is often associated with functional morphological adaptations concerning the tooth crown morphology. Some predominantly herbivorous lizards (e.g., *Angolosaurus skoogi*, *Tracheloptychus petersi*, *Gallotia stehlini*, *Corucia zebrata*) show mesially flattened teeth with tendencies toward multicuspidity. Even among night lizards some multicuspoid forms evolved; the presence of lateral cusps is also associated with a dietary shifting toward herbivory here (e.g.,

Lepidophyma smithii, *Xantusia riversiana*). However, some marine snail shell fragments were found in stomachs of *X. r. riversiana* from San Nicolas Island. BRATTSTROM (1952) assumes that the presence of these small shell fragments suggests occasional foraging about the beach for marine isopods and amphipods. Another explanation for the ingestion of shell fragments is the voluntary ingestion of these fragments for calcium support. A comparable behavior was observed in two species of the agamid genus *Uromastyx* in the indoor vivaria of the author. Several *Uromastyx* individuals which are usually vegetarian ingested shell fragments of terrestrial snails (*Cepaea* sp.) for calcium support.

In *Egernia cunninghami*, the morphology of the teeth, which show conspicuous similarities to herbivore lizards of other genera, indicates a functional morphological adaptation to a plant-dominated diet. The tooth crowns are mesially and distally expanded and thus almost in contact with each other, together forming a straight cutting edge. A comparable morphology is found in the genus *Becklesius* from the Upper Jurassic of Guimarota, suggesting a certain percentage of plant matter in the diet of this fossil taxon.

Stomach contents analyses show a small amount of plant matter in many lizards (e.g., *Zootoca vivipara*), which was probably ingested involuntarily. When foraging, lizards often ingest the leaves, the blades of grass, or the twigs the arthropod prey is sitting onto. This is confirmed by observations on the feeding behavior of captive specimens of various scincomorph taxa, showing that lizards often ingest plant matter together with the true arthropod prey. In large species (e.g., *Tupinambis merianae*), sometimes even pieces of bark stick to the prey (especially if soft fruits are eaten) and consumed involuntarily (own observation).

The subrecent Cape verde giant skink *Macrosclincus coctei* was feeding on an almost exclusively herbivorous diet. The question why two insular and herbivorous giant skinks like *Macrosclincus coctei* and *Corucia zebrata* developed completely different dental morphologies (multicuspid teeth in *M. coctei* and lanceolate unicuspid teeth in *C. zebrata*) can only be solved under functional morphological viewpoints, and the consideration of the climatic conditions of their habitats. *M. coctei* was spread on arid islands, which were inhabited by plants with a solid

cuticula. The numerous lateral cusps of the tooth crowns were used for chopping up the resistant plant matter as a preliminary stage of the chemical break-down of its ingredients during the process of digestion. *C. zebrata*, on the other hand, inhabits a tropical archipelago with humid climatic conditions and consumes soft plants and fruits requiring no serrations to be chopped up. This shows the strong dependence of the dental morphology upon outer influences; especially the dietary composition causes evolutionary adaptations to a high degree. Interestingly, only the shape of the crown apex is modified in phytophagous lizards, while "all of the other family-specific features remain unchanged" (VOROBYEVA & CHUGUNOVA 1991). Accordingly, the tooth implantation as well as the mode of tooth replacement in these highly specialized herbivores remain the same as in ancestral forms, whereas the tooth crown morphology completely differs from related taxa.

The extraordinarily high dental adaptability gives rise to a vast cladogenesis in many scincomorph families. For example, the lygosomine genus *Ctenotus* includes a large number of syntopic species all of which depend at least partly upon termite prey. This diverse saurofauna could evolve because termites with their numerous guilds offer various types of prey. Each *Ctenotus* species obviously favors a certain caste of termites. Dietary specialization thus enables lizard genera to evolve numerous syntopic species, which do not compete with their congenetics.

The use of tools for the purpose to break down stiff food items is rather unusual in scincomorphans. However, the lygosomine *Mabuya wrightii*, which is endemic to the Seychelles, is highly specialized in its feeding habits since it consumes the eggs of sea swallows. *M. wrightii* presses the eggs out of the nests with its body so that the eggs roll against rocks and break (HENKEL & SCHMIDT 1995); the spilt contents are then consumed. Sometimes several lizards share one egg. Another skink using a special technik to break down stiff foods is the scincine *Novoeumeces schneideri*. The inverted durophagous dentition of this skink with large anterior and small posterior teeth is interpreted as an adaptation to a partly durophagous diet accompanied by a specialized feeding behavior. In strong contrast to other durophagous lizards, which use their enlarged posterior teeth for the crushing of hard bodied prey (e.g., most

Tiliqua species, *Hemisphaeriodon gerrardi*, *Dracaena guianensis*), *Novoeumeces schneideri* uses rocks to crush the shells of its prey items. Thus, anteriorly situated crushing teeth are more useful to concentrate the forces against the resisting objects which in most cases are rocks or logs. The skink separates the shell fragments from the soft parts with the help of its tongue and swallows only the soft parts of the prey item, thereby rendering any posterior crushing teeth superfluous.

Another unusual feeding behavior was recorded for *Eumeces laticeps*; this scincine is specialized in actively rousing prey animals and therefore strongly contrasts the sit-and-wait hunting technique of other skinks. *E. laticeps* uses prey odor discrimination for detecting hidden prey. The location of prey items takes place inside and under rotting logs as well as beneath surface litter (COOPER 1989).

The foraging technique of the teiid *Dracaena guianensis* strongly contrasts with most other scincomorphans. Representatives of this durophagous species predominantly consume water snails (ROGNER 1994), but also feed on terrestrial gastropods. RAND (1964) observed *D. guianensis* foraging underwater. The lizards were completely submerged in approximately 30 cm deep water and hunted for snails which were brought to the surface and swallowed there. These large teiids also consume mussels (CONANT 1955). A precise description of the crushing process is given in DALRYMPLE (1979): "The snail is picked up in the jaws, the head is dorsiflexed, the bite relaxed, and the snail rolls toward the back of the tooth row. The lizard then crushes the shell, removing shell fragments with its tongue before swallowing the snail." However, the teeth of the upper and lower jaws of *D. guianensis* do not meet in occlusion (DALRYMPLE 1979); this strongly contrasts the chewing mechanisms of other large teiids like *Dicrodon guttulatum*. For these herbivores a perfect occlusion is necessary to chop up the fibres of their plant food.

The lygosomine *Egernia kingii* gives evidence for an actualistic comparison since the dentition of this species strongly resembles the dental morphology of the Upper Jurassic *Becklesius* from Guimarota. *E. kingii* is not only distributed on the Australian mainland, but it also dominates the herpetofauna of many islands at the coast of Australia. Among other items, this skink feeds on carrion washed ashore. Since the dietary spectrum of

Becklesius must have been comparable due to the similarities found in tooth crown morphology, this observation supports the theory of periodical marine incursions, which greatly influenced the environment of the Upper Jurassic Guimarota ecosystem.

4.1.7.2 Statistics

The dentitions of numerous taxa of recent scincomorphans were investigated for this study. Nevertheless, the numbers of conspecific individuals were too low to allow any statistical interpretation. Most taxa are represented by less than six specimens due to either a lack of osteological material or to the complicated process of producing the casts. Only a few taxa are represented by more than six individuals (e.g., *Cordylus polyzonus* (8), *Cordylus warreni* (7), *Gallotia caesaris* (8), *Gallotia galloti* (8), *Lacerta agilis* (9), *Lacerta viridis* (10), *Podarcis muralis* (8), *Podarcis pityusensis* (7), *Podarcis sicula* (10), *Timon lepidus* (17), *Chalcides ocellatus* (10), *Corucia zebata* (7), *Mabuya multifasciata* (9), *Scincus scincus* (7), *Tiliqua rugosa* (11), *Ameiva ameiva* (10), *Ameiva chrysoleama* (7), *Ameiva plei* (8), *Callopietes maculatus* (7), *Cnemidophorus tigris* (7), *Tupinambis merianae* (8), *Xantusia henshawi* (12)), but even these are not enough specimens to apply mathematical methods in a reliable manner. In addition, the higher numbers of individuals in these species often represent specimens of various subspecies; this complicates the situation and makes any statistical usability impossible.

4.1.7.3 Ontogenetic implications

The morphology of lizards teeth underlies ontogenetic changes to a lesser degree than does the tooth number, which continually increases with increasing age of the individual (e.g., *Corucia zebata*). In species including individuals with bicuspid, tricuspid, or multicuspid teeth, the number of lateral cusps not always depends on the age of the individual. In *Lacerta viridis* e.g., which usually has bicuspid teeth, some tricuspid teeth can be found in individuals belonging to different age classes. The appearance of tricuspid teeth in *Lacerta viridis* was already mentioned by ROCEK (1980): "A limited

number of posterior teeth may be tricuspid with a small third cusp distal to the main cusp.”. Accordingly, bicuspidity and tricuspidity are not related to age or body size in *Lacerta viridis*. This leads to the conclusion that the number of cusps is at least in this well known species an individual character rather than being of taxonomical value. This explanation is confirmed by similar conditions in other taxa (e.g., *Timon lepidus*, several *Ameiva* species), which also show individual differences in the number of lateral cusps. Nevertheless, some ontogenetic differences do exist in certain taxa: Adult specimens of *Ameiva plei* and *Tupinambis merianae* show unicuspid posterior crushing teeth, whereas these teeth are bicuspid or tricuspid and distinctly pointed in juvenile specimens. This reduction of lateral cusps is due to extensive wear and probably to dietary changes during ontogeny (e.g., *Tupinambis merianae* shifts from a predominantly insectivorous diet to a more molluscivorous and plant-dominated diet). Ontogenetic changes concerning the composition of the diet are common in many lizard taxa, but these trophic changes do not necessarily imply a remodulation of the dental morphology (e.g., *Teira dugesii*). Juveniles of *Scincus scincus* show a more larvae-dominated diet than adults; this is a result of a special need of proteins during the growing process (HARTMANN 1989a) and agrees with the larvae-dominated diets of several smaller burrowing skinks. Probably the small subterminal mouth of a burrowing skink does not allow the grasping and holding of agile and hard prey like mature beetles.

Scincella lateralis is the first scincid lizard with thoroughly described dentition (TOWNSEND et al. 1999). These authors observed no ontogenetic or sexual variation in tooth crown morphology; however, ontogenetic changes in tooth size and tooth number were noticed, with significantly more teeth in the dentaries of adults than in the dentaries of juveniles. An ontogenetic increasing of the tooth number was observed during research for this thesis in several taxa (e.g., *Corucia zebrata*, *Tiliqua rugosa*). An allometric growth of the dentaries was not indicated in any of the species of which individuals from different age classes were available for this study. The proportions of the dentaries and the dentitions mostly stayed the same throughout the entire ontogenetic row, so that juvenile dentaries are

miniatures of the adult ones, with only a lower number of teeth.

Distinct ontogenetic changes in tooth morphology take place in several *Ameiva* species; these morphological reshaping are especially well documented for *Ameiva plei*: The posterior teeth of young *Ameiva plei*-specimens are tricuspid with well developed mesial and distal side cusps and pointed central main cusps. This tooth morphology strongly contrasts the tooth morphology found in individuals of higher individual age; in these older individuals, the five to seven posteriormost teeth are perfectly globular. The globular shape of the posterior teeth is interpreted here as a result of intensive wear. Therefore, no striations were found in the crushing teeth of *Ameiva plei*. This observation strongly contrasts other durophagous taxa, in which the development of crushing teeth is not a result of wear. The striations in those “primarily durophagous” lizards are formed during amelogenesis.

In many scincomorph taxa each age-class adopts foraging tactics which increase the chances to find the most valuable prey. PAULISSEN (1987) observed different prey preferences among various age groups in *Cnemidophorus sexlineatus* and recorded that grasshopper-like insects are the most valuable prey for adults, whereas plant and ground arthropods are the most valuable prey for juveniles.

Older individuals sometimes show malfunctions of the mode of tooth replacement. The solely available specimen of *Sphenomorphus variegatus*, SRK 00.297, shows a pathological replacement mode which was described in this thesis for *Lygosoma afra* as “multiple replacement”. SRK 00.297 lived in my stock for several years and reached a high individual age, which probably is not reached under natural conditions due to the high predatory pressure in the wild. Obviously the parameters of tooth replacement change in older individuals so that the mechanism of tooth replacement no longer functions. New replacement teeth are steadily developed while the older tooth generations have not fallen out. The result of this malfunction is the development of up to four parallel tooth rows, as seen in SRK 00.297. Interestingly, the old *Lygosoma afra* specimen had problems in handling and “chewing” its prey (BROSCHINSKI, pers. comm.), whereas the *Sphenomorphus variegatus* specimen did not

show any age-related difficulties concerning its feeding behavior. It was still able to grasp and handle its prey even shortly before it died (own observation).

A secondary row of posterior teeth was recorded in the literature for *Crotaphytus* (Iguanidae): “seemingly by the fusion of replacement teeth lingually and ventrally to the teeth they would normally replace; this gives an apparent expansion of the biting surface and perhaps forms an area in which crushing could occur.” (ESTES & WILLIAMS 1984). Unfortunately the individual age of the *Crotaphytus*-specimen was not mentioned, but it can be assumed that it was an older individual (like the examined *Sphenomorphus variegatus*-specimen with multiple tooth rows) due to the development of multiple tooth rows being age dependent.

4.1.7.4 The relationships between body size and trophic structure

The majority of all recent scincomorphans are small to medium-sized lizards, measuring 15 to 40 cm in total length (TL; from the tip of the snout to the tip of the tail). These small or medium-sized taxa show a generalized arthropod-dominated diet. The dietary spectrum of these insectivorous lizards often depends strongly on prey availability. However, exceptions do exist since some small to medium-sized scincomorphans are highly specialized feeders: e.g., the sand-swimming scincine *Scincus scincus* (18 cm TL), which prefers larvae and pupae of Coleoptera, as well as seeds; the durophagous scincine *Novoeumeces schneideri* (approximately 40 cm TL, some subspecies grow larger) shows a strong preference for terrestrial snails; the desert dwelling gerrhosaurine *Angolosaurus skoogi* (25 cm TL) is almost strictly vegetarian as well as the xantusiid *Xantusia riversiana* (20 cm TL), while the zonosaurine *Tracheloptychus petersi* (22 cm TL) is partly frugivorous.

The small or even miniaturized scincomorphans, which remain under 15 cm in total length, prey almost exclusively on minute arthropods or their larvae. This group includes some worm skinks which exceed 15 cm TL, but are also treated as miniaturized lizards due to their worm-like body shape. Most of these small forms are myrmecophageous or prey on tiny spiders: e.g., the lacertid *Lacerta parva* (15

cm TL); the scincine worm skink *Typhlacontias gracilis* (20 cm TL); the lygosomine *Ablepharus grayanus* (12 cm TL); and many other representatives.

Some recent scincomorphans grow to an astonishing large body size. The group of the large scincomorphans includes lizards which measure more than 50 cm in total length. Several highly specialized feeders belong to this group: the almost strictly molluscivorous teiid *Dracaena guianensis* (120 cm TL); the herbivorous teiid *Dierodon guttulatum* (approximately 90 cm TL); the phytophagous lygosomine *Corucia zebrata* (70 cm TL); the durophagous lygosomine *Tiliqua gigas* (58 cm TL), and the predominantly vegetarian giant lacertid *Gallotia stehlini* (80 cm TL). However, the largest recent scincomorphans, *Tupinambis merianae* (140 cm TL), is an opportunistic feeder.

4.1.7.5 Functional morphology

The tooth crown morphologies of many lizards are the results of phylogenetically adaptations for a certain trophic structure. Accordingly, the dental morphological features enable the lizard optimizing the handling of its prey. For example, the arrangement of the cuspides linguales et distales parallel to the distomesial axis of the tooth row as found in *Cordylus peersi* not only allows an increasing of the biting forces, but also an orientation of these forces into three directions. These directions concern the direction of the tooth tips themselves and the two lingually oriented axes of the two cusps. The possibilities of the prey escaping are reduced by the doubled penetration of the feeding object and the angle of orientation of the cusps. This tooth crown configuration helps in holding the prey even when the jaws are slightly opened. Under functional morphological aspects, straight cusps are useful for grasping soft prey animals, whereas lingually recurved cusps are more suitable for the grasping of prey animals with a strong cuticula (SUMIDA & MURPHY 1987). This observation allows comparisons between recent and fossil taxa under an actualistic point of view and furthermore makes a reconstruction of the prey spectrum of fossil lizards possible.

The dentitions of some recent scincomorphans species differ strongly from the dentitions of their congenetics, suggesting an

adaptation to a trophic structure which somehow differs from the trophic structures of related species. An impressive example is the lygosomine *Tiliqua nigrolutea*. In strong contrast to other *Tiliqua* species, which show exclusively durophageous dentitions, the teeth of *T. nigrolutea* are conical and pointed. *T. nigrolutea* represents the only montanous species of the genus *Tiliqua*. These unusual bluetongue skinks are well adapted to montanous habitats characterized by low temperatures and humid climatic conditions. The food spectrum of *T. nigrolutea* is also adapted to this extraordinary alpine habitat and consists of snails, slugs, insects (predominantly beetles, cicadas, and caterpillars), spiders, leaves, flowers, and fruits. Small-sized vertebrates like smaller skinks are also preyed on (HAUSCHILD et al. 2000). In addition to the aforementioned items, stomach contents analyses of fresh road kills of this species also found mushrooms, grass, and seeds (WEBB & SIMPSON 1985). In the summer, *T. nigrolutea* consumes vast numbers of christmas beetles, *Anaplognathus* sp. By examining the stomach contents of a specimen of *T. nigrolutea* in 1836, Charles DARWIN was one of the first biologists to note that blue-tongue skinks are partly herbivorous (SHINE & HUTCHINSON 1991). A diet consisting of soft items like slugs and plant matter is well compatible with the unique dental morphology of *T. nigrolutea* from a functional morphological point of view. The pointed teeth are very useful in grasping and penetrating the soft bodies of slugs or caterpillars which inhabit the cool and often humid habitat of this skink, whereas a durophageous dentition, which is important for the shell-crushing *Tiliqua* species of arid habitats, is not required by the alpine *T. nigrolutea*.

The dentition of the African lacertid *Holaspis guentheri* strongly resembles the dentitions found in the cordyline genus *Platysaurus*. Both taxa have numerous homodont teeth which lack any mesial or distal side cusps usually found in lacertid teeth. This morphological convergence corresponds with the similarities of the habitats of *Holaspis guentheri* and *Platysaurus* species; individuals of both genera inhabit vertical rock walls or the bark of tree trunks, where they actively forage for small arthropods. In addition, both genera have distinctly flattened bodies as an adaptation to the narrow crevices they often hide in.

The partly frugivorous *Gallotia galloti* also consumes seeds additionally to its arthropod-dominated diet (VALIDO & NOGALES 1994). BROSCHINSKI (pers. comm.) offered bird food to wild *G. galloti* on La Palma; the lizards skilfully separated the grains from their capsules with chewing movements of the jaws. The pointed tricuspid tooth crowns of *G. galloti* are ideal for the handling of grains. In comparison with the fossil material, the absence of lizards with pointed tricuspid tooth crowns in the Upper Jurassic assemblage from Guimarota appears conclusive since grasses had not evolved in the Mesozoic.

Another functional adaptation is the development of extremely pointed teeth (often associated with myrmecophagy) lacking any enamel striations. For example, the extremely pointed teeth of the lygosomine *Sphenomorphus muelleri* require less force to penetrate the cuticula of arthropod prey items. EVANS & SANSON (1998) stated that "strong or stiff foods are most efficiently broken down by minimizing contact area between the tooth and the food". However, not only strong food items (e.g., arthropods with a stiff cuticula) require a pointed morphology of the tooth crowns. Another type of prey requiring pointed tooth tips in the predator is represented by minute insects, especially termites and ants. The diet of the teiid *Cnemidophorus hyperythrus* consists mainly (85.05 %) of termites (MEDICA 1967). This termite-dominated diet corresponds well with the extremely pointed tooth tips of *C. hyperythrus*. Only pointed tooth tips enable the myrmecophageous lizards to pierce the minute corpus of their prey. Pointed conical teeth are also common among various burrowing skinks. For example, the diet of the sand skink *Neoseps reynoldsi*, whose limbs are strongly reduced, consists mainly of termites and beetle larvae; these prey items are predominantly caught and eaten while burrowing (CONAN & COLLINS 1998). The short mandibles require a strong adductor musculature, which again requires a relatively large area of attachment. This is given by the elevated coronoid (Fig. 119). However, the secretive feeding habits of subterranean lizards make detailed studies extremely difficult and require additional investigation.

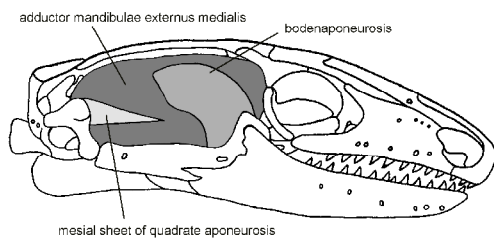


Fig. 118: The trigeminal jaw adductor musculature in the burrowing skink *Acontias meleagris* (after RIEPPEL 1981); right lateral view.

Certain characters may vary within a taxon, while other characters are constant in a diversity of taxa. This makes the taxonomical usability of dental morphologies complicated and compound the classification of fossil lizards. Accordingly, the application of dental morphological characters demands critical consideration. This problem was already noticed by other authors; HOTTON (1955) e.g. remarked that “In some cases, closely related forms have different dentitions, indicating divergent evolution with respect to dentition; in other cases, distantly related forms have similar dentitions, indicating evolutionary convergence with respect to dentition.”. In some rare cases the genetic manifestation of certain features plays a more important role than functional morphological adaptations. Accordingly, the inclusion of hard prey items does not always result in the development of a durophagous dentition, which is best proved by the consumption of snails in the anguid *Gerrhonotus* and the iguanid *Liolaemus*, neither of which shows durophagous adaptations (ESTES & WILLIAMS 1984).

4.1.7.6 Problems

The absolute ages of most recent lizard genera or lineages are difficult to distinguish. The phylogenetical relationship of the Australian lygosomine genera *Tiliqua* and *Egernia* shows these difficulties: The genus *Tiliqua* probably evolved from the genus *Egernia*. Immunological studies suggest a common ancestor of *Tiliqua rugosa* and *Egernia frerei* 12 million years ago. However, the fossil record does not support this argumentation since *Tiliqua pusilla* is known already from the middle Miocene. This shows that sometimes different methods lead to different results

especially concerning the determination of the absolute age of certain lizard clades.

4.2 The fossil Scincomorpha from Guimarota

4.2.1 Geological setting of the Guimarota mine

The coal mine of Guimarota is located 1.5 km south of the Central Portuguese provincial town of Leiria. This corresponds to the following geographical co-ordinates (after the Carta Militar de Portugal (sheet Leiria, No. 297)): 142.75 NS / 307.50 EW or the degree of longitude 8°48' / of latitude 39°43' (after SEIFFERT 1973).

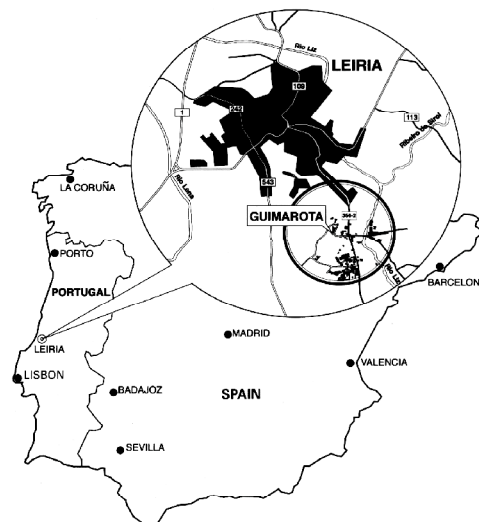


Fig. 119: Position of the Guimarota mine, Leiria, Portugal. From MARTIN & KREBS (2000).

The coal seams were mined during the first half of the 20th century; however, the mines were only of local importance. The exploration of the lignites was discontinued in the 1960s. In 1959, the high vertebrate content of the Guimarota mine was discovered by W. G. KÜHNE; this was shortly before the mines were closed for commercial mining in 1961. Afterwards, the mines were only reopened for scientific purposes. An excavation in 1972 under Prof. Dr. S. HENKEL, Berlin, whose goal

was to explore the mammal fauna of this locality, brought additional lizard material to light, which was investigated by SEIFFERT (1973). Later excavations (until 1982) completed the collection of lizard remains.

The stratigraphic position of the outcrop of the Guimarota mine was determined as Lower Kimmeridgian based on the following ostracod assemblage (from SEIFFERT 1973): *Cetacella inermis* MARTIN, 1958, *Dicrorygma kimmeridgensis* KILENYI, 1969, *Poisia bicostata* HELMDACH, 1968, *Poisia clivosa* HELMDACH, 1968, *Theriosynoecum hemigygnon* HELMDACH, 1968, *Theriosynoecum wyomingense* (BRANSON, 1935), and *Timiriasevia mackerrowi* BATE, 1965.

The two coal beds of the Guimarota mine (each being approximately 20 m thick) dip southwards at an angle of 22°. The coals are marly coals with a high percentage of non inflammable components. The coal seams are separated by intercalated limestone (approximately 5 m thick). Unfortunately, the vertebrate-bearing beds do not contain marine index fossils and therefore, the exact dating is difficult (MARTIN & KREBS 2000). The later authors assigned the “Guimarota-beds” to the Alcobaca Formation, which is correlated with the Ammonite zones “*divisum*” (Lower Kimmeridgian) and “*mutabilis*” (Upper Kimmeridgian).

Beyond the basis of the 2. Lusitanian lignite series a shelly layer, which contains the bivalves *Isognomon* and *Trigonia*, is supposed to mark the stratigraphic division between the Upper Oxfordian and the Lower Kimmeridgian (SEIFFERT 1973).

The paleoenvironmental situation of the “Guimarota-beds” is less disputed than their absolute age. The sediments were deposited in a shallow lagoon with freshwater inlets, located within the Lusitanian basin. The salinity of the water in this small lagoon varied to a large extent, since both marine and freshwater organisms were found. Because clastic sediments are not represented within the layers, a low relief of the hinterland is assumed (MARTIN & KREBS 2000). The eastern rim of the opening North Atlantic ocean was represented by extensive coastal plains; here, dense vegetation flourished.

The vertebrate fauna of the Guimarota mine includes Osteichthyes (Holostei and Teleostei), Chondrichthyes (Selachii), Lissamphibia (Anura, Urodela), Chelonia

(Cryptodira), Lepidosauria (Eosuchia, Lacertilia), Archosauria (Crocodilia, Pterosauria, Saurischia, Ornithischia), and Mammalia (Docodonta, Multituberculata, Pantotheria). The lizards of the Guimarota mine were formerly investigated by BROCHINSKI (2000), who mentions remains of the scincomorphans *Saurillodon*, *Becklesius*, and *Paramacellodus* as well as remains of the anguimorphans lizards *Dorsetisaurus* and *Parviraptor*.

Usually the potential for preservation of vertebrate remains in coal lagerstätten is low since phosphatic and carbonatic fossils are destroyed by the humin acids, which result from decaying processes from plants; nevertheless, the fossils from the Guimarota mine are well preserved. This leads to the assumption that the humin acids were neutralized by carbonatic waters. These waters possibly originated from the limestones, which the Guimarota coal seam is intercalated in. Another source of the carbonatic waters are the coals themselves since they are not pure, but rather represent coaly marls petrographically (GLOY 2000). The actualistic equivalent of these neutralization processes is found in the mangroves and fresh-water swamps of the Everglades, which are located on a carbonate platform; therefore the swamp deposits are directly neutralized by water dissolving the underlying carbonatic beds. The extraordinarily well preservation of bony remains and its biodiversity makes the Guimarota mine the most important fossil lagerstätte of the world for Late Jurassic mammals and other small terrestrial vertebrates.

4.2.2 Systematic palaeontology

4.2.2.1 Family **Paramacellodidae** ESTES, 1983

(Diagnosis: see ESTES 1983, and RICHTER 1994)

Upper Jurassic and Lower Cretaceous Cordyliformes from England, Portugal, Spain, North Africa, East Africa, Asia, and North America.

The Paramacellodidae include the genera *Paramacellodus*, *Becklesius*, *Pseudosaurillus*, *Sharovisaurus*, *Balnealacerta*, and *Mimobecklesisaurus*. Traditionally *Saurillodon*

was also included within the Paramacellodidae, but it shows striking scincoid affinities that warrant a tentative classification of this genus within the Scincoidea.

The Paramacellodidae are probably the ancestral form of the extant Cordyliformes, which are restricted to the Southern hemisphere.

Becklesius ESTES, 1983

Species typica: *Becklesius hoffstetteri* (Seiffert, 1973)

Referred taxa: *Becklesius cataphractus* RICHTER, 1994, *Becklesius hoffstetteri* (SEIFFERT, 1973), *Becklesius* sp.

Number of examined specimens: dentaries of approximately 16 adults and numerous additional fragments.

Range:

Upper Jurassic of Great Britain (Swanage) and Portugal, Lower Cretaceous of Spain and Morocco. One specimen from the Upper Jurassic of Tanzania is tentatively classified as *Becklesius* by BROSCINSKI (1999).

Diagnosis (after HOFFSTETTER (1967), SEIFFERT (1973), ESTES (1983), and RICHTER (1994)):

Teeth chisel-shaped; up to a maximum of 26 teeth per dentary; lingual surfaces of the tooth crowns concave; prominent enamel striations at the lingual surfaces of the tooth crowns; tooth crowns mesially expanded; crista mesialis longer than crista distalis; cuspis labialis formed by cristae mesialis et distalis; pronounced anguli mesialis et distalis; well-defined but flattened lingual cuspule (cuspis lingualis *sensu* RICHTER (1994) formed by two apically converging main striae (striae dominantes anterior et posterior); weak heterodonty with caudal tendencies to extremely mesially expanded tooth crowns with angular shape and gradually elongated crista distalis; tooth neck bulbous; teeth wide spaced in specimens with higher individual age; processus coronoideus relatively long; distinct attachment surface of the musculus pterygomandibularis at the dentary; pterygoid dentition present.

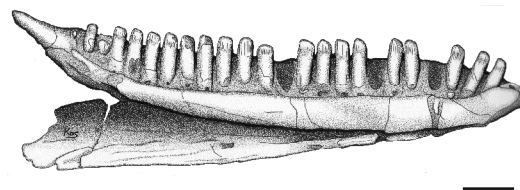


Fig. 120: *Becklesius hoffstetteri* (specimen Gui. Squ. 74)
Complete left dentary; lingual view
Scale bar: 1.0 mm

Description:

The dentaries of the examined *Becklesius*-individuals bear 22 (specimen Gui. Squ. 65) to 25 (specimen Gui. Squ. 63) tooth positions. The tooth shafts are cylindrical, whereas the lingual surfaces of the tooth crowns are curved inward. The tooth crowns are almost blunt. The mesial widths of the tooth crowns are enlarged compared to the diameters of the tooth necks. The posterior tooth crowns are particularly widened in the specimens Gui. Squ. 65 and Gui. Squ. 70. The degree of this expansion is comparable with the expanded posterior teeth in the extant scincids *Egernia cunninghami* and *Egernia kingii*. The crista mesialis is always longer than the crista distalis, it often even exceeds the double length of the crista distalis. The pronounced culmines lateres are long and in basal direction often reach the tooth necks. The anguli mesiales et distales are very pronounced in most individuals, especially in posterior teeth. The tooth cusps are situated in a slightly posterior position in anterior and central teeth, but a gradual shifting into a more central position is observable in posterior teeth. The apices of the anterior teeth are recurved. The cusps of the central and posterior teeth are divided into an almost blunt cuspis labialis (apical angle: 110-120°) and a pointed cuspis lingualis (apical angle: ca. 50°). The tips of the two cusps are situated in the immediate vicinity of each other. The cuspis lingualis is formed by the prominent striae dominantes anterior et posterior. The concave lingual surfaces of the tooth crowns are heavily striated with approximately seven or eight additional striae. The distinct additional striae of *Becklesius* are arranged almost parallel and they decrease apically before reaching the apical portions of the cusps. Striations on the crown surface are probably symplesiomorphic for scincomorphans (GAO & FOX 1996). The labial enamel surfaces of *Becklesius* are

unwrinkled. The ratio toothlength:diameter of tooth neck is 3.5:1.0. The resorption pits are circular or apically elongated and are situated centrally at the tooth bases.

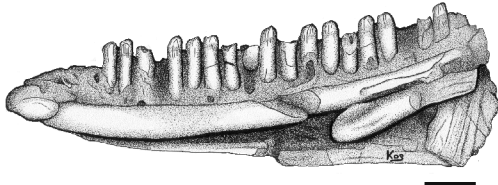


Fig. 121: *Becklesius hoffstetteri* (specimen Gui. Squ. 63)
Complete right dentary; lingual view
Scale bar: 1.0 mm

Conclusions concerning trophic structure:

The dentition of *Becklesius* belongs to an ecotype, which among extant scinciforms is represented by several scincid taxa. The general habitus of the teeth of *Becklesius* is accordingly comparable to the habitus of the teeth in *Egernia cunninghami*, *Egernia kingii*, and *Egernia striolata*. As the trophic structures of these extant taxa are without exception omnivorous, a comparable diet consisting of arthropods as well as leaves and other plant matter should be assumed for *Becklesius*.

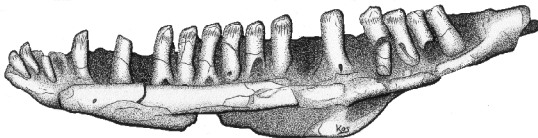


Fig. 122: *Becklesius hoffstetteri* (specimen Gui. Squ. 65)
Right dentary, showing mesially broadened tooth crowns; lingual view
Scale bar: 1.0 mm

The tooth crown ornamentation in *Becklesius* strongly resembles the pattern of striations in the living entomophagous cordylid *Cordylus cataphractus*. As the diet of *C. cataphractus* consists predominantly of termites, crickets, beetle larvae with strong chitinous shells, and other lizards, the striations seem to be useful in leading the teeth through the cuticula of the arthropods in order to handle or crack the prey. The presence of striations indicates a powerful stroke (RENSBERGER 1995). The stress of the bite can be directed and concentrated if striae are

developed, what results in a collapsing of the chitinous cuticula of the prey items. Concerning the former data, *Becklesius* was most probably a well adapted insectivore, which also accepted occasional plant matter in its diet.

Remarks:

SMITH & CHISZAR (1989) assumed a derivation of striate types from cuspidate types.

Becklesius probably was distributed also in the Upper Jurassic of Tanzania. An isolated lower jaw-fragment from the "Mittlere Sauriermergel" of Tendaguru was tentatively referred to the genus *Becklesius* by BROSCINSKI (1999) on the basis of similar tooth crown morphologies. This is the first evidence for the Paramacellodidae in the Southern hemisphere.

Dermal armor seems to be absent in the *Becklesius*-material from Guimarota, which strongly contrasts the well developed osteoderms found in *Becklesius* from the Early Cretaceous of Spain (BROSCINSKI 2000).

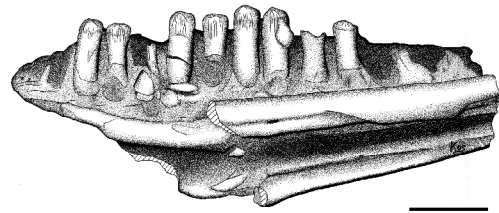


Fig. 123: *Becklesius hoffstetteri* (specimen Gui. Squ. 171)
Fragmentary left dentary, showing distinctly broadened tooth crowns; lingual view
Scale bar: 1.0 mm

Paramacellodus HOFFSTETTER, 1967

Species typica: *Paramacellodus oweni* HOFFSTETTER, 1967

Referred taxa: *Paramacellodus marocensis* RICHTER 1994, *Paramacellodus sinuosus* RICHTER 1994, *Paramacellodus oweni* HOFFSTETTER, 1967, *Paramacellodus* sp. (Morrison-Formation, Upper Jurassic, Wyoming (USA)), *Paramacellodus* sp. (Lower Cretaceous, Galve (Spain)).

Number of examined specimens: dentaries of approximately 7 adults and numerous additional fragments.

Range:

Upper Jurassic of Great Britain (Swanage), Colorado and Wyoming, Lower Cretaceous of Spain, Morocco and Transbaikalia (Asia).

Diagnosis (after HOFFSTETTER (1967), ESTES (1983), and RICHTER (1994)):

Teeth blunt-conical and slightly recurved; lingual surfaces of tooth crowns concave and striated; tooth shafts slightly expanded at the bases; ca. 24 teeth in dentary; teeth are of lanceolate shape; narrowly spaced dentition; anguli mesialis et distalis not pronounced (except in several posterior teeth); pointed cuspis labialis; tooth necks only moderately convex; few parallelly arranged and apically converging striae; striae dominantes without pars furcata; lingual surfaces of tooth crowns are posterolingually directed and therefore appear slightly recurved; large resorption pits at the bases of the teeth; crista dentalis slightly angular; pterygomandibularis facet on dentary absent (ESTES 1983) or present (RICHTER 1994); head and body covered by osteoscutes.

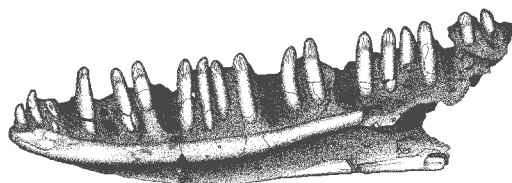


Fig. 124: *Paramacellodus oweni*
(specimen Gui. Squ. 58)
Complete right dentary; lingual view
Scale bar: 1.0 mm

Description:

All examined *Paramacellodus*-specimens were identified as *Paramacellodus oweni*. The well preserved and complete *Paramacellodus*-dentaries from the Guimarota mine bear approximately 24 (at least 23, maximally 25) tooth positions above strong subdental shelves (“laminae horizontales” *sensu* BROSCHINSKI & SIGOGNEAU-RUSSELL 1996). The teeth are narrowly spaced (Gui. Squ. 54, Gui. Squ. 57, Gui. Squ. 58, Gui. Squ. 59) or more widely spaced (Gui. Squ. 55, Gui. Squ. 60). This variability of the widths of interdental spaces lies within the possible intraspecific variability in extant scincomorphans. The tooth shafts are slender and cylindrical. The tooth crowns show

concave lingual surfaces. The degree of this inward curvature is highest in the immediate vicinity of the culmines lateres. The cristae mesialis et distalis are almost the same length what leads to a central position of the apex. The cusps of most teeth are divided into a blunt cuspis labialis and a more pointed cuspis lingualis. The cuspis lingualis is formed by the sharp edged cristae mesialis et distalis and shows an apical angle of approximately 90°, whereas the cuspis labialis is formed by the striae dominantes anterior et posterior and shows an apical angle of approximately 30°. The tips of both cusps are situated in the immediate vicinity of each other. In several teeth the two cusps are linked by a short and only slightly concave carina intercuspidalis. About five additional striae are developed at the concave inner surface of each tooth crown. The striae are arranged in parallel but converge apically underneath the cusps. The ornamentation varies greatly within this taxon. In several specimens the pattern of striations is very complex (e. g. Gui. Squ. 54, Gui. Squ. 58, Gui. Squ. 59, Gui. Squ. 60, Gui. Squ.61), whereas the striations are only weakly developed in other individuals (e. g. Gui. Squ. 55, Gui. Squ. 57). These additional striae can be situated between the striae dominantes as well as on the surfaces between the culmines lateres and the striae dominantes. tooth bases. The Meckelian sulcus is open.

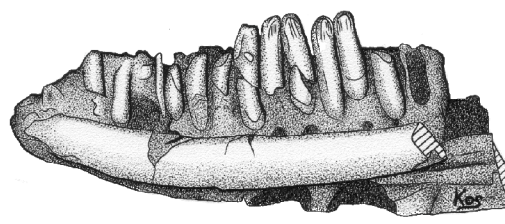


Fig. 125: *Paramacellodus oweni*
(specimen Gui. Squ. 227)
Fragmentary right dentary; tooth crowns showing complex patterns of striations; lingual view
Scale bar: 1.0 mm

In most teeth of *Paramacellodus* the relatively long striae are covering the entire lingual surface of the tooth crown. The striations decrease in the posterior teeth and the labial surfaces of all teeth are unwrinkled. The cristae mesialis et distalis transfer gradually into the culmines lateres in basal direction without forming anguli. The culmines lateres are prominent and long, and they run in a wide

sinus and decrease at the lingual surfaces of the tooth necks. The tooth crowns and the apical portions of the tooth necks rise above the labial wall of the dentary. The ratio toothlength:diameter of tooth neck is 4.9:1.0. The resorption pits are of circular shape and situated centrally at the Intraspecific variability:

Specimen Gui. Squ. 227 (fragment of a right dentary), specimen Gui. Squ. 246 (fragment of the snout region of a right dentary), specimen Gui. Squ. 248 (left dentary in matrix, bearing 22 tooth positions; posterior teeth robust), and specimen Gui. Squ. 259 (fragment of left dentary with a single preserved tooth) show transversal expansions of the tooth bases which strongly resemble the extremely expanded tooth bases in the extant cordylid *Cordylus giganteus*.

Conclusions concerning trophic structure:

The dentition of *Paramacellodus* strongly resembles the dentition of several species of the extant gerrhosaurid genus *Zonosaurus*. *Zonosaurus* taxa often show a similar pattern of striations (*Z. laticaudatus*, *Z. quadrilineatus*) as *Paramacellodus*, but in contrast to *Paramacellodus* there are prominent anguli developed in *Zonosaurus*. The *Zonosaurus* species prey on diverse arthropods and consume additional sweet soft fruits. A partly omnivorous diet is also assumed for *Paramacellodus*, especially as the paleoenvironmental habitat of this genus (swamp forests) is comparable to the habitat of the extant Madagascan *Zonosaurus* (damp tropical forests, riverbanks).

Among the Scincidae, many taxa show a tooth crown morphology which is comparable to the complex tooth crown morphology of *Paramacellodus* (*Carlia fusca*, *Dasia olivata*, *Emoia cyanura*, *Emoia nigromarginata*, *Emoia trossula*, *Eumeces fasciatus*, *Lamprolepis smaragdina*, and *Mabuya bistrriata*). In these species the striations are dominated by two main striae and anguli are absent. Interestingly, all of these skinks are forest dwellers with arboricole tendencies. The diets of these skinks are dominated by arthropod prey, which they hunt for in rotting stumps, where insects are abundant in damp forests. Since most of these lizard species are not closely related, the complex tooth crown morphology seems to be the result of a convergent evolution. Therefore, using actualistic methods, a similar foraging behavior and trophic structure can be assumed for *Paramacellodus*. This assumption perfectly

corresponds with the sedimentological background of *Paramacellodus*. The lizard inhabited damp tropical forrests, which are preserved as coals (Lignite Beds, Guimarota). The development of prominent anguli (like in *Becklesius* and *Zonosaurus*) obviously agrees with an at least partly frugivorous diet. The absence of these anguli indicates a shifting towards a higher percentage of insect prey, as it is found in the above mentioned forrest dwelling skinks and assumed for the fossil *Paramacellodus oweni*. The most efficient tooth shape to penetrate hard food items has short crest lengths (EVANS & SANSON 1998). These authors proved by punching experiments with beetles that "teeth of the same shape but at different scales require different forces to penetrate". The apical angles of *Paramacellodus* are smaller than in *Becklesius* and therefore the teeth require significantly less force and energy to penetrate the exocuticle of the prey. This corroborates the assumption of an arthropod-dominated trophic structure in *Paramacellodus* and a more omnivorous diet in *Becklesius*.

Remarks:

The phylogenetic youngest *Paramacellodus*-specimens originate from the Lower Cretaceous of Transbaikalia (Asia) (AVERIANOV & SKUTCHAS 1999). The Paramacellodidae were assumed to be the stem group of the Cordyliformes (BROSCHINSKI & SIGOGNEAU-RUSSELL 1996). A cladistic analysis made by EVANS & CHURE (1998), which is based on the discovery of almost complete *Paramacellodus*-skulls, proved a sister group relationship of *Paramacellodus* to Scincoidea as a whole, rather than to Cordyliformes.

4.2.2.2 Family ?Scincidae GRAY, 1825

Saurillodon ESTES, 1983

Species typica: *Saurillodon proraformis* (SEIFFERT, 1973)

Referred taxa: *Saurillodon henkeli* (SEIFFERT, 1973), *Saurillodon proraformis* (SEIFFERT, 1973), *Saurillodon marmorensis* (EVANS 1998).

Number of examined specimens: complete and

fragmentary dentaries of several hundred individuals.

Range:

Upper Jurassic (Kimmeridgian) of Portugal (Guimarota Lignite mine, Leiria), Middle Jurassic (Bathonian) of Kirtlington, Oxfordshire, England, and the Late Jurassic Morrison Formation of Colorado (Fruita).

Diagnosis (after SEIFFERT (1973), and ESTES (1983):

The dentary is short and shows a low (9-16) number of conical teeth; tooth crowns blunt; limb reduction; zygosphenes-zygantrum articulations in the vertebrae; referred to the Scincidae by SEIFFERT (1973) and tentatively referred to the Paramacellodidae by ESTES (1983).

Saurillodon henkeli (SEIFFERT, 1973)

Range:

Upper Jurassic (Kimmeridgian) of Portugal.

Diagnosis (after SEIFFERT (1973), and ESTES (1983):

Predominantly as for *Saurillodon proraformis*, but the shape of the dentary is more slender in *Saurillodon henkeli*; pterygomandibularis muscle scar on the prearticular is less prominent than in *S. proraformis*; tooth number is higher (15-16) than in *Saurillodon marmorensis* (9-12) (EVANS 1998).

Description:

The dentaries of *S. henkeli* bear 15 to 16 tooth positions. The ventral margin of the dentary is straight and the dentary is of gracile shape. The subdental ridge is deep.

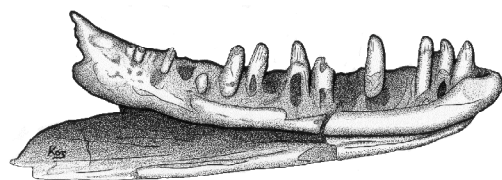


Fig. 126: *Saurillodon henkeli* (specimen Gui. Squ. 121)
Complete left dentary; lingual view
Scale bar: 1.0 mm

Specimen Gui. Squ. 121 as a typical representative of this species shows

moderately slender teeth with cylindrical shafts and conical cusps. The apical halves of the teeth rise above the labial wall of the dentary. The anteriormost teeth are forward inclined. The tooth cusps are unicuspid and moderately pointed. The lingual surfaces of the tooth cusps are slightly flattened. The culmines lateres often reach the lingual surfaces of the tooth necks. The lingual surfaces of the tooth crowns are sometimes faintly striated. The striae are extremely fine and run parallel. The pattern of striations is best developed in specimen Gui. Squ. 234. The labial surfaces of the teeth are unwrinkled. The ratio tooth length:diameter of tooth neck is 3.2:1.0. The resorption pits of *S. henkeli* are ventrally expanded. The lamina horizontalis is less broad than in *S. proraformis* and thins posteriorly. The labial wall of the dentary is rather low. The Meckelian sulcus is open. Multiple neurovascular foramina (mental foramina) are situated at the anterior portion of the labial wall of the dentary. These foramina indicate a highly sensitive snout region which is typical for burrowing lizards. The number and arrangement of these foramina varies individually. The snout tip is slightly pointed, which is a characteristic feature of burrowing lizards.

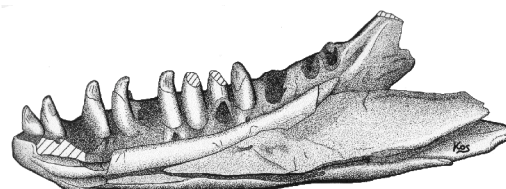


Fig. 127: *Saurillodon henkeli* (specimen Gui. Squ. 49)
Complete right dentary; the tooth crowns are distinctly recurved in this individual; lingual view
Scale bar: 1.0 mm

Conclusions concerning trophic structure:

The dentition of *S. henkeli* strongly resembles the dentition of the extant burrowing skink *Acontias meleagris*. The proportions of the teeth and of the tooth bearing bones, the tooth numbers, and the patterns of striations are almost identical in both taxa. Since these taxa belong to the same morphotype, the trophic structures are probably comparable. *A. meleagris* preys on earth worms, beetle larvae, millipedes, amphibians, worm snakes, and shows cannibalistic tendencies. The foraging

takes place directly underneath the ground surface. The mainly soft prey items can be grabbed by the slightly recurved and relatively long anterior teeth. A shortening of the mandibles and the reduction in tooth numbers is a typical character of many subterranean dwelling lizards.

Discussion:

SEIFFERT (1973) described a “remarkable similarity” of the lower jaw of *S. henkeli* with the jaws of the scincid *Chalcides chalcides*. This observation cannot be confirmed here. The lower jaw of *C. chalcides* is more elongated, the teeth are longer, the tooth cusps are less pointed, and the tooth number is higher (18-20) than in *S. henkeli*.

S. henkeli is the most abundant species of the burrowing ecotype among the Guimarota assemblage. The following specimens are referred to this species: Gui. Squ. 31, Gui. Squ. 35, Gui. Squ. 36, Gui. Squ. 37, Gui. Squ. 38, Gui. Squ. 39, Gui. Squ. 40, Gui. Squ. 41, Gui. Squ. 43, Gui. Squ. 45, Gui. Squ. 48, Gui. Squ. 49, Gui. Squ. 51, Gui. Squ. 53, Gui. Squ. 121, Gui. Squ. 131, Gui. Squ. 133, Gui. Squ. 134, Gui. Squ. 137, Gui. Squ. 138, Gui. Squ. 139, Gui. Squ. 141, Gui. Squ. 144, Gui. Squ. 145, Gui. Squ. 151, Gui. Squ. 152, Gui. Squ. 153, Gui. Squ. 157, Gui. Squ. 158, Gui. Squ. 159, Gui. Squ. 162, Gui. Squ. 165, Gui. Squ. 166, Gui. Squ. 167, Gui. Squ. 168, Gui. Squ. 175, Gui. Squ. 179, Gui. Squ. 181, Gui. Squ. 186, Gui. Squ. 187, Gui. Squ. 189, Gui. Squ. 192, Gui. Squ. 193, Gui. Squ. 196, Gui. Squ. 199, Gui. Squ. 201, Gui. Squ. 202, Gui. Squ. 204, Gui. Squ. 205, Gui. Squ. 206, Gui. Squ. 207, Gui. Squ. 210, Gui. Squ. 213, Gui. Squ. 217, Gui. Squ. 220, Gui. Squ. 223, Gui. Squ. 224, Gui. Squ. 226, Gui. Squ. 230, Gui. Squ. 232, Gui. Squ. 234, Gui. Squ. 237, Gui. Squ. 238, Gui. Squ. 244, Gui. Squ. 249, Gui. Squ. 254, Gui. Squ. 260, Gui. Squ. 276, Gui. Squ. 283, Gui. Squ. 286, Gui. Squ. 302, Gui. Squ. 303, Gui. Squ. 307, Gui. Squ. 314, Gui. Squ. 316, Gui. Squ. 319, Gui. Squ. 321, Gui. Squ. 325, Gui. Squ. 337, Gui. Squ. 343, Gui. Squ. 346. The proportions of the teeth and tooth bearing bones slightly vary among these specimens, but the degree of the variations lies (compared with extant taxa) within the parameters of intraspecific variability.

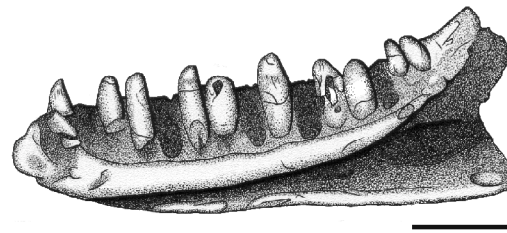


Fig. 128: *Saurillodon henkeli* (specimen Gui. Squ. 179)
Complete right dentary; the teeth of this specimen are blunt; lingual view
Scale bar: 1.0 mm

Remarks:

Since the positions of the posteromedial foramina vary individually in the extant fossorial *Typhlosaurus aurantiacus* (HEEVER, VAN DEN 1976), the arrangement of these foramina in fossil lizards is considered not to be of taxonomic value.

Saurillodon proraformis (SEIFFERT, 1973)

Remark:

Most dentaries examined by SEIFFERT were edentulous, accordingly the tooth crown morphology was scarcely noticed sufficiently in former studies.

Range:

Upper Jurassic (Kimmeridgian) of Portugal.

Diagnosis (after SEIFFERT (1973), and ESTES (1983):

Dentary is relatively short, deep, robust, and of boat-like shape; teeth conical with posterolingually orientated cusps; open broad Meckelian groove, sometimes closed by splenial (which is lost in most specimens due to preservation; however, facets on the underlying portions of the dentary often indicate the initial presence of the splenial); apical third of the teeth surpass the margin of the dental parapet; resorption pits large; tooth number is higher (15-16) than in *Saurillodon marmorensis* (9-12) (EVANS 1998).

Description:

Saurillodon proraformis is not as abundant in the Guimarota-material as was expected. Specimen Gui. Squ. 161 is a well preserved right dentary with an almost complete tooth row, of which only the most anterior tooth is lost. The tooth bases are firmly implanted by bone of attachment. The

subdental ridge is deep. The dentary is characterized by a convex ventral margin and a slightly concave dorsal margin of the labial wall ("boat-like shape" *sensu* SEIFFERT (1973) and ESTES (1983)). The dentary bears 16 tooth positions, three of these are represented as empty loci. The teeth are robust and short. The apical thirds of the teeth rise above the labial wall of the dentary. The tooth shafts are cylindrical. The lingual surfaces of the tooth crowns are slightly flattened, apart from that the tooth crowns are conical. The tooth tips are unicuspid, pointed and oriented in posterolingual direction. The intensity of this recurvature decreases in the posterior teeth. The lingual surfaces of the apices are faintly striated in the teeth of the central portion of the tooth row. The distances between the striae are regular and they converge apically. The labial surfaces of the teeth are unwrinkled. The ratio toothlength:diameter of tooth neck is 3.2:1.0. The resorption pits of *S. proraformis* are of circular shape and situated centrally at the tooth bases. The lamina horizontalis is broad throughout its entire length. The Meckelian sulcus is open.

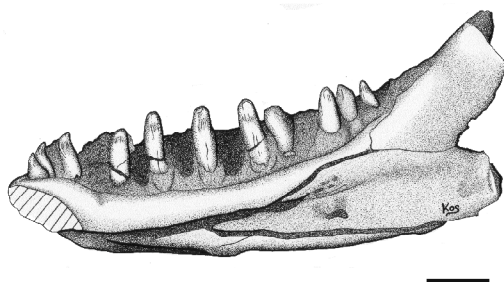


Fig. 129: *Saurillodon proraformis* (specimen Gui. Squ. 43)
Complete right dentary with 11 preserved teeth and 5 empty loci; lingual view
Scale bar: 1.0 mm

Intraspecific variability:

Specimen Gui. Squ. 43 is classified as *S. proraformis* even if it differs from specimen Gui. Squ. 161 in the relations between the heights of the dentaries and the lengths of the teeth (dentary of Gui. Squ. 161 is higher, teeth are smaller and more recurved than in Gui. Squ. 43). Proportional differences to a certain degree were also observed between individuals within numerous extant scincomophan taxa.

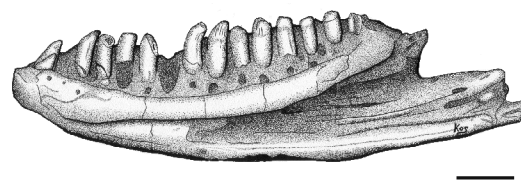


Fig. 130: *Saurillodon proraformis* (specimen Gui. Squ. 161)
Complete right dentary of robust shape demonstrating intraspecific variability; lingual view
Scale bar: 1.0 mm

Conclusions concerning trophic structure:

Among extant scincomorphans the dentition of *S. proraformis* is most closely resembled by the acontine skinks. The smaller *Acontias* species consume maggots, beetle larvae, termites, earth worms, millipedes, amphibians, worm snakes, and juvenile conspecifics. The lower jaws of *S. proraformis* are of comparable size as the lower jaws of the smaller *Acontias* species. The scale of the dentition plays an important role for its functional morphology (EVANS & SANSON 1998). As the examined dentaries of *Acontias gracilicauda*, *A. meleagris*, and *A. percivali* are of comparable size as the dentaries of *S. proraformis*, a comparable ecotype can be assumed for these lizards. The fang-like recurved teeth of the anterior portion of the tooth row are an adaptation to the soft prey items (predominantly larvae) which these burrowing skinks prey on.

Discussion:

The dental morphology represented by the Upper Jurassic *S. proraformis* is found among extant scincomorphans only in acontine skinks, but the general shapes of the dentaries differ greatly as they are boat-shaped in *S. proraformis* whereas the dentaries of the examined *Acontias*-specimens are more gracile and show a straight ventral margin. The teeth are more narrow spaced in *S. proraformis* than they are in *Acontias*. Apart from that, the dental morphologies of the fossil and the recent specimens are similar. *Saurillodon* represents the Mesozoic equivalent of the acontine morphotype.

The limbs of *Saurillodon* are only slightly reduced (BROSCHINSKI 2000) which strongly contrasts with the total loss of limbs in the acontine skinks. Extant scincomorphans genera (Cordylidae: *Tetradactylus*, Scincidae: *Lerista*, *Chalcides*) prove a gradual reduction of limbs within the genus, so it cannot be excluded that

one or more *Saurillodon* species were possibly legless.

***Saurillodon gigas* sp. nov.**

Derivation of name:

From Greek “gigas” meaning giant, referring to the large and robust size of the dentary in this species.

Holotype:

Gui. Squ. 126 - an almost complete right dentary, bearing 15 tooth positions, eight of which are preserved as empty loci; perhaps an additional posterior tooth position, which is lost together with the posteriormost portion of the dentary.

Referred material:

Gui. Squ. 198 - a badly preserved right dentary of short and robust habitus, bearing 14 tooth positions.

Gui. Squ. 250 - fragment of a left dentary; tip of a robust snout with 4 preserved teeth.

Gui. Squ. 211 - a badly preserved right dentary, bearing 15 tooth positions.

Type locality:

Guimarota mine, Leiria, Portugal (see chapter “Geological setting of the Guimarota mine”).

Type horizon:

Guimarota Lignite Beds.

Age:

Kimmeridgian, Upper Jurassic.

Differential diagnosis:

Dentary is short, deep, robust, and of boat-like shape with distinctly convex ventral margin; teeth robust with short cylindrical shafts and blunt conical crowns; large teeth; lingual surfaces of tooth crowns slightly flattened; tooth crowns slightly recurved; open broad Meckelian groove; apical thirds of the teeth rise above the margin of the dental parapet; resorption pits small.

Description:

Specimen Gui. Squ. 126 is an almost complete and relatively large right dentary. The dentary is conspicuously robust and short. The tip of the snout is pointed. The subdental shelf is extremely broad over its entire length. The posterior portion of the dentary is lost so that the shape of the coronoid process is unknown. The splenial facet, a rough portion of the surface of the subdental shelf, is reaching forward to the height of tooth position 11. The teeth of *Saurillodon gigas* are relatively large and robust. The apical third

rises above the labial wall of the dentary. The tooth shafts are predominantly cylindrical, only the tooth bases and necks of the anteriormost teeth are transversally widened. The anterior teeth are hardly inclined anteriorly. The lingual surfaces of the tooth crowns are lingually flattened. The cusps are unicuspid, blunt and slightly recurved. The posterior teeth are even more robust than the anterior teeth. The culmines lateres are weak. All enamel surfaces are unwrinkled. The ratio of toothlength:diameter of tooth neck is 2.9:1.0 in anterior and 2.3:1.0 in posterior teeth. The resorption pits are small and of circular shape.

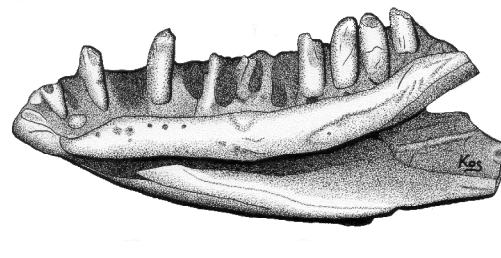


Fig. 131: *Saurillodon gigas* sp. nov. (specimen Gui. Squ. 126) Almost complete right dentary (holotype); lingual view
Scale bar: 1.0 mm

Discussion:

The dentary of *S. gigas* is even more robust than in *S. proraformis* (SEIFFERT, 1973). The new species shows distinctly larger teeth compared to *S. proraformis* and other taxa of the genus. The subdental shelf is broader developed and more massive than in its congenetics. Additionally, the dentary of *S. gigas* differs from other *Saurillodon* species in its distinct vertical expansion. *S. gigas* coincides with its congenetics in a reduced number of mandibular teeth (approximately 14 tooth positions per dentary) (opposing *Chalcidosaurus guimarotensis* gen. et sp. nov., which shows 21-23 teeth in each mandible). The ventral margin of the dentary is distinctly convex (opposing *Saurillodon henkeli* (SEIFFERT, 1973), *Saurillodon gracilis* sp. nov., in accordance with *Saurillodon proraformis* (SEIFFERT, 1973), *Saurillodon palacontiformis* sp. nov., and *Saurillodon tenuidens* sp. nov., all of which are less massive build).

Conclusions concerning trophic structure:

An extant counterpart of *S. gigas* is not known. The prey items of this robust

burrowing species must have been less soft bodied than the prey of other *Saurillodon* species since the teeth of *S. gigas* are more robust, less pointed, larger, and less inclined anteriorly.

S. gigas is the most robust of all taxa which are included in the genus *Saurillodon*. As the diets of the larger extant acontine skinks consist to a high percentage of vertebrate prey, a comparable trophic structure is likely for *S. gigas*. Many extant acontine skinks prey on other burrowing lizards, their own offspring, and worm snakes (*Typhlops* sp.). The great diversity of smaller burrowing species and their offspring in the Guimarota-paleo-environment meant a perfect food supply for a comparably large and strong species like *S. gigas*. The low frequency of *S. gigas* (4 *S. gigas*-individuals versus approximately 300 individuals of other *Saurillodon* species) within the Guimarota-assemblage confirms a predator-prey-relationship between *S. gigas* and its congenetics.

***Saurillodon gracilis* sp. nov.**

Derivation of name:

From Latin “gracilis” meaning gracile, referring to the gracile and slender shape of the dentary and the teeth in this species.

Holotype:

Gui. Squ. 136 - an almost complete left dentary, bearing 16 tooth positions, six of which are preserved as empty loci, one tooth position bears a minute replacement tooth.

Referred material:

Gui. Squ. 142 - an almost complete left dentary, bearing 14 tooth positions; slightly less elongated jaw than the Holotype; apices almost straight and hardly recurved; lingual surfaces of tooth crowns flattened and faintly striated.

Gui. Squ. 155 - fragment of the central portion of a right dentary.

Gui. Squ. 270 – fragment of the posterior portion of a left dentary, badly preserved.

Type locality:

Guimarota mine, Leiria, Portugal.

Type horizon:

Guimarota Lignite Beds.

Age:

Kimmeridgian, Upper Jurassic.

Differential diagnosis:

Dentary is slender, gracile and elongated; dentary shows perfectly straight

ventral margin; teeth relatively long with cylindrical shafts and pointed, recurved conical crowns; open narrow Meckelian groove; apical halves of the teeth rise above the labial wall of the dentary; anterior teeth strongly forward inclined; lingual surfaces of tooth crowns sometimes faintly striated; resorption pits large.

Description:

Specimen Gui. Squ. 136 is an almost complete left dentary. The jaw bone of *Saurillodon gracilis* is shallow, long, and gracile. The subdental shelf thins posteriorly. The symphyseal region is badly preserved. The ventral margin of the dentary is straight. The dentary bears 16 tooth positions. The apical halves of the long teeth rise above the labial wall of the dentary. The tooth bases are firmly implanted by bone of attachment. While the anterior teeth are forward inclined, the teeth in the central and posterior portions of the tooth row are almost straight. The posterior teeth are very small. The tooth shafts are shaped cylindrical, whereas the tooth crowns are conical and pointed. The tips of the teeth are unicuspid without exception and posterolingually directed. The 9th tooth of specimen Gui. Squ. 136 shows a faint striation at the lingual surface of the tooth crown (similar striations are also present in specimen Gui. Squ. 142). The six uniform striae converge apically. The labial enamel surfaces are unwrinkled. The ratio of toothlength:diameter of tooth neck amounts to 3.8:1.0. The resorption pits are large and dorsally expanded.

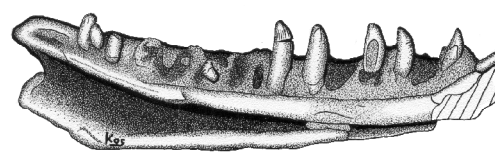


Fig. 132: *Saurillodon gracilis* sp.nov. (specimen Gui. Squ. 136)
Complete left dentary (holotype); lingual view
Scale bar: 1.0 mm

Discussion:

As a unique feature, the dentary of *S. gracilis* is extremely slender compared to other *Saurillodon* species, it is even distinctly more gracile than in *Saurillodon henkeli* (SEIFFERT, 1973). The dental parapet is lower than in any other *Saurillodon* species and the subdental shelf is rather narrow. The teeth are conical,

recurved, and rather long (contra *Saurillodon gigas* sp. nov. and *Saurillodon palacontiformis* sp. nov., both showing shorter and more bulky teeth, contra *Saurillodon tenuidens* sp. nov., showing more elongated teeth). As in other *Saurillodon* species, the tooth number of *S. gracilis* is reduced (14-16 tooth positions per dentary, opposing 21-23 tooth positions in each mandible of *Chalcidosaurus guimarotensis* gen. et sp. nov.). The ventral margin of the dentary is straight/linear (opposing *Saurillodon proraformis* (SEIFFERT, 1973), *Saurillodon gigas* sp. nov., *Saurillodon palacontiformis* sp. nov., and *Saurillodon tenuidens* sp. nov.; in accordance with *Saurillodon henkeli* (SEIFFERT, 1973)).

Conclusions concerning trophic structure:

The dentition of *S. gracilis* strongly resembles the dentition of the extant scincid *Typhlacontias gracilis*. It differs from this extant burrowing skink in a slightly higher number of teeth (16 in *S. gracilis* versus 13 in *T. gracilis*) and a slightly shorter shape of the dentary. The tooth shape and morphology as well as the width of the interdentary spaces of both taxa are similar. *Typhlacontias* preys on termites, ants, small beetles, and ant-lions. Since *T. gracilis* and *S. gracilis* represent a similar morphotype, the diet of *S. gracilis* probably consisted of comparable small-sized and mainly soft prey items.

Discussion of the assumed trophic structure:

Even if the dental morphology of *S. gracilis* strongly resembles the dental morphology of an extant myrmecophageous burrowing skink with a preference for termites, the prey compound of *S. gracilis* must have differed, since the fossil record of termites dates back only to the Cretaceous. Probably *S. gracilis* preyed on comparably small and soft arthropod larvae.

***Saurillodon palacontiaformis* sp. nov.**

Derivation of name:

From the Greek “palaeos” meaning ancient, and the extant South African scincid genus *Acontias*, whose morphotype strongly resembles the morphotype of the genus *Saurillodon*.

Holotype:

Gui. Squ. 148 – an almost complete left dentary, bearing 13 tooth positions, three of which are preserved as empty loci; posteriormost portion of dentary is lost.

Referred material:

Only holotype.

Type locality:

Guimarota mine, Leiria, Portugal.

Type horizon:

Guimarota Lignite Beds.

Age:

Kimmeridgian, Upper Jurassic.

Differential diagnosis:

The teeth in the short mandible of *Saurillodon palacontiformis* are extremely narrowly spaced, short, and whorl-shaped; the widths of the tooth necks are larger than the widths of the tooth crowns and the tooth bases; the tooth crowns are moderately pointed; the six anteriormost teeth are forward inclined; broad sympsical portion of the lamina horizontalis; resorption pits minute and circular; tooth bases firmly implanted by bone of attachment.

Description:

Specimen Gui. Squ. 148 (Holotype; left dentary) presents a unique dentition which justifies the status of the new species *S. palacontiaformis*. The dentary bears 13 tooth positions. Ten of these tooth positions are occupied by retracted teeth, whereas three tooth positions are represented as empty loci. The teeth are stout and hardly rise above the labial wall of the dentary. The whorl-like shape of the teeth differs greatly from the predominantly conical teeth of other *Saurillodon* species.

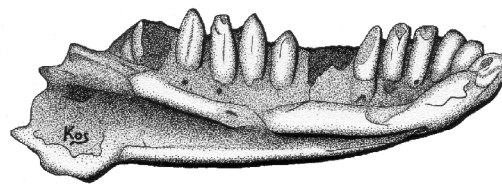


Fig. 133: *Saurillodon palacontiformis* sp. nov. (specimen Gui. Squ. 148)
Complete left dentary (holotype); lingual view
Scale bar: 1.0 mm

The teeth in tooth positions 1, 4, 5, and 6 show distinct apical wear facets. The distal portions of the first and the 6th tooth are abraded. The apical angles amount to 80°, which is extremely large. Faint longitudinal furrows are developed at the lingual surfaces of the posterior teeth (This is assumed to be an individual character: In the extant lacertid *Ichnotropis squamulosa* comparable furrows

can be present or absent individually). The ratio of toothlength:diameter of tooth neck amounts to 2.4:1.0. Resorption processes take place at the bases of almost all teeth. The resorption pits are small and circular.

Discussion:

S. palacontiformis strongly resembles *Saurillodon proraformis* (SEIFFERT, 1973) in the general shape of the dentary, but the ventral margin of the dentary is less convex in *S. palacontiformis*; it further differs from all other *Saurillodon* species in the unusually bulky habitus of the teeth. The teeth are shorter than in its congenetics and hardly rise above the dental parapet. *S. palacontiformis* coincides with other *Saurillodon* species in an extremely reduced number of mandibular teeth (contra *Chalcidosaurus guimarotensis* gen. et sp. nov.).

Conclusions concerning trophic structure:

The dentition of *S. palacontiformis* probably indicates a partially durophagous diet as it is represented in several extant *Chalcides* species that prey on occasional terrestrial snails.

Discussion:

A sympatric distribution of closely related species is not unusual among extant lizards. Morphological and behavioral adaptations toward certain microhabitats allow the overlapping of diverse species in several genera (*Acontias*, *Emoia*, *Lerista* (Scincidae), *Zonosaurus* (Gerrhosauridae)). Therefore, an assemblage of several sympatric *Saurillodon* species is likely and represents the situation found in extant Scincomorpha. Interestingly, sympatry of several congenetic species is especially common in extant fossorial or burrowing skinks. Probably the competition in burrowing lizards is more restricted to microhabitats than to larger areas as a result of a lack in visual sense.

Teeth which hardly rise above the labial wall of the dentary are among recent Scincomorphans only represented in the fossorial skinks *Chalcides mionecton*, *Hemiergis millewae*, and *Lerista punctatovittata*. All these skinks show limb reduction.

Comments:

Specimen Gui. Squ. 277 also shows extremely short and stout teeth which hardly rise above the labial wall of the dentary. Since only the posterior teeth are short (the tooth crowns are blunt and appear intensively worn), whereas the anterior teeth are longer and

resemble the dental habitus of *S. henkeli*, specimen Gui. Squ. 277 is not referred to *S. palacontiformis*. It more likely represents a *S. henkeli*-specimen of high individual age with strongly worn posterior teeth.

***Saurillodon tenuidens* sp. nov.**

Derivation of name:

From Latin “tenuis” meaning slender, and “dens” meaning tooth, referring to the unusual slender and long teeth in this species.

Holotype:

Gui. Squ. 44 – a fragment of a right dentary, bearing 9 tooth positions. The anterior portion of the dentary and the posteriormost portion of the tooth row are lost.

Referred material:

Only holotype.

Type locality:

Guimarota mine, Leiria, Portugal.

Type horizon:

Guimarota Lignite Beds.

Age:

Kimmeridgian, Upper Jurassic.

Differential diagnosis:

Dentary is posteriorly elongated; dentary shows slightly convex ventral margin; broad subdental shelf; teeth extraordinarily long, slender and recurved; tooth shafts cylindrical; tooth crowns conical; open narrow Meckelian groove; apical quarters of the teeth rise above the labial wall of the dentary; posterior teeth slightly more robust; sometimes faint striations developed on lingual surfaces of tooth crowns; resorption pits small and circular.

Description:

The holotype of *Saurillodon tenuidens* (specimen Gui. Squ. 44) is a fragmentary right dentary. The anterior portion of the tooth row is lost. The dentary is posteriorly expanded. The Meckelian groove is open and narrow. The subdental shelf is broad. Only nine tooth positions are preserved, but these teeth distinctly differ from the teeth of other *Saurillodon* species. The central portion of the tooth row is represented by four complete teeth. These teeth are narrowly spaced and extraordinarily long and slender. The shafts are cylindrical and the tooth crowns are conical with pointed apices. The teeth are strongly hook-like and bend in the posterior direction. The lingual surfaces of the tooth crowns sometimes show extremely faint striations. The

tooth shafts show several transversal cracks. Only the tooth bases and parts of the tooth necks of four posterior teeth are preserved. These teeth are slightly more robust than the above described central teeth. The tooth crowns are abraded. The ratio of toothlength:diameter of tooth neck amounts to 5.8:1.0 in the central teeth. The resorption pits are circular and situated in medial positions at the tooth bases.

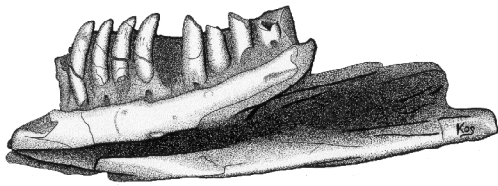


Fig. 134: *Saurillodon tenuidens* sp. nov. (specimen Gui. Squ. 44) Posterior portion of a fragmentary right dentary (holotype); lingual view
Scale bar: 1.0 mm

Discussion:

The teeth of *Saurillodon tenuidens* are longer and distinctly more slender than in any other *Saurillodon* species. The subdental shelf is rather broad (almost as broad as in *Saurillodon gigas* sp. nov.). The teeth are distinctly caudally directed (contra *Saurillodon henkeli* (SEIFFERT, 1973), *Saurillodon proraformis* (SEIFFERT, 1973), *Saurillodon gigas* sp. nov., *Saurillodon palacontiformis* sp. nov., *Chalcidosaurus guimarotensis* gen. et sp. nov.; in accordance with the more gracile *Saurillodon gracilis* sp. nov.). *S. tenuidens* coincides with *Saurillodon palacontiformis* sp. nov. in the distinctly narrowly spaced arrangement of the teeth, but differs clearly from the latter in possessing extremely long teeth (contra the bulky habitus of the teeth in *S. palacontiformis* sp. nov.). The ventral margin of the dentary is convex (resembling *Saurillodon proraformis* (SEIFFERT, 1973), *Saurillodon gigas* sp. nov., and *Saurillodon palacontiformis* sp. nov.; opposing *Saurillodon henkeli* (SEIFFERT, 1973) and *Saurillodon gracilis* sp. nov.).

Conclusions concerning trophic structure:

Tooth elongation in lizards is often associated with a dietary shift toward particularly minute or slippery prey items (e.g., the diet of the semiburrowing limbless *Anguis fragilis* (Anguimorpha)). The diet of *S.*

tenuidens most likely consisted of earthworms, beetle larvae, and slugs.

Discussion of the functional morphology:

Among extant scincomorphans the dentition of *S. tenuidens* resembles the dentition of the longtoothed scincid *Sphenomorphus muelleri*, but there are major differences at closer view. The tooth crown morphology is more complex in *S. muelleri*, the tooth crowns are more angled and the teeth are more widely spaced in this recent skink than they are in the new *Saurillodon* species. Apart from these morphological differences the teeth of both taxa are of comparable size (almost 1 mm total length). From the functional morphological point of view, the size of a tooth plays an important role since an increase in tooth volume means more force and energy are required to drive through insect prey (EVANS & SANSON 1998). The general shapes and sizes of the teeth are comparable in the extant and the fossil form. This convergence predicts an optimized length of this long recurved tooth morphotype at a total length of about 1 mm for insectivorous taxa.

Ontogenetic changes in the genus *Saurillodon* ESTES, 1983

The new material from Guimarota included several juvenile individuals of the genus *Saurillodon*.

Specimen Gui. Squ. 189 (tentatively referred to *S. henkeli*); right dentary of small size bearing 15 tooth positions. The teeth are relatively short and show recurved apices. The enamel surfaces are unwrinkled.

Specimen Gui. Squ. 195 (*Saurillodon* sp.); right dentary bearing 16 tooth positions. The teeth are short and conical.

Specimen Gui. Squ. 231 (*Saurillodon* sp.); minute right dentary with 16 tooth positions. This individual probably was a neonate.

Specimen Gui. Squ. 253 (*Saurillodon* sp.); badly preserved left dentary of minute size.

Specimen Gui. Squ. 340 (tentatively referred to *S. henkeli*); minute left dentary.

These dentaries of juvenile *Saurillodon*-individuals are miniatures of the dentaries of the adult specimens. No evidences of an allometric growth of the tooth-bearing bones and the dentitions were observed.

Chalcidosaurus gen. nov.

Species typical: *Chalcidosaurus guimarotensis* gen. et sp. nov.

Derivation of name:

From the extant scincid genus *Chalcides* referring to the similar dental proportions of the two genera, and the Greek *sauros* meaning lizard.

Range:

Upper Jurassic (Kimmeridgian) of Portugal (Guimarota Lignite mine, Leiria).

Differential diagnosis:

The length of the dentary is moderate, each dentary shows 21-23 conical teeth; tooth crowns blunt; posterior teeth anteriorly inclined; lingual surfaces of tooth crowns often striated.

Discussion:

The dentary of *Chalcidosaurus* is longer than in *Saurillodon* and shows a distinctly higher number of conical teeth (21-23 tooth positions in *Chalcidosaurus* versus 9-16 tooth positions in *Saurillodon*). The new genus clearly differs from paramacelodid taxa in its less complex ornamentation of the tooth crowns, its lower tooth numbers (21-23 in *Chalcidosaurus* versus more than 25 tooth positions in most paramacelodids), and its comparatively short dentaries.

Chalcidosaurus guimarotensis gen. et sp. nov.

Derivation of name:

From the locality Guimarota in Portugal, where the holotype originated from.

Holotype:

Gui. Squ. 174 - a complete left dentary, bearing 23 tooth positions.

Referred material:

Gui. Squ. 169 - an almost complete left dentary with approximately 23 tooth positions, only four of which are occupied by complete teeth.

Gui. Squ. 203 - a badly preserved right dentary, bearing 21 tooth positions, only one of which bears a tooth with a complete apex; dentary straight and long.

Gui. Squ. 212 - an almost complete right dentary with approximately 23 tooth positions, only six of which are occupied by complete teeth.

Type locality:

Guimarota mine, Leiria, Portugal.

Type horizon:

Guimarota Lignite Beds.

Age:

Kimmeridgian, Upper Jurassic.

Differential diagnosis:

As for genus.

Description:

Specimen Gui. Squ. 174 is a slender dentary, which shows a convex ventral margin. The subdental shelf slightly broadens anteriorly. The symphyseal region is rather robust. The dentary bears 23 tooth positions, 14 of which are represented as fully erected teeth while the others are preserved as empty loci. *Chalcidosaurus guimarotensis* shows a slight tendency toward heterodonty. The anterior teeth are very slender, whereas the posterior teeth are becoming gradually more robust. The tooth shafts of the anterior teeth are cylindrical and the tooth crowns are of conical shape. The tooth bases of the posterior teeth are expanded and therefore the outer shapes of these teeth are conical. The anterior as well as the posterior teeth are anteriorly inclined whereas the central teeth are straight. The tooth crowns are unicuspid and blunt. The lingual surfaces of the tooth crowns often show faint striations. The striae converge apically. A maximum of eight striae is developed per tooth. The labial surfaces of the tooth crowns are unwrinkled. The ratio of toothlength:diameter of tooth neck is 3.8:1.0.

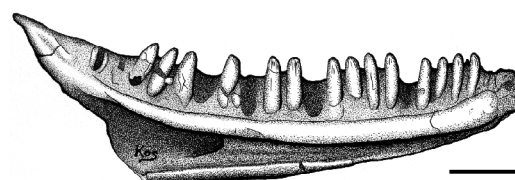


Fig. 135: *Chalcidosaurus guimarotensis* gen. et sp. nov. (specimen Gui. Squ. 174) Complete left dentary (holotype); lingual view Scale bar: 1.0 mm

Specimen Gui. Squ. 169 strongly resembles the morphology of specimen Gui. Squ. 174, but the bases of the posterior teeth are not expanded. This character together with the small size of the dentary gives evidence for a juvenile individual. The anterior teeth of Gui. Squ. 169 are posteriorly inclined what might be a result of post mortem deformation since the anterior region of the dentary was cracked.

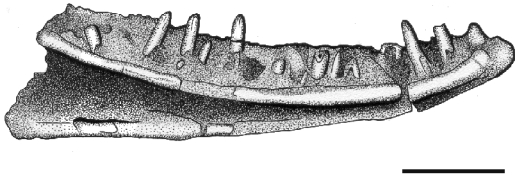


Fig. 136: *Chalcidosaurus guimarotensis* gen. et sp.nov. (specimen Gui. Squ. 169) Almost complete left dentary (paratype); lingual view Scale bar: 1.0 mm

Specimen Gui. Squ. 212 differs from the other specimens of *C. guimarotensis* in showing a straight ventral margin of the dentary. This single character state is treated as an individual variation (different shapes of the ventral margins of dentaries within a taxon are common among extant skinks), and specimen Gui. Squ. 212 is tentatively classified as *C. guimarotensis*.

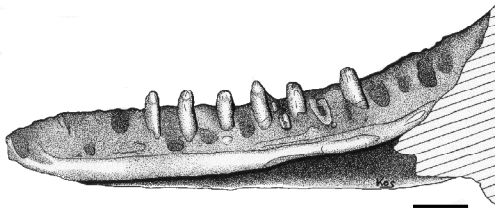


Fig. 137: *Chalcidosaurus guimarotensis* gen. et sp.nov. (specimen Gui. Squ. 212) Complete right dentary (paratype), posterior portion is covered by matrix; lingual view Scale bar: 1.0 mm

Discussion:

As for genus.

Conclusions concerning trophic structure:

The tooth morphology of *C. guimarotensis* is generally comparable with the tooth morphology of some extant arboreal skinks (genus *Carlia*). However, there are minor differences in tooth crown morphologies since the tooth crowns of *Carlia* are divided into a cuspis lingualis and a cuspis labialis whereas the apices of *C. guimarotensis* are unicuspid. Apart from morphological differences, the number of teeth in the dentaries of both genera differ very much since *Carlia* belongs to the taxa with the highest tooth numbers. The dentition of the recent *Chalcides chalcides* strongly resembles the dentition of *C. guimarotensis* in terms of tooth morphology as well as in the number of teeth. In contrast to *C. guimarotensis* the posterior

teeth of *C. chalcides* are not inclined anteriorly and the dentary is of a more shallow habitus. *C. guimarotensis* accordingly most likely consumed small insects, but the precise compound of its diet remains unclear as no extant representative shows perfectly identical features of dental morphology.

Discussion:

C. guimarotensis was less adapted to a burrowing lifestyle than the *Saurillodon* species. It probably was a semifossorial lizard comparable to most extant *Chalcides*.

4.2.3 Reconstruction of the habitat

4.2.3.1 Results

The investigation of numerous well preserved scincomorphan dentaries from the Guimarota mine yielded many formerly at best superficially known or even unknown details concerning the functional morphology of the teeth, the taxonomy of the lizard assemblages, and the paleo-environmental situation of the Guimarota ecosystem. Since all scincomorphan taxa from Guimarota are still represented by living counterparts of corresponding morphotypes, many actualistic conclusions can be drawn by direct comparison. The common paramacellodid *Becklesius hoffstetteri* for example shows mesially expanded tooth crowns with well developed lingual striations; this morphotype is also represented by the recent scincid *Egernia kingii*, which additionally to its basic diet feeds on carrion washed ashore. However, dental morphologies are greatly influenced by adaptations for a certain diet in numerous recent taxa; thus, based on their similar dentitions, a comparable trophic structure can be assumed for *Egernia kingii* and *Becklesius hoffstetteri*. Accordingly, the consumption of the aforementioned carrion is plausible also for *Becklesius* and confirms the presence of marine ingressions in the Upper Jurassic Guimarota ecosystem.

The absence of lizards with a tricuspid tooth crown morphology in the Guimarota material is possibly due to the absence of grasses in the Mesozoic. As shown in the recent lacertid *Gallotia galloti*, grasses and seeds may form an important food source for lizards with a tricuspid dental condition. The three pointed cusps help separating the grains from their capsules while the lizard performs

chewing movements of the jaws.

Becklesius hoffstetteri shows distinctly mesially expanded tooth crowns. This dental morphology is favorable for cutting plant tissues more efficiently. However, the teeth of *Becklesius* lack lateral cusps or serrations, thus a strictly vegetarian diet can be excluded for this paramacelodid. A higher percentage of plant matter results in even more widened tooth crowns than found in *Becklesius* and also in the development of lateral cusps in almost all families of the Scincomorpha (Gerrhosauridae: *Angolosaurus skoogi*, Lacertidae: *Gallotia stehlini*, Scincidae: *Macroscolecus coctei*, Xantusiidae: *Xantusia riversiana*). The apical angles of *Paramacelodus* are smaller than in *Becklesius* and therefore the teeth require significantly less force and energy to penetrate the exocuticle of the prey. This corroborates the assumption of an arthropod-dominated trophic structure in *Paramacelodus* and a more omnivorous diet in *Becklesius*.

The lizard assemblages from Guimarota yielded a surprisingly high percentage of burrowing forms. This allows actualistic comparisons with extant burrowing and semifossorial taxa, most of which are scincids. The distinct abundance of fossorial lizards in the Guimarota assemblage is not surprising after taking into consideration some data from recent lizard communities: In a study area in Kinchega, Australia, HENLE (1989) recorded a total reptile biomass of 0.1-1.1 kg/ha for diurnal food generalists opposed by a biomass of 22 kg/ha for the burrowing skink *Lerista lineata* and 60 kg/ha for the burrowing *Lerista elegans* in the Banksia woodland in Western Australia. These data convincingly demonstrate the high percentage of burrowing lizards in recent ecosystems. Accordingly, the abundance of fossorial lizards in the Guimarota community no longer seems to be astonishing.

In the fossil material from Guimarota, the common genus *Saurillodon* represents the Mesozoic equivalent of the acontine morphotype. Accordingly, conclusions concerning the feeding behavior and the paleoecology of the *Saurillodon* species can be drawn by direct comparison with recent representatives of its morphotype. A burrowing lifestyle requires several modifications concerning the morphology of the skull. The extant acontine *Typhlosaurus* is a sand swimming lizard and does not live in a

burrow, consequently prey may be approached from any angle which makes a terminal position of the mouth unnecessary (HEEVER, VAN DEN 1976). The subterminal mouth and shortened tooth row of *Typhlosaurus* allow a relatively great force of bite (HEEVER, VAN DEN 1976). A similarly inferior position of the mouth can be assumed for the Jurassic *Saurillodon* since it also shows shortened mandibles with reduced tooth numbers, but additional material, especially of the skull, is required before further conclusions can be drawn. In lizards, the miniaturization of the skull is another important adaptation to burrowing (RIEPEL 1981). A reduced diameter of head and body also allows a reduction of the widths of the tunnels which are constructed by these lizards. The short lower jaws and the reduced tooth numbers in burrowing lizards are characteristics that strongly coincide with this miniaturization.

Saurillodon gigas is the most robust of all taxa which are included in the genus *Saurillodon*. As the diets of the larger extant acontine skinks consist to a high percentage of vertebrate prey, a comparable trophic structure is likely for *S. gigas*. Many extant acontine skinks prey on other burrowing lizards, their own offspring, and worm snakes (*Typhlops* sp.). The great diversity of smaller burrowing species and their offspring in the Guimarota-paleo-environment meant a perfect food supply for a comparably large and strong species as *S. gigas*. The low frequency of *S. gigas* (4 *S. gigas*-individuals versus approximately 300 individuals of other *Saurillodon* species) within the Guimarota-assemblage confirms a predator-prey-relationship between *S. gigas* and its congenetics. A gap in the fossil record can be excluded due to the robustness of the dentaries. Further evidence of a predator-prey-relationship between *S. gigas* and its congenetics is given by the feeding behavior of the partly subterranean recent skink *Eremiascincus richardsonii*, which was observed eating smaller skinks (*Lerista* sp., small *Ctenotus* sp.) (HUTCHINSON, pers. comm.). *E. richardsonii* is a nocturnal lizard with slightly reduced limbs, which "swims" in loose soil and sand, or inhabits other animal burrows by day. *Saurillodon gigas* obviously occupied a comparable target niche within the Jurassic Guimarota ecosystem. With its strong mandibles and teeth it was even better equipped for saurophagy than the extant *Eremiascincus richardsonii*.

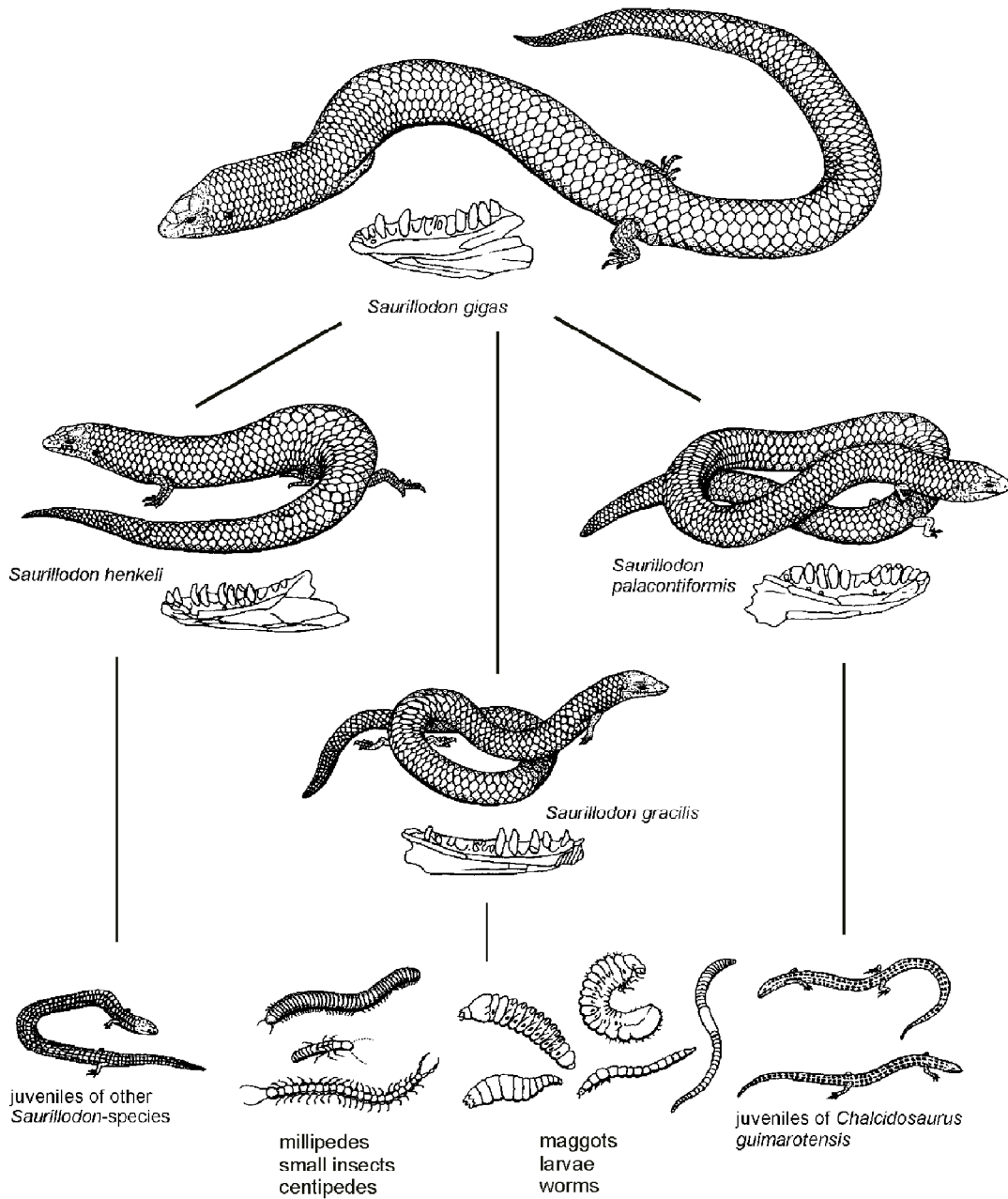


Fig. 138: Food chain in the subterranean ecosystem of Guimarota. The life community was dominated by the robust *Saurillodon gigas*, which probably preyed on other burrowing lizards, but also on maggots, larvae, and other subterranean invertebrates. The remaining *Saurillodon* species were more or less adapted to a diet consisting of soft maggots, insect larvae, worms, and occasionally juvenile burrowing lizards. The presence of limbs in the reconstructed lizards is hypothetical due to a lack of articulated skeletons. BROSCCHINSKI (2000) recorded limb elements in a *Saurillodon*-specimen, which is at least partly articulated. However, since many recent genera of burrowing lizards include legless forms beneath forms with well developed limbs, the presence of legless *Saurillodon* taxa is rather likely due to this actualistic background.

The dental morphology of the gracile *Saurillodon gracilis* strongly resembles the dental morphology of the recent legless burrowing skink *Typhlacontias gracilis*, which is a specialized myrmecophageous feeder. Its diet consists mainly of termites. However, the prey compound of *S. gracilis* must have differed, since the fossil record of termites dates back only to the Cretaceous. Probably *S. gracilis* preyed on comparably small and soft arthropod larvae. Aside from this, having extremely pointed unicuspid teeth, *S. gracilis* was also well equipped for grasping small arthropods possessing a strong cuticula since the extremely pointed teeth require less force to penetrate the cuticula of arthropod prey items. EVANS & SANSON (1998) claimed that "strong or stiff foods are most efficiently broken down by minimizing contact area between the tooth and the food". This minimizing of the contact area between tooth and prey is given in *S. gracilis* and, to a minor degree, in most other *Saurillodon* species from Guimarota.

A new possibly scincid lizard, *Chalcidosaurus guimarotensis* gen. et sp. nov., was less adapted to a burrowing lifestyle than the *Saurillodon* species. Compared to *Saurillodon*, *Chalcidosaurus* shows higher tooth numbers and slightly elongated dentaries. It was probably a semifossorial lizard comparable to most extant *Chalcides* (Scincinae).

In recent scincids, a vertical microhabitat stratification was observed by BROWN (1991). The substrate preferences of Australian burrowing skinks indicate a microhabitat segregation which strongly influences the prey types chosen by the lizards. Accordingly, several species of sympatric burrowing skinks with different prey preferences may coexist. The number of sympatric fossorial species is even higher under humid conditions (HENLE 1989). This observation fits well with the diverse fossorial herpetofauna of the Guimarota mine, which probably represents a humid paleo-environment. HENLE (1989) stated that "the potential for competition is so strong that fossorial guilds of reptiles are only stable if all species are morphologically and ecologically well separated ...". In the fossil Guimarota material this morphological separation is well documented by the various shapes of the mandibles found in burrowing lizards.

The classification of some fossil dentaries is difficult due to the problem to distinguish between taxonomical and individual characters. Indeed, a case of intraspecific variability is demonstrated by specimen Gui. Squ. 43, which is classified as *Saurillodon proraformis* even if it differs from other conspecific specimens in the relations between the heights of the dentaries and the lengths of the teeth (e.g., the dentary of Gui. Squ. 161 is higher, the teeth are smaller and more recurved than in Gui. Squ. 43). Proportional differences to a certain degree were also observed between individuals within numerous extant scincophan taxa (e.g., *Mabuya perroteti*). However, the dentaries of juvenile *Saurillodon*-individuals are miniatures of the dentaries of the adult specimens. No evidences of an allometric growth of the tooth-bearing bones and the dentitions were observed.

Other authors also worked on the problem of the taxonomic significance of dental characteristics in lizards. VOROBYEVA & CHUGUNOVA (1991) noticed that the morphology of lizard dentitions includes adaptations of feeding mechanisms and adaptations to certain food items; the same authors made an attempt to separate "the more stable features from variable ones in dental morphology and replacement". The majority of the taxonomically useful characters they found were either restricted to groups outside the Scincomorpha, or the differences concerning features of the upper jaws (e.g., the presence of a diastema between premaxillar and maxillar teeth which separates racerunners from other lizards). Of course there are numerous dietary adaptations influencing the form and function of lizard teeth (e.g., the multicuspid tooth crowns in the phytophagous *Macroscincus coctei*; the pointed teeth in larvae-consuming burrowing lizards) which confirm the strong dependence of tooth morphology from the trophic structure of the lizard. On the other hand, the functional morphological adaptations of lizard dentitions to a special diet should not be overrated, because stomach contents often reflect prey availability rather than prey selection. Prey availability seems to play an important role in the nutrition of lizards, which is proved by island populations of herbivorous iguanas, *Ctenosaura pectinata*, which occasionally prey on defenseless birds (GRANT 1967). Therefore it is obvious that dental

characteristics not always require a defined diet, but are at least partly to be considered as the result of a stable genome.

Among recent scincomorphans some pathological abnormalities were found, which may also occur in fossil forms. The lower jaw of an *Egernia stokesii* individual (SRK 00.073) was strongly deformed (especially the articular complex) by a rhachitic disease. In this specimen, several teeth have fallen out, or are no longer arranged vertically to the longitudinal axis of the dentary. Additionally, the retro-articular bows upward. Another abnormality is the development of numerous parallel tooth rows as described above for *Lygosoma afra* and *Sphenomorphus variegatus* as “multiple replacement”. Since “multiple replacement” seems to occur predominantly in old individuals, it is probably a rare feature in wild populations, which almost always underly a predatory pressure. Nevertheless, if ever found in fossil lizards, the “multiple replacement” can be used as an indicator for a long life span of the specimen.

The extraordinarily preservation of the fossil lizard remains from Guimarota is remarkable; only few bacteria are able to produce enzymes capable of breaking down the organic matrix of dentine (BRADFORD 1954). Additional biochemical reasons allow a longtime preservation of lizard (and other vertebrate) teeth; the “enamel structure is altered very little during fossilization because the content of organic components is very small and the inorganic phase (hydroxyapatite crystals) is of low solubility” (KOENIGSWALD et al. 1993).

4.3 The fossil Scincomorpha from the Bavarian Freshwater Molasse

4.3.1 Geological settings and fossil contents of the Scincomorpha-bearing localities

Two localities of the Bavarian Freshwater Molasse yielded remains of fossil scincids and/or fossil cordylids; those are Petersbuch 2 and Rembach. Lithologically, Petersbuch 2 represents a fissure filling, whereas the lower Bavarian locality Rembach is dominated by marls. Due to the taphonomy of the rare fishes found in these sediments, the marls are

interpreted as a paleo-soil in a floodplain environment.

In addition to *Bavariascincus mabuyaformis* gen. et sp. nov., the locality Rembach yielded remains of several other ectothermic vertebrates: *Channa* ssp., *Chamaeleo* sp., Gekkonidae indet., *Miolacerta* sp., *Lacerta* sp., *Ophisaurus* sp. 1, *Ophisaurus* sp. 2, Anguidae indet., *Blanus* sp., and Serpentes indet.

However, the vertebrate assemblage of the locality Petersbuch 2 is even more diverse. In addition to *Bavaricordylus ornatus* gen. et sp. nov. and *Bavariascincus mabuyaformis* gen. et sp. nov., the locality Petersbuch 2 yielded remains of numerous other lower vertebrates: *Albanerpeton inexpectatum*, *Salamandra sansaniensis*, *Mertensiella* sp., *Chioglossa meini*, *Salamandrina* sp., *Chelotriton pliocenicus*, *Triturus helveticus*, *Triturus* sp., *Albionbatrachus* sp. 1, *Albionbatrachus* sp. 2, *Latonia ragei*, *Pelobates* sp., *Eopelobates* sp., *Bufo viridis*, *Rana (ridibunda)* sp., *Chamaeleo* sp., *Miolacerta* sp., *Lacerta* sp., *Ophisaurus fejfari*, *Ophisaurus* sp., *Pseudopus moguntinus*, *Varanus hofmanni*, cf. *Iberovaranus* sp., and Serpentes indet. Altogether, these taxa are well adapted to dryer habitats (BÖHME, M., pers. comm.).

4.3.2 Systematic palaeontology

4.3.2.1 Family Cordylidae GRAY, 1837

Diagnosis (after ESTES 1983, MCDOWELL & BOGERT 1954; OLMO & ODIERNA 1980; RIEPPEL 1980):

Posterior adductor not extending far into Meckelian canal; differentiation of the musculus adductor mandibulae externus. Cordylids are usually robust-bodied lizards with strongly keeled or very spiny tails. Osteoderms are well developed dorsally from head to tail. Their chests and bellies bear a lighter osteoderm shield and often abutting, smooth scales. Scales are arranged in circles around the body.

Bavaricordylus gen. nov.

Species typica: *Bavaricordylus ornatus* gen. et sp. nov.

Derivation of name:

From Latin "Bavaria" referring to the locality (in the German state of Bavaria), where the specimen was excavated, and the probably closely related recent genus *Cordylus*.

Range:

Lower Miocene (lower MN4, approximately 18 Myr) of South Germany (fissure filling Petersbuch 2).

Diagnosis:

Prominent and broad subdental shelf; labial surface of dentary appears rough, probably as an attachment for osteoderms; teeth robust with laterally expanded tooth crowns; distinct striations on lingual surfaces of tooth crowns; weak striations on labial surfaces of tooth crowns.

Bavaricordylus ornatus gen. et sp. nov.

(Pl. XV, Figs. 10-13)

Derivation of name:

From the striking pattern of striations (ornamentation) of the tooth crowns.

Holotype:

M 16 - a fragment of the central portion of a left dentary with 3 preserved teeth.

Referred material:

Only holotype.

Type locality:

Petersbuch, Bavaria, Germany.

Horizon:

Fissure filling (lower MN4).

Age:

Lower Miocene (18 Myr).

Diagnosis:

As for genus.

Description:

The holotype of *Bavaricordylus ornatus* is a fragment of the central portion of a left dentary. The labial surface of the dentary is sculptured with rough facets for the attachment of dermal bones. The jaw fragment bears three well preserved teeth. The teeth are widely spaced, robust shaped and show transversally expanded tooth bases and flattened flanks. Only the tooth crowns rise above the labial

wall of the dentary. The tooth crowns are blunt and of slightly larger widths than the tooth shafts. The culmines lateres are prominent and with their ventral portions reach the tooth shafts. At the immediate vicinity of the culmines lateres, the lingual surfaces of the tooth crowns are concave. The anguli mesiales et distales are well developed and represent the transition zone between the culmines lateres and the occlusal cutting edges. The crista mesialis is always longer than the crista distalis. Apically, the cristae form the blunt cuspis labialis (apical angle ca. 150°). Approximately 20 prominent striae are situated at the lingual surfaces of the tooth crowns. The striae converge apically. Many of these striae bifurcate in basal direction. The lingual striations are dominated by two main striae, the striae dominantes anterior et posterior, which apically form the moderately pointed cuspis lingualis. These lingual cusps are situated in the immediate vicinity of the cuspides labiales, but in a slightly lower position. The labial surfaces are less intensively striated. The labial striae converge apically and are very uniform, in contrast to the lingual striations a derivation of striae dominantes is not developed here. The ratio of toothlength:diameter of tooth neck is 2.9:1.0.

Conclusions concerning trophic structure:

The dentition of *B. ornatus* strongly resembles the dentition of the recent cordylid *Codylus cataphractus*, which preys on termites, beetle-larvae, caterpillars, crickets, moth-larvae, eggs, and other lizards (Lacertidae). A comparable diet probably was consumed by *B. ornatus*.

Discussion:

B. ornatus shared its environment with numerous Lacertidae and Anguimorpha, which are both common in the sediments of the Bavarian Freshwater Molasse. Since its extant equivalent, *C. cataphractus*, shows saurophageous tendencies, a partially saurophageous diet in *B. ornatus* was made possible by the presence of other lizards in this habitat. The dentitions of the two species differ in a few characters, which are believed to be of only minor functional morphological value. The number of striae per tooth is generally smaller in *C. cataphractus* (it varies between individuals) and the labial striations, which are present in *B. ornatus*, are absent in *C. cataphractus*. Labial striations are developed among extant scincomorphans almost exclusively in durophageous taxa (e. g. in the

scincids *Hemisphaeriodon* and *Tiliqua*, and the teiid *Tupinambis*), so that an at least partially durophagous diet can be assumed for *B. ornatus*.

Cordylids were rare during the Lower Miocene of Central Europe, but their presence was already proved with the discovery of (the probably closely related) *Palaeocordylus bohemicus* (ROCEK 1984). The beginning of the Miocene was marked by the return of tropical climatic conditions and the collision of Eurasia with Africa. These processes allowed the immigration of a new squamate fauna to Europe as well as the re-immigration of squamate lineages which were extinct in Europe during the cooler and drier Oligocene, but survived in Africa. Among these lineages were Varanidae, Scolecophidia, Chamaeleonidae, Viperidae, Elapidae, and probably Scincidae (RAGE & AUGÉ 1993). The Lower Miocene appearance of *B. ornatus* in Southern Germany corresponds well with the immigration of the diverse other squamate lineages.

Comment:

Since osteoscutes at the lower jaws are only developed in girdled and plated lizards, specimen M 16 is tentatively referred to the Cordylidae.

4.3.2.2 Family ?Scincidae GRAY, 1825

Diagnosis (after ESTES 1983, GREER 1970, READ 1986, RIEPPEL 1980):

Anterior pterygoid processes overlap palantines to form a secondary palatal structure; multiple unit osteoderm structure; femoral pores absent; parietal downgrowth clasps processus ascendens tecti synotici.

Bavariascincus gen. nov.

Species typica: *Bavariascincus mabuyaformis* gen. et sp. nov.

Derivation of name:

From Latin Bavaria referring to the locality where the specimens were excavated, and the recent scincid genus *Scincus*.

Range:

Lower Miocene (lower MN4, approximately 18 Myr (fissure filling Petersbuch 2) to upper MN4, approximately 17

Myr (Rembach; floodplain deposits, paleosoil)) of South Germany.

Diagnosis:

Subdental shelf broad and straight; teeth slender with laterally expanded tooth crowns; prominent striations on lingual surfaces of tooth crowns; cristae mesiales distinctly longer than cristae distales; apices divided into cuspidae linguales et labiales.

Bavariascincus mabuyaformis gen. et sp. nov.
(Pl. XV, Figs. 14-15; Pl. XVI, Fig. 1)

Derivation of name:

From the extant scincid genus *Mabuya*, whose dentition strongly resembles the dentition of this Miocene taxon.

Holotype:

M 15b - an almost complete right dentary, anteriormost portion of the dentary is lost.

Referred material:

M 15a - a fragment of the posterior portion of a left dentary.

M 17 - a fragment of the anterior portion of a right dentary.

Localities:

Petersbuch and Rembach, both in Bavaria, Germany.

Horizons and ages:

Fissure filling (lower MN4; ca. 18 Myr) and floodplain deposits/ paleosoil (upper MN4; ca. 17 Myr), Lower Miocene.

Diagnosis:

As for genus.

Description:

The fragmentary dentaries of *Bavariascincus mabuyaformis* show moderately robust subdental shelves and high cristae dentales *sensu* ROCEK (1984). The teeth are labially attached to the dental parapet almost over their entire length, with only the tooth crowns rising above the labial wall of the dentary. The flanks are flattened. The tooth shafts are slender, long, and slightly expanded transversally. The tooth crowns are blunt and lingually flattened or concave (the inward curvature is most distinct in the immediate vicinity of the culmines lateres). The widths of the tooth crowns are larger than the widths of the tooth shafts. The crista mesialis is longer than the crista distalis which leads to a posterolingual orientation of the cusp. The culmines lateres are prominent and long, they run down onto the lingual surfaces of the tooth

necks. The angulus mesialis and the angulus distalis both are well developed. The apices are divided into a cuspis labialis and a lower situated cuspis lingualis. The cuspis labialis is formed by the cristae mesialis et distalis, whereas the cuspis lingualis is formed by a system of cutting edges which run parallel to the cristae mesialis et distalis in a more lingual position (the cristae linguales anterior et posterior which were observed also in many extant genera of the Scincidae). The lingual surfaces of the tooth crowns are striated. The striae are very prominent, straight, and arranged parallel to the longitudinal axis of the tooth. They are restricted to the flattened or concave portions of the teeth and end underneath the cusps without reaching them. There are five or six striae to be found in each tooth. The labial surfaces of the teeth are unwrinkled. The ratio of toothlength:diameter of tooth neck is 5.0:1.0. The resorption pits are dorsally expanded.

Conclusions concerning trophic structure:

Many taxa of extant Scincidae evolved a similar or at least comparable dental morphology like *B. mabuyiformis*, but most of these taxa are not closely related to each other. Therefore, they are considered to be of the same ecotype. The extant taxa which developed a dentition comparable to *B. mabuyiformis* are predominantly opportunistic feeders with a preference for arthropod prey. Therefore *B. mabuyiformis* most likely was a generalized skink consuming a great variety of arthropods.

Discussion:

The dental morphology of *B. mabuyiformis* strongly resembles the dental morphologies of many extant scincids like *Emoia aneityumensis*, *Emoia cyanura*, *Emoia sanfordi*, *Emoia trossula*, *Eugongylus albifasciolatus*, *Eugongylus rufescens*, *Eulamprus tympanum*, *Eumeces gilberti*, *Lamprolepis smaragdina*, *Mabuya bistrinata*, *Mabuya carinata*, *Mabuya multifasciata*, *Mabuya quinquetaeniata*, *Mabuya wrightii*, and *Sphenomorphus striatopunctatus*. Interestingly, many of these extant taxa are not closely related to each other. Therefore, this dental morphology must have evolved several times in different populations and is assumed to be an ecotype more than of taxonomic value. The prominent parallel striae are useful for leading the tooth crowns through the cuticula of the arthropod prey items.

4.3.2.3 Comments regarding the remains of Lacertidae and Anguimorpha from the Bavarian Freshwater Molasse

Numerous fossil Lacertidae and Anguimorpha were excavated at localities in the Tertiary Freshwater Molasse of Southern Germany and France. Though most of these lizard remains are of Miocene age, the oldest sample dates back to Middle Oligocene (Möhren 12 (MP21), ca. 33 Myr) and the youngest sample probably contains subrecent material (Ronheim 1 bei Harburg (MP22), ca. 32 Myr to subrecent (fissure filling)). The dentitions of these lizard remains proved a great diversity of tooth crown morphologies, which allow comparisons with extant taxa and conclusions concerning the trophic structures of these Tertiary lizards (table 1).

Sample	Locality and age	Extant taxon of comparable dental morphotype	Trophic structure
M 1 (A)	Möhren 12 (MP21), fissure filling; ca. 33 Myr.	<i>Gastropholis echinata</i> (Lacertidae)	probably insectivorous
M 9 (B)	Gallenbach 2b (Lower MN6), floodplain deposits, paleosoil; ca. 14.7 Myr.	<i>Lacerta agilis</i> (Lacertidae)	insectivorous
M 24 (B)	Goldberg bei Pflaumloch/ Ries (Lower MN6), limnic; ca. 14.4 Myr.	<i>Lacerta agilis</i> (Lacertidae)	insectivorous
M 10 (C)	Laimering 3 (Lower MN6), floodplain deposits, paleosoil; ca. 14.6 Myr.	<i>Lacerta agilis</i> (Lacertidae)	insectivorous
M 13 (C)	Merkur Nord (Lower MN3), palustric; ca. 20 Myr.	<i>Lacerta agilis</i> (Lacertidae)	insectivorous
M 22 (B)	Goldberg bei Pflaumloch/ Ries (Lower MN6), Upper Miocene fissure filling in freshwater carbonate; ca. 14.4 Myr.	<i>Podarcis hispanica</i> and <i>Zootoca vivipara</i> (Lacertidae)	predominantly insectivorous
M 23 (B)	Ronheim 1 bei Harburg (MP22), Middle Oligocene and subrecent fissure filling; ca. 32 Myr.	<i>Timon pater</i> (Lacertidae)	predominantly insectivorous; occasional gastropod and vertebrate prey
M 4 (B)	Schönenberg (Lower MN5), fluvial channel filling; ca. 16.5 Myr.	<i>Lacerta princeps</i> (Lacertidae)	probably insectivorous with occasional gastropod and vertebrate prey
M 12 (D)	Walda 1 (Middle MN5), fluvial channel filling; ca. 16.0 Myr.	<i>Timon pater</i> (Lacertidae)	predominantly insectivorous; occasional gastropod and vertebrate prey
M 10 (B)	Laimering 3 (Lower MN6), floodplain deposits, paleosoil; ca. 14.6 Myr.	<i>Lacerta viridis</i> (Lacertidae)	predominantly insectivorous with omnivorous tendencies
M 8 (A)	Unterempfenbach 1b (Middle MN5), floodplain deposits, paleosoil; ca. 15.8 Myr.	<i>Tupinambis merianae</i> (Teiidae), posterior teeth	omnivorous with preference for gastropods and eggs (durophagous)

Table 1: Comparisons between the lizard remains from the Bavarian Freshwater Molasse with recent lizards in terms of tooth crown morphology.

4.3.3 Composition of the saurofauna and trophic relationships

The Bavarian Freshwater Molasse yielded a fragment of a left dentary from a new cordylid, *Bavaricordylus ornatus* gen. et sp. nov., as well as two fragmentary dentaries from a new lizard, *Bavariascincus mabuyaformis* gen. et sp. nov., which was tentatively referred to the Scincidae here. The tooth crown morphology of *B. ornatus* is rather peculiar due to the presence of some labial wrinklins and the numerous prominent lingual striations. Since labial striations are developed among extant scincomorphans almost exclusively in durophagous taxa (e. g., in the scincids *Hemisphaeriodon* and *Tiliqua*, and the teiid *Tupinambis*), an at least partially durophagous diet can be assumed for *B. ornatus*.

The dental morphology of *Bavariascincus mabuyaformis* strongly resembles the dental morphologies of many extant scincids like *Emoia aneityumensis*, *Emoia cyanura*, *Emoia sanfordi*, *Emoia trossula*, *Eugongylus albifasciolatus*, *Eugongylus rufescens*, *Eulamprus tympanum*, *Eumeces gilberti*, *Lamprolepis smaragdina*, *Mabuya bistriata*, *Mabuya carinata*, *Mabuya multifasciata*, *Mabuya quinquetaeniata*, *Mabuya wrightii*, and *Sphenomorphus striatopunctatus*. Interestingly, many of these extant taxa are not closely related to each other. Therefore, this dental morphology must have evolved several times in different taxa and is assumed to be an ecotype more than of taxonomic value. The prominent parallel striae are useful for leading the tooth crowns through the cuticula of the arthropod prey items.

4.4 Results and conclusions

The description of new fossil species on the basis of isolated dentaries in this thesis was maintained since distinct morphological characters or clear differences in relations separated these individuals from other dentaries. These interspecific differences are of the same dimensions as jaw related osteological differences between extant scincomorph species. Unfortunately, several extant species show a high degree of intraspecific variation of the dentition, which sometimes even overlaps the degree of interspecific variability (e.g., in several species of the lacertid genus *Podarcis*, or the teiid

genera *Ameiva* and *Cnemidophorus*). The importance of the intraspecific variation in the dentition of lizards was also observed by ROCEK (1980). The *Lacerta viridis*-specimens examined by ROCEK varied individually in terms of tooth shape, general pattern of dentition, and the mode of tooth replacement.

The Scincidae are probably the most successful lizard family; they gave rise to 1000-1200 extant species and are distributed almost worldwide: scincids inhabit a wide variety of ecosystems in Australia, Asia, Africa, Europe, and the Americas. Nevertheless the Scincidae are poorly represented in the fossil record since they are not recorded in pre-Miocene deposits from Asia, Africa, or Australia, were they are widespread today (GAO & FOX 1996). The oldest record of the Scincidae is probably provided by fragmentary dentaries from the Lower Cretaceous of Spain (RICHTER 1994). If *Saurillodon* is really of scincid relationship, the Scincidae would already have been highly diversified at the end of the Jurassic period, including specialized burrowing forms. The scarcity of articulated individuals of Mesozoic scincomorphans, and the relative abundance of disarticulated, isolated elements allow the assumption that many scincid dentaries are hidden beyond specimens which were referred to the Paramacellodidae (many characteristics that divide the two groups are highly equivocal, like the depth or the shape of the subdental shelf).

The scincids *Penemabuya antecessor* GAO & FOX, 1996 from the Upper Cretaceous (Aquilan) Milk River Formation of Alberta, *Orthrioscincus mixtus* GAO & FOX, 1996 from the Upper Cretaceous Oldman Formation (Judithian) of Alberta (a scincid species with a tooth morphology similar to that of the extant *Gerrhosaurus*), and *Aocnodromeus currugatus* GAO & FOX, 1996 from the Upper Cretaceous (Aquilan) Milk River Formation of Alberta (this species shows molariform posterior teeth and striated tooth crowns) prove a high diversity of this family at the end of the Mesozoic.

Scincid remains are abundant in Tertiary deposits: *Palaeoscincosaurus middletoni* SULLIVAN & LUCAS, 1996 from the Early Paleocene (Puercan) of Colorado was tentatively referred to the Scincidae (SULLIVAN & LUCAS 1996). *P. middletoni* strongly resembles the Late Cretaceous to Late Paleocene North American scincomorph

Contogenys sloani (which is more gracile) in terms of tooth morphology; GAO & FOX (1996) tentatively located *Contogenys sloani* to the Xantusiidae.

All Scincomorpha have in common the polyphyodont condition (teeth are replaced throughout the entire life-span of an individual), but the dental morphologies often greatly vary even in smaller taxonomic groups. The variability of lizard dentitions was proved on the basis of numerous extant species. In several genera (e.g., *Ameiva*, *Cnemidophorus* (both Teiidae), *Podarcis* (Lacertidae)), the dentitions are almost uniform in all examined species, whereas a large number of extant species displays a great variability of dental morphologies even in closely related species. This is especially true for the Scincidae which evolved a large diversity of tooth crown morphologies. It appears very difficult to distinguish between the taxonomic usability of a morphological character and the functional morphological influence which this character underlies. Often the taxonomic importance of a dental character is coupled with a functional morphological advantage for the lizard (e.g., the conical teeth of the recent slug-eating alpine *Tiliqua nigrolutea*, which strongly contrast the durophagous dentition of lowland *Tiliqua* species). Many recent scincomorphan species are clearly recognizable by their dentitions (e.g., *Angolosaurus skoogii*, *Cordylus giganteus*, *Gallotia stehlini*, *Acontias plumbeus*, *Chalcides ocellatus*, *Corucia zebrata*, *Egernia kingii*, *Egernia stokesi*, *Hemisphaeriodon gerrardi*, *Macrosincus coctei*, *Novoeumeces schneideri* vel *Novoeumeces algeriensis*, *Sphenomorphus muelleri*, *Tiliqua nigrolutea*, and *Cnemidophorus lemniscatus*), but most of these taxa proved to consume highly specialized diets so that the uniquenesses of their dental morphologies are clearly the results of adaptations. These specialized dentitions often evolved on a species level, since the dental morphologies of congenetics in most cases are fundamentally different. Examples of species which clearly contrast the dental morphologies of their congenetics are *Cordylus giganteus*, *Gallotia stehlini*, *Acontias plumbeus*, *Egernia kingii*, *Egernia stokesi*, *Sphenomorphus muelleri*, *Tiliqua nigrolutea*, and *Cnemidophorus lemniscatus*. If the giant scincid *Macrosincus coctei* really turns out to be (as assumed by GREER (1976)) a close relative of the representatives of the genus

Mabuya which inhabit the same archipelago, it also can be included in the row of taxa which distinctly differ from closely related species in terms of dental morphology. The above proves that changes concerning the dental morphology of lizards often happen in a short period of time. These changes include tooth numbers, tooth shapes and proportions as well as the patterns of striations. The most important prerequisite for this rapid evolutionary process is of course a high mutation rate, which is well documented in many investigated scincomorphan taxa by numerous morphological differences between conspecific individuals (e.g., *Mabuya perroteti*, *Gerrhosaurus flavigularis*, *Ichnotropis squamulosa*). On the other hand, constant characters do exist and can therefore be applied for taxonomical examinations. One of these mostly unchanged features is the presence of the cuspis lingualis, which is formed by two dominant striae on the lingual surfaces of the tooth crowns in many cordylids (*Chamaesaura macrolepis* (here not always present), *Cordylus cataphractus*, *Cordylus johnstoni*, *Cordylus peersi*, *Cordylus polyzonus*, *Cordylus tropidosternum*, and *Pseudocordylus microlepidotus* (here not always present)). But even if most Cordylidae show these two main striae, this is not a derived character restricted to this family alone since this characteristic feature is also wide spread among the Scincidae, the Gerrhosauridae (predominantly in the genus *Zonosaurus*), and even the Lacertidae (e.g., *Acanthodactylus erythrurus*, *Darevskia chlorogaster*, *Gastropholis echinata*, *Iberolacerta monticola*, *Lacerta agilis*, *Lacerta cappadocica*, *Teira dugesii*, and *Timon pater*).

An additional important fact for the classification of fossil scincomorphans is the occasional occurrence of pathological deformations in isolated teeth (e.g., *Podarcis sicula*, *Egernia kingii*) or entire dentitions (e.g., *Lygosoma afra*, *Sphenomorphus variegatus*) in extant specimens. The occurrence of these abnormalities indicates a probable presence of dental pathological deformations in fossil taxa as well.

The technical methods which were used in this thesis for casting collection specimens are highly recommended since the casts proved to be exact replicas of the original jaws and even allowed for the taking of SEM-images.

5. Summary

The monophyly of the Scincomorpha is still an unsolved problem. According to ESTES (1983) the Scincomorpha are a monophyletic group. In strong contrast to this opinion and based on a phylogenetic analysis, LEE (1998) stated that “scincids and cordylids are not related to lacertiforms as previously thought, but to anguimorphs”; according to LEE “most of the characters supporting scincomorph monophyly are highly equivocal.” Another link in a possible paraphyly of the Scincomorpha is given by HARRIS et al. (2001), who posited a sister group relationship of the Teiidae to all other squamates. Since the resolution of these higher taxonomic questions is not the purpose of this thesis, the author follows the traditional grouping of the Scincomorpha *sensu* ESTES (1983).

Among the lizard assemblages from the Guimarota mine the diverse species of the genus *Saurillodon* are relatively abundant. In terms of the reduction of tooth numbers as well as the general dental morphology, the mandibles of *Saurillodon* strongly resemble the mandibles of the extant Acontinae, a Southern African subfamily of specialized burrowing skinks with pointed, conical, and to a certain degree recurved teeth. This type of dentition is best suited to the grasping of soft-bodied maggots, larvae, and worms, all of which share their subterranean habitats with the predatory burrowing skinks. In lizards, a burrowing or fossorial lifestyle is mostly associated with the reduction or loss of limbs. Among scincomorphans legless taxa are known within the Cordyliformes, the Scincidae, and the Teiidae (BERGER-DELL’MOUR 1983). An intermedial status between quadruped and legless forms often exists when the “target niche” is already occupied by another taxon. The transition from quadruped to legless forms is primarily a morphological process since many quadruped lizards already move in a serpentine manner. A comparable form of locomotion can be assumed for the *Saurillodon* species from the Guimarota mine. Burrowing diapsid reptiles from the Jurassic were already known in the literature. One of these is *Tamaulipasaurus morenoi* CLARK & HERNANDEZ, 1994, which belongs either to Archosauromorpha or Lepidosauromorpha (CLARK & HERNANDEZ 1994). Many extant burrowing lizards return to

the ground surface to swallow their prey. Even the amphisbaenid *Blanus cinereus*, which is perfectly adapted to a subterraneous lifestyle, feeds above the ground surface. The lizards bite tiny pieces from beetle larvae and do not swallow the prey items in a single piece (pers. obs. at six captive individuals of *B. cinereus* (taken from the wild in Morocco)). A comparable behavior was observed in the fossorial gymnophthalmine *Bachia bresslaui*, a taxon with extremely reduced limbs (COLLI et al. 1998). Stomach contents of *B. bresslaui* contained insect larvae, scorpions, ants, beetles, and spiders. Probably fossil burrowers like *Saurillodon* also fed outside their burrows. Generally, burrowing lizards tend to avoid the swallowing of prey animals in one piece. This observation is proved by the stomach contents of the acontine *Typhlosaurus braini* HAACKE, 1964 which consisted of well masticated insects (HAACKE 1964). Soft bodied prey items are digested more rapidly (BROWN 1991). The preference of soft bodied items by most burrowing scincids is correlated to their thigmotherm metabolism since the digestion of hard bodied prey might be problematical for an organism which totally depends upon the temperature of its subterraneous surroundings.

The dentitions of the following extant species of burrowing, fossorial or semi-fossorial skinks were investigated for this study: *Acontias gracilicauda*, *Acontias meleagris*, *Acontias percivali*, *Acontias plumbeus*, *Anomalopus leuckartii*, *Brachymeles boulengeri*, *Brachymeles tridactylus*, *Chalcides chalcides*, *Chalcides sexlineatus*, *Feylinia currori*, *Hemiergis decresiensis*, *Hemiergis millewae*, *Hemiergis peronii*, *Janetaescincus braueri*, *Lerista bougainvillii*, *Lerista planiventralis*, *Lerista punctatovittata*, *Lygosoma afra*, *Melanoseps occidentalis*, *Neoseps reynoldsi*, *Saiphos equalis*, *Saproscincus mustelinus*, *Scelotes bipes*, *Scelotes gronovii*, *Sphenops sepsoides*, and *Typhlacontias gracilis*. Of all these more or less limb-reduced scincid species, the acontine skinks evolved the highest modification concerning dental morphology: the shortened mandibles bear a highly reduced number of long, conical, and recurved teeth with more or less pointed apices. A similar dentition is found in the Upper Jurassic *Saurillodon*. Unfortunately, no material of the six endemic genera of fossorial limb-reduced skinks from Madagascar, *Androgo*, *Pygomeles*, *Voeltzkowia*, *Cryptoscincus*, *Paracontias*, and

Pseudacontias, was available for comparison since these taxa are extremely rare (NUSSBAUM & RAXWORTHY 1995).

The patterns of striation are already developed in embryonic replacement teeth because tooth enamel cannot be remodeled after mineralization. Therefore all biomechanical adaptations in enamel must first be established in the genome. During the process of tooth replacement the functional teeth which are to be replaced are at least partially destroyed by odontoclasts (large multinucleate cells) which resorb dentine (EDMUND 1969). The process of tooth replacement is effected by individual age, temperature, season, and disease. After the replacement tooth erupts through the soft tissues, the development of its final height and the inclination happens very rapidly (e.g., within three days in *Anguis fragilis*). The functional life of teeth can vary greatly within different areas of the jaw (COOPER 1966).

Striations of the tooth enamel are widely spread among extant as well as fossil scincomorphan species, but they are not considered to be an apomorphic scincomorphan characteristic since striations are also developed at the tooth crowns of some Iguanidae (*Chamaeleolis chamaeleonides*, *Chamaeleolis porcus*, and *Diplolaemus bibroni*) (ESTES & WILLIAMS 1984), Chamaeleonidae (SCHLEICH 1984), Anguimorpha (SULLIVAN & LUCAS 1996; pers. obs.), and Shinisauridae (pers. obs. in *Shinisaurus crocodilurus*, formerly referred to Xenosauridae). Despite the presence of striations no complex patterns of striation are known for these groups. Striations of the lingual tooth crown surfaces were also observed in fossil Lacertidae (e.g., in the Lower Miocene *Lacerta* (inc. sed.) *poncenatensis* MÜLLER, 1996) (MÜLLER 1996).

The wrinkles observed in an individual of *Zonosaurus laticaudatus* (specimen ZFMK 7256) at the exposed dentine surfaces beneath the flaked-off enamel layer prove that the boundary plane between the dentine and the enamel (EDJ *sensu* SANDER 1999, short for "enamel dentine junction"; here starts the amelogenesis) is not always a smooth plane.

The time scales in which the single scincomorphan families evolved seem to vary distinctly. While most species of the Cordylidae and the Gerrhosauridae appear rather conservative, a rapid cladogenesis takes

place within the Lacertinae (HARRIS et al. 2001).

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I Appendix

This thesis is founded on the following specimens:

Extant Taxa:

Cordylidae:

Chamaesaura macrolepis SDS 59533 (cast), *Chamaesaura macrolepis* SDS 59535 (cast), *Chamaesaura macrolepis* ZFMK 7822 (cast), *Cordylus cataphractus* SDS 68129 (cast), *Cordylus cataphractus* SRK 00.147, *Cordylus cataphractus* ZFMK 7808 (cast), *Cordylus cataphractus* ZFMK 7818 (cast), *Cordylus cordylus* SRK 00.045, *Cordylus cordylus* SRK 00.047, *Cordylus cordylus* SRK 00.148, *Cordylus giganteus* SRK 00.150, *Cordylus giganteus* SRK 00.160, *Cordylus giganteus* ZFMK 7816 (cast), *Cordylus giganteus* ZFMK 7817 (cast), *Cordylus johnstoni* SDS 63039 (cast), *Cordylus peersi* SRK 00.060, *Cordylus peersi* ZFMK 29406 (cast), *Cordylus polyzonus* BMNH 63.2.21.28 (cast), *Cordylus polyzonus* SRK 00.044, *Cordylus polyzonus* SRK 00.048, *Cordylus polyzonus* SRK 00.085, *Cordylus polyzonus* SRK 00.236, *Cordylus polyzonus* SRK 00.238, *Cordylus polyzonus* ZFMK 9192 (cast), *Cordylus p. polyzonus* ZFMK 7805 (cast), *Cordylus tropidosternum* BMNH 1977.1238-1241 (cast), *Cordylus tropidosternum* SRK 00.001, *Cordylus tropidosternum* SRK 00.002, *Cordylus tropidosternum* SRK 00.049, *Cordylus tropidosternum* SRK 00.079, *Cordylus tropidosternum* SRK 00.149, *Cordylus tropidosternum* SRK 00.292, *Cordylus tropidosternum jonesii* SRK 00.237, *Cordylus tropidosternum jonesii* ZFMK 14849 (cast), *Cordylus t. tropidosternum* ZFMK 7810 (cast), *Cordylus ukingensis* SRK 00.022, *Cordylus warreni* SRK 00.046, *Cordylus warreni* SRK 00.066, *Cordylus warreni* SRK 00.097, *Cordylus warreni* SRK 00.145, *Cordylus warreni* SRK 00.146, *Cordylus warreni* SRK 00.228, *Cordylus warreni* ZFMK 7809 (cast), *Platysaurus* sp. SDS 46999 (cast), *Platysaurus capensis* SRK 00.067, *Platysaurus capensis* SRK 00.188, *Platysaurus capensis* ZFMK 7821 (cast), *Platysaurus capensis* ZFMK 14833 (cast), *Platysaurus intermedius rhodesianus* BMNH 1908.5.20.3 (cast), *Pseudocordylus microlepidotus* BMNH 64.2.21.27 (cast), *Pseudocordylus microlepidotus* ZFMK 7806 (cast), *Pseudocordylus microlepidotus* ZFMK 7820 (cast)

Gerrhosauridae:

Angolosaurus skoogi ZFMK 7819 (cast), *Gerrhosaurus* sp. SRK 00.223, *Gerrhosaurus flavigularis* AMNH 73607 (cast), *Gerrhosaurus flavigularis* IFSZ 14774 (cast), *Gerrhosaurus flavigularis* USNM KdQ 134 (cast), *Gerrhosaurus flavigularis fitzsimonsi* ZFMK 7813 (cast), *Gerrhosaurus major* IFSZ 19148 (cast), *Gerrhosaurus major* SRK 00.156, *Gerrhosaurus major* ZFMK 7815 (cast), *Gerrhosaurus major* ZFMK 56403 (cast), *Gerrhosaurus nigrolineatus* IFSZ 14773 (cast), *Gerrhosaurus validus* IFSZ 16340 (cast), *Gerrhosaurus validus* SRK 00.154, *Gerrhosaurus validus* SRK 00.155, *Tracheloptychus madagascariensis* ZFMK 27678 (cast), *Tracheloptychus petersi* ZFMK 8903 (cast), *Zonosaurus haraldmeieri* ZFMK 7812 (cast), *Zonosaurus laticaudatus* ZFMK 57148 (cast), *Zonosaurus laticaudatus* ZFMK 7256 (cast), *Zonosaurus madagascariensis* BMNH 63.5.14-4. (cast), *Zonosaurus maximus* ZFMK 7802 (cast), *Zonosaurus maximus* ZFMK 7825 (cast), *Zonosaurus quadrilineatus* ZFMK 7804 (cast)

Lacertidae:

Acanthodactylus boskianus SRK 00.118, *Acanthodactylus boskianus* SRK 00.119, *Acanthodactylus boskianus* SRK 00.207, *Acanthodactylus boskianus* SRK 00.213, *Acanthodactylus boskianus asper* ZFMK 4084 (cast), *Acanthodactylus erythrurus* AC-VIII Priv. Coll. EVANS (cast), *Acanthodactylus erythrurus* SDS 65156 (cast), *Acanthodactylus erythrurus* ZFMK 7873 (cast), *Acanthodactylus pardalis* SRK 00.246, *Acanthodactylus pardalis latastasii* BMNH 1920.1.20.2715 (cast), *Acanthodactylus scutellatus* SRK 00.117, *Acanthodactylus scutellatus* SRK 00.275, *Acanthodactylus vulgaris* BMNH 1907.6.22.-20 (cast), *Algyroides marchi* A3 Priv. Coll. EVANS (cast), *Algyroides marchi* A 25 juv. Priv. Coll. EVANS (cast), *Algyroides marchi* Priv. Coll. EVANS, non cataloged (cast), *Algyroides marchi* SRK 00.038, *Algyroides nigropunctatus* SRK 00.031, *Archaeolacerta bediagae* SRK 00.120, *Archaeolacerta bediagae* SRK 00.120, *Darevskia chlorogaster* BMNH, non cataloged (cast), *Darevskia chlorogaster* SRK 00.070, *Darevskia rudis* SRK 00.171, *Darevskia rudis bischoffi* ZFMK 1739 (cast), *Darevskia rudis bischoffi* ZFMK 1740 (cast), *Darevskia rudis bischoffi* ZFMK 1741 (cast), *Eremias arguta* SRK 00.094, *Eremias arguta* SRK 00.210, *Eremias scripta* SRK 00.208, *Eremias scripta* SRK 00.211,

Eremias velox BMNH 1920.1.20.389 (cast), *Eremias velox* SRK 00.209, *Eremias velox* SRK 00.212, *Gallotia atlantica* BMNH 1967.1496 (cast), *Gallotia atlantica* ZFMK 34964 (cast), *Gallotia a. atlantica* ZFMK 4117 (cast), *Gallotia caesaris* SRK 00.113, *Gallotia caesaris* ZFMK 4113 (cast), *Gallotia caesaris* ZFMK 4114 (cast), *Gallotia caesaris gomeræ* SRK 00.346, *Gallotia caesaris gomeræ* ZFMK 4106 (cast), *Gallotia caesaris gomeræ* ZFMK 4108 (cast), *Gallotia caesaris gomeræ* ZFMK 4110 (cast), *Gallotia caesaris gomeræ* ZFMK 4111 (cast), *Gallotia galloti* IFSZ 42311 (cast), *Gallotia galloti* ZFMK 7832 (cast), *Gallotia galloti* ZFMK 7834 (cast), *Gallotia galloti eisentrauti* ZFMK 1816 (cast), *Gallotia galloti eisentrauti* ZFMK 1817 (cast), *Gallotia g. galloti* ZFMK 4102 (cast), *Gallotia g. galloti* ZFMK 4115 (cast), *Gallotia g. galloti* ZFMK 4133 (cast), *Gallotia stehlini* BMNH 1967.1.1738-57 (cast), *Gallotia stehlini* ZFMK 4097 (cast), *Gallotia stehlini* ZFMK 4099 (cast), *Gallotia stehlini* ZFMK 7876 (cast), *Gastropholis echinata* BMNH 1903.7.28.4 (cast), *Holaspis guentheri* SRK 00.033, *Iberolacerta cyreni* ZFMK 4068 (cast), *Iberolacerta cyreni* ZFMK 7861 (cast), *Iberolacerta cyreni* ZFMK 7862 (cast), *Iberolacerta monticola* I.MB-31, Priv. Coll. EVANS (cast), *Iberolacerta monticola* I.M-6, Priv. Coll. EVANS (cast), *Iberolacerta monticola* Priv. Coll. EVANS Lm 6 (cast), *Iberolacerta monticola* LMM-76, Priv. Coll. EVANS (cast), *Iberolacerta monticola* Priv. Coll. EVANS Lmm 76 (cast), *Iberolacerta monticola* Priv. Coll. EVANS Lmm 81 (cast), *Ichnotropis capensis* USNM 058611 (cast), *Ichnotropis capensis* IFSZ 13943 (cast), *Ichnotropis squamulosa* BMNH, non cataloged (cast), *Lacerta agilis* IFSZ 61996 (cast), *Lacerta agilis* SRK 00.108, *Lacerta agilis* SRK 00.109, *Lacerta agilis* ZFMK 4089 (cast), *Lacerta agilis* ZFMK 4090 (cast), *Lacerta agilis* ZFMK 7827 (cast), *Lacerta a. agilis* ZFMK 4050 (cast), *Lacerta agilis grusinica* SRK 00.032, *Lacerta agilis grusinica* SRK 00.111, *Lacerta bilineata* SRK 00.091, *Lacerta cappadocica urmiana* ZFMK 4065 (cast), *Lacerta danfordi* ZFMK 4066 (cast), *Lacerta graeca* SRK 00.263, *Lacerta laevis* SRK 00.090, *Lacerta laevis* ZFMK 4067 (cast), *Lacerta laevis* ZFMK 7831 (cast), *Lacerta laevis* ZFMK 7863 (cast), *Lacerta schreiberi* SX-1, juv., Priv. Coll. EVANS (cast), *Lacerta schreiberi* Priv. Coll. EVANS S7 (cast), *Lacerta schreiberi* SRK 00.110, *Lacerta schreiberi* ZFMK 7836 (cast), *Lacerta trilineata* SRK 00.092, *Lacerta trilineata* ZFMK 4057 (cast), *Lacerta trilineata* ZFMK 4058 (cast), *Lacerta trilineata* ZFMK 7869 (cast), *Lacerta trilineata gica* ZFMK 4059 (cast), *Lacerta trilineata major* ZFMK 3509 (cast), *Lacerta viridis* BMNH 1920.1.20.725 (cast), *Lacerta viridis* Priv. Coll. EVANS, non cataloged (cast), *Lacerta viridis* SRK 00.175, *Lacerta viridis* SRK 00.182, *Lacerta viridis* SRK 00.265, *Lacerta viridis* ZFMK 4053 (cast), *Lacerta viridis* ZFMK 4054 (cast), *Lacerta viridis* ZFMK 4061 (cast), *Lacerta viridis* ZFMK 4062 (cast), *Lacerta viridis meridionalis* ZFMK 4056 (cast), *Meroles suborbitalis* USNM 292594 (cast), *Nucras lalandii* ZFMK 7830, *Omanosaura jayakari* BMNH 1971.1480 (cast), *Omanosaura jayakari* SRK 00.089, *Parvilacerta parva* SRK 00.266, *Philochortus hardeggeri* BMNH 1905.10.58.9 (cast), *Podarcis bocagai* Priv. Coll. EVANS PB 14 (cast), *Podarcis bocagai* PB-44, Priv. Coll. EVANS (cast), *Podarcis bocagai* PB-57, Priv. Coll. EVANS (cast), *Podarcis erhardii* SRK 00.214, *Podarcis e. erhardii* ZFMK 955 (cast), *Podarcis filfolensis* BMNH 1909.10.30.56 (cast), *Podarcis hispanica* Priv. Coll. EVANS H-5 (cast), *Podarcis hispanica* Priv. Coll. EVANS H-31 (cast), *Podarcis lilfordi* SRK 00.095, *Podarcis lilfordi* SRK 00.115, *Podarcis lilfordi* ZFMK 21648 (cast), *Podarcis melisellensis* SRK 00.082, *Podarcis muralis* SRK 00.267, *Podarcis muralis* SRK 00.272, *Podarcis muralis* SRK 00.273, *Podarcis muralis* SRK 00.274, *Podarcis muralis* ZFMK 4070 (cast), *Podarcis muralis liolepis* USNM 220261 (cast), *Podarcis muralis nigriventris* SRK 00.116, *Podarcis muralis nigriventris vel. bruggemanni* SRK 00.037, *Podarcis peloponnesiaca* SRK 00.093, *Podarcis peloponnesiaca* ZFMK 4074 (cast), *Podarcis peloponnesiaca* ZFMK 4075 (cast), *Podarcis peloponnesiaca* ZFMK 4095 (cast), *Podarcis p. peloponnesiaca* ZFMK 7867 (cast), *Podarcis pityusensis* SRK 00.024, *Podarcis pityusensis* SRK 00.025, *Podarcis pityusensis* SRK 00.030, *Podarcis pityusensis* SRK 00.239, *Podarcis pityusensis* SRK 00.241, *Podarcis pityusensis* SRK 00.242, *Podarcis pityusensis* SRK 00.243, *Podarcis sicula* SRK 00.028, *Podarcis sicula* SRK 00.029, *Podarcis sicula* SRK 00.035, *Podarcis sicula* SRK 00.112, *Podarcis sicula* SRK 00.114, *Podarcis sicula* ZFMK 1729 (cast), *Podarcis sicula campestris* SRK 00.036, *Podarcis sicula campestris* ZFMK 4093 (cast), *Podarcis sicula campestris* ZFMK 4094 (cast), *Podarcis s. sicula* ZFMK 4092 (cast), *Podarcis taurica* ZFMK 7865 (cast), *Psammodromus algirus* USNM 199210 (cast), *Psammodromus algirus* ZFMK 4086 (cast), *Psammodromus algirus* ZFMK 7864 (cast), *Psammodromus hispanicus* BMNH 1920.1.20.1159 (cast), *Takydromus formosanus* BMNH 18231 (cast), *Takydromus septentrionalis* SRK 00.162, *Takydromus septentrionalis* ZFMK 14830 (cast), *Takydromus septentrionalis* ZFMK 14831 (cast), *Takydromus sexlineatus* SRK 00.096, *Takydromus sexlineatus* SRK 00.268, *Takydromus sexlineatus* SRK 00.269, *Takydromus sexlineatus* SRK 00.270, *Takydromus sexlineatus* SRK 00.271, *Takydromus sexlineatus* SRK 00.303, *Teira d. dugesii* ZFMK 4076 (cast), *Teira d. dugesii* ZFMK 4077 (cast), *Teira d. dugesii* ZFMK 4079 (cast), *Timon lepidus* K-12 Priv. Coll. EVANS (cast), *Timon lepidus* Priv. Coll. EVANS K17 (cast), *Timon lepidus* K-17, juv., Priv. Coll. EVANS (cast), *Timon lepidus* K-37 Priv. Coll. EVANS (cast), *Timon lepidus* SRK 00.088, *Timon lepidus* SRK 00.178, *Timon lepidus* SRK 00.215, *Timon lepidus* SRK 00.229, *Timon lepidus* SRK 00.247, *Timon lepidus* SRK 00.264, *Timon lepidus* SRK 00.295, *Timon lepidus* SRK 00.325, *Timon lepidus* ZFMK 7800 (cast), *Timon lepidus* ZFMK 7801 (cast), *Timon lepidus* ZFMK 7838 (cast), *Timon lepidus* ZFMK 7866 (cast), *Timon lepidus* ZFMK 21650 (cast), *Timon pater* BMNH 1974.24.91 (cast), *Timon pater* IFSZ 27816 (cast), *Timon pater* ZFMK 4060 (cast), *Timon pater* ZFMK 7870 (cast), *Timon princeps* ZFMK 7877 (cast), *Zootoca vivipara* SRK 00.245, *Zootoca vivipara* SRK 00.336, *Zootoca vivipara* ZFMK 4063 (cast)

Scincidae:

Ablepharus grayanus BMNH 91.9.14.8 (cast), *Ablepharus lineo-ocellatus* BMNH XI.4A (cast), *Ablepharus wahlbergi* BMNH 1933.7.1.156 (cast), *Acontias g. gracilicauda* AMNH 48507 (cast), *Acontias meleagris* BMNH 63.2.21.21 (cast), *Acontias meleagris* SRK 00.042, *Acontias meleagris* SRK 00.053, *Acontias meleagris* SRK 00.055, *Acontias meleagris* SRK 00.056, *Acontias meleagris* SRK 00.062, *Acontias percivali* SRK 00.054, *Acontias plumbeus* BMNH 49.6.29.-38 (cast), *Anomalopus leuckartii* SRK 00.332, *Brachymeles boulengeri taylori* USNM 305967 (cast), *Brachymeles boulengeri taylori* USNM 305968 (cast), *Brachymeles tridactylus* USNM 229623 (cast), *Carlia fusca* USNM 323689 (cast), *Carlia fusca* USNM 323696 (cast), *Carlia storri* SRK 00.193, *Chalcides* sp. SRK 00.103, *Chalcides bedriagai* ZFMK 14823 (cast), *Chalcides chalcides* SRK 00.277, *Chalcides chalcides* SRK 00.278, *Chalcides mionecton* SRK 00.360, *Chalcides ocellatus* BMNH 63.2.21.29 (cast), *Chalcides ocellatus* BMNH 1920.1.20.784 (cast), *Chalcides ocellatus* SRK 00.104, *Chalcides ocellatus* SRK 00.333, *Chalcides ocellatus* USNM 313453 (cast), *Chalcides ocellatus* ZFMK 9199 (cast), *Chalcides ocellatus* ZFMK 9200 (cast), *Chalcides o. ocellatus* ZFMK 7850 (cast), *Chalcides o. ocellatus* ZFMK 7851 (cast), *Chalcides sexlineatus* SRK 00.124, *Chalcides sexlineatus* SRK 00.125, *Chalcides s. sexlineatus* ZFMK 35135 (cast), *Chalcides viridanus* SRK 00.126, *Chalcides v. viridanus* ZFMK 49964 (cast), *Corucia zebrata* SDS 62346 (cast), *Corucia zebrata* SDS 66311 (cast), *Corucia zebrata* SDS 66314 (cast), *Corucia zebrata* SRK 00.174, *Corucia zebrata* ZFMK 5226 (cast), *Corucia zebrata* ZFMK 5227 (cast), *Corucia zebrata* ZFMK 53535 (cast), *Cryptoblepharus boutoni* BMNH 1947.3.3.34 (cast), *Cryptoblepharus boutoni* SDS 65005 (cast), *Cryptoblepharus boutoni* SRK 00.353, *Cryptoblepharus poecilopleurus* USNM 337782 (cast), *Cryptoblepharus poecilopleurus* USNM 337797 (cast), *Ctenotus regius* SRK 00.170, *Cyclodomorphus melanops* SRK 00.191, *Dasia olivacea* ZFMK 14828 (cast), *Egernia cunninghami* SRK 00.138, *Egernia cunninghami* SRK 00.220, *Egernia cunninghami* ZFMK 21646 (cast), *Egernia depressa* SRK 00.198, *Egernia dorsalis* BMNH 1908.2.25.9. (cast), *Egernia inornata* SRK 00.176, *Egernia inornata* SRK 00.186, *Egernia kingii* SRK 00.107, *Egernia kingii* SRK 00.121, *Egernia kingii* SRK 00.151, *Egernia stokesii* SRK 00.073, *Egernia stokesii* SRK 00.161, *Egernia stokesii* ZFMK 14820 (cast), *Egernia striolata* SRK 00.173, *Egernia striolata* ZFMK 1482 (cast), *Egernia whitii* IFSZ 14262 (cast), *Emoia aneityumensis* BMNH 1956.1.3.63 (cast), *Emoia caeruleocauda* USNM 122578 (cast), *Emoia caeruleocauda* USNM 323699 (cast), *Emoia cyanura* SDS 18028 (cast), *Emoia cyanura* SDS 66245 (cast), *Emoia cyanura* USNM 249750 (cast), *Emoia jakati* USNM 512284 (cast), *Emoia nigra* SRK 00.076, *Emoia nigromarginata* USNM 334060 (cast), *Emoia ponapea* USNM 521740 (cast), *Emoia sanfordi* AMNH R40169 (cast), *Emoia slevini* USNM 536082 (cast), *Emoia trossula* SDS 66261 (cast), *Emoia trossula* USNM 249744 (cast), *Emoia trossula* USNM 249745 (cast), *Eremiascincus richardsonii* BMNH 1908.5.28.54-55 (cast), *Eremiascincus richardsonii* SRK 00.172, *Eugongylus albifasciolatus* BMNH 98.5.27.-13 (cast), *Eugongylus rufescens* BMNH 97.12.10.73 (cast), *Eulamprus tympanum* SRK 00.168, *Eumeces* sp. SRK 00.071, *Eumeces ater* IFSZ 18018 (cast), *Eumeces fasciatus* AMNH 92742 (cast), *Eumeces fasciatus* USNM 220267 (cast), *Eumeces fasciatus* USNM 313457 (cast), *Eumeces gilberti* SDS 63115 (cast), *Eumeces gilberti* SDS 63134 (cast), *Eumeces gilberti* USNM 5310 (cast), *Eumeces gilberti rubricaudatus* SDS 63125 (cast), *Eumeces inexpectatus* USNM 332755 (cast), *Eumeces laticeps* AMNH R-110724 (cast), *Eumeces laticeps* USNM 9242 (cast), *Eumeces laticeps* USNM 525729 (cast), *Eumeces longirostris* USNM 217505 (cast), *Eumeces marginatus* USNM 17851 (cast), *Eumeces marginatus* USNM 17853 (cast), *Eumeces obsoletus* AMNH 68919 (cast), *Eumeces schwarzei* USNM 113603 (cast), *Eumeces skiltonianus* USNM 234041 (cast), *Eumeces skiltonianus* SDS 63107 (cast), *Eumeces skiltonianus* SDS 63112 (cast), *Eumeces skiltonianus* SDS 68049 (cast), *Eumeces skiltonianus* SDS 63156 (cast), *Eumeces tunganus* USNM 82751 (cast), *Eumecia anchietae* BMNH 1906.7.6.4. (cast), *Eurylepis taeniolatus* AMNH 110170 (cast), *Feylinia currori* IFSZ 14562 (cast), *Hemiergus decresiensis* SRK 00.255, *Hemiergus decresiensis* SRK 00.257, *Hemiergus decresiensis* SRK 00.261, *Hemiergus decresiensis* SRK 00.279, *Hemiergus decresiensis* SRK 00.280, *Hemiergus millewae* SRK 00.258, *Hemiergus millewae* SRK 00.259, *Hemiergus millewae* SRK 00.281, *Hemiergus peronii* SRK 00.187, *Hemiergus peronii* SRK 00.282, *Hemisphaeriodon gerrardi* BMNH 1882.210 (cast), *Hemisphaeriodon gerrardi* SRK 00.081, *Hemisphaeriodon gerrardi* SRK 00.157, *Hemisphaeriodon gerrardi* SRK 00.159, *Janetaescincus braueri* BMNH 1910.3.18.33 (cast), *Lamprolepis smaragdina* SRK 00.080, *Lamprolepis smaragdina* USNM 507550 (cast), *Lamprolepis smaragdina* ZFMK 14824 (cast), *Lamprolepis smaragdina* ZFMK 14825 (cast), *Lamprolepis smaragdina philippinica* USNM 340061 (cast), *Lampropholis delicata* SDS 63231 (cast), *Lampropholis delicata* SDS 63057 (cast), *Lampropholis delicata* SDS 63231, *Lampropholis delicata* USNM 279295 (cast), *Leiopisma austracaledonicum* ZFMK 14826 (cast), *Leiopisma telfairii* IFSZ 13587 (cast), *Lerista bougainvillii* SRK 00.262, *Lerista bougainvillii* SRK 00.283, *Lerista planiventralis* BMNH 1954.1-2.21 (cast), *Lerista punctatovittata* SRK 00.253, *Lerista punctatovittata* SRK 00.256, *Liopelis belli* IFSZ 13718 (cast), *Lipinia leptosoma* USNM 507554 (cast), *Lipinia noctua* SDS 18018 (cast), *Lipinia noctua* USNM 249758 (cast), *Lipinia pulchella* USNM 509419 (cast), *Lipinia rabori* USNM 305975 (cast), *Lygosoma afra* SRK 00.018, *Lygosoma afra* SRK 00.019, *Lygosoma afra* SRK 00.293, *Lygosoma bouringii* USNM 72277 (cast), *Mabuya* sp. SRK 00.184, *Mabuya* sp. ZFMK 4120 (cast), *Mabuya affinis* ZFMK 9196 (cast), *Mabuya aureopunctata* BMNH 95.11.12.70 (cast), *Mabuya bistrata* USNM 292407 (cast), *Mabuya bistrata* USNM

292410 (cast), *Mabuya brevicollis* SRK 00.106, *Mabuya carinata* SRK 00.197, *Mabuya carinata* SRK 00.249, *Mabuya carinata* SRK 00.251, *Mabuya carinata* SRK 00.252, *Mabuya cumingi* USNM 499004 (cast), *Mabuya elegans* USNM 336439 (cast), *Mabuya gravenhorstii* USNM 336440 (cast), *Mabuya gravenhorstii* USNM 336441 (cast), *Mabuya mabouya alliacea* SRK 00.127, *Mabuya macularia* SRK 00.206, *Mabuya macularia* SRK 00.250, *Mabuya macularis comorensis* BMNH 77.8.9.8 (cast), *Mabuya madagascariensis* SRK 00.051, *Mabuya madagascariensis* SRK 00.075, *Mabuya madagascariensis* SRK 00.087, *Mabuya multifasciata* SRK 00.050, *Mabuya multifasciata* SRK 00.105, *Mabuya multifasciata* SRK 00.200, *Mabuya multifasciata* SRK 00.201, *Mabuya multifasciata* SRK 00.217, *Mabuya multifasciata* SRK 00.218, *Mabuya multifasciata* SRK 00.222, *Mabuya multifasciata* USNM 509421 (cast), *Mabuya multifasciata* ZFMK 9195 (cast), *Mabuya perroteti* SRK 00.074, *Mabuya perroteti* SRK 00.086, *Mabuya perroteti* SRK 00.219, *Mabuya perroteti* SRK 00.221, *Mabuya quinquetaeniata* SRK 00.122, *Mabuya seychellensis* BMNH 1976.289 (cast), *Mabuya striata* SRK 00.202, *Mabuya unimarginata* SDS 60425 (cast), *Mabuya vittata* SRK 00.123, *Mabuya vittata* ZFMK 9194 (cast), *Mabuya wrightii* BMNH 1956.1.15.60 (cast), *Macroscoincus coctei* Priv. Coll. EVANS, non cataloged (original), *Melanoseps occidentalis* BMNH 1907.5.22.6A (cast), *Mochlus fernandi* BMNH 88.829.-3 (cast), *Mochlus s. sundevalli* AMNH 40723 (cast), *Morethia obscura* SRK 00.190, *Neoseps reynoldsi* USNM 48762 (cast), *Novoeumeces algeriensis* SRK 00.136, *Novoeumeces schneideri* BMNH 1920.1.20.2702 (cast), *Novoeumeces schneideri* SRK 00.043, *Novoeumeces schneideri* SRK 00.083, *Panaspis africana* BMNH 1906.3.30.54 (cast), *Pseudemoia entrecasteauxii* SRK 00.254, *Saiphos equalis* SRK 00.356, *Saiphos equalis* SRK 00.358, *Saproscincus mustelinus* SRK 00.260, *Scelotes bipes* BMNH XVII.2.F (cast), *Scelotes gronovii* BMNH 97.5.15.8 (cast), *Scincella lateralis* AMNH R-16974 (cast), *Scincella lateralis* USNM 332758 (cast), *Scincopus fasciatus* BMNH 1906.5.7.5 (cast), *Scincus mitranus* BMNH 1973.405 (cast), *Scincus scincus* BMNH 1909.7.2834 (cast), *Scincus scincus* IFSZ 19076 (cast), *Scincus scincus* IFSZ 19107 (cast), *Scincus scincus* SDS 65230 (cast), *Scincus scincus* SRK 00.069, *Scincus scincus* SRK 00.204, *Scincus s. cucullatus* ZFMK 14832 (cast), *Sphenomorphus aignanus* BMNH 1946.8.15.48 (cast), *Sphenomorphus dussumieri* BMNH 1946.8.15.42 (cast), *Sphenomorphus indicus* AMNH 34884 (cast), *Sphenomorphus indicus* BMNH 1965.1064 (cast), *Sphenomorphus leptofasciatus* SRK 359, *Sphenomorphus muelleri* BMNH 88.3.21.-5. (cast), *Sphenomorphus muelleri* SRK 00.034, *Sphenomorphus scutatus* USNM 507555 (cast), *Sphenomorphus solomonis* SRK 00.357, *Sphenomorphus striatopunctatus* BMNH 1948.1.7.60 (cast), *Sphenomorphus variegatus* SRK 00.297, *Sphenops sepsoides* BMNH 64.2-21.34 (cast), *Sphenops sepsoides* SRK 00.061, *Sphenops sepsoides* SRK 00.077, *Tiliqua* sp. IFSZ 13589 (cast), *Tiliqua* sp. IFSZ 61997 (cast), *Tiliqua gigas* BMNH 1910.4.26.29 (cast), *Tiliqua gigas* SRK 00.065, *Tiliqua gigas* SRK 00.144, *Tiliqua gigas* ZFMK 5224 (cast), *Tiliqua gigas* ZFMK 7852 (cast), *Tiliqua gigas* ZFMK 14829 (cast), *Tiliqua nigrolutea* SRK 00.177, *Tiliqua nigrolutea* SRK 00.230, *Tiliqua occipitalis* SRK 00.248, *Tiliqua rugosa* IFSZ 13606 (cast), *Tiliqua rugosa* SDS 68063 (cast), *Tiliqua rugosa* SDS 68064 (embryo) (cast), *Tiliqua rugosa* SRK 00.232, *Tiliqua rugosa* SRK 00.311, *Tiliqua rugosa* SRK 00.332, *Tiliqua rugosa* ZFMK 5231 (cast), *Tiliqua rugosa* ZFMK 5235 (cast), *Tiliqua rugosa* ZFMK 21642 (cast), *Tiliqua rugosa* ZFMK 21643 (cast), *Tiliqua rugosa* ZFMK 21644 (cast), *Tiliqua scincoides* IFSZ 27821 (cast), *Tiliqua scincoides* ZFMK 21645 (cast), *Tiliqua s. scincoides* SRK 00.231, *Tribolonotus gracilis* SRK 00.139, *Tribolonotus novaeguineae* BMNH 1905.11.29.10, *Tribolonotus novaeguineae* SRK 00.041, *Tropidophorus beccarii* BMNH 1929.12.22.103 (cast), *Tropidophorus brookei* BMNH 1900.1.23.15 (cast), *Tropidophorus grayi* SRK 00.052, *Tropidophorus grayi* SRK 00.084, *Tropidophorus herdmorei* BMNH 1964.964 (cast), *Tropidophorus robinsoni* BMNH 1933.5.13.27, *Typhlacontias gracilis* USNM 159338 (cast)

Teiidae:

Ameiva ameiva SDS 66589 (cast), *Ameiva ameiva* SRK 00.057, *Ameiva ameiva* SRK 00.058, *Ameiva ameiva* ZFMK 21641 (cast), *Ameiva ameiva* ZFMK 59019 (cast), *Ameiva ameiva* ZFMK 59021 (cast), *Ameiva ameiva* ZFMK 59022 (cast), *Ameiva ameiva* ZFMK 59023 (cast), *Ameiva ameiva* ZFMK 59024 (cast), *Ameiva ameiva* ZFMK 59026 (cast), *Ameiva auberi* SDS 65988 (cast), *Ameiva auberi sabulicolor* USNM 220666 (cast), *Ameiva auberi sabulicolor* USNM 220669 (cast), *Ameiva bifrontata* ZFMK 21640 (cast), *Ameiva chrysoleama* SDS 64800 (cast), *Ameiva chrysoleama boekeri* USNM 259527 (cast), *Ameiva chrysoleama parvioris* USNM 259531 (cast), *Ameiva chrysoleama parvioris* USNM 259532 (cast), *Ameiva chrysoleama regularis* USNM 225056 (cast), *Ameiva chrysoleama umbratilis* USNM 225051 (cast), *Ameiva chrysoleama umbratilis* USNM 225053 (cast), *Ameiva corax* USNM 236387 (cast), *Ameiva corax* USNM 236388 (cast), *Ameiva corax* USNM 236391 (cast), *Ameiva corax* USNM 236392 (cast), *Ameiva dorsalis* SDS 63967 (cast), *Ameiva dorsalis* SDS 63968 (cast), *Ameiva erythrocephala* USNM 236237 (cast), *Ameiva erythrocephala* USNM 236238 (cast), *Ameiva erythrocephala* USNM 236244 (cast), *Ameiva exsul* USNM 314244 (cast), *Ameiva exsul* USNM 314245 (cast), *Ameiva exsul deseichensis* USNM 221745 (cast), *Ameiva festiva* USNM 313854 (cast), *Ameiva festiva* USNM 319232 (cast), *Ameiva festiva* USNM 536493 (cast), *Ameiva fuscata* USNM 158908 (cast), *Ameiva griswoldi* USNM 218350 (cast), *Ameiva griswoldi* USNM 218353 (cast), *Ameiva griswoldi* USNM 218354 (cast), *Ameiva lineolata* SDS 64831 (cast), *Ameiva lineolata privigna* SDS 64832 (cast), *Ameiva plei* SDS 63727 (cast), *Ameiva*

plei SDS 63976 (cast), *Ameiva plei* SDS 63986 (cast), *Ameiva plei* USNM 236377 (cast), *Ameiva plei* USNM 236379 (cast), *Ameiva plei* USNM 236381 (cast), *Ameiva plei* USNM 236383 (cast), *Ameiva plei* USNM 236394 (cast), *Ameiva pluvianotata* SDS 64011 (cast), *Ameiva pluvianotata* SDS 64014 (cast), *Ameiva pluvianotata* USNM 236523 (cast), *Ameiva pluvianotata* USNM 236524 (cast), *Ameiva pluvianotata* USNM 236525 (cast), *Ameiva quadrilineata* SDS 46993a (cast), *Ameiva quadrilineata* USNM 319266 (cast), *Ameiva quadrilineata* USNM 319270 (cast), *Ameiva surinamensis* IFSZ 62019 (cast), *Ameiva surinamensis* IFSZ 62020 (cast), *Ameiva taeniura* USNM 55053 (cast), *Ameiva undulata* SDS 46992 (cast), *Ameiva wetmorei* SDS 67839 (cast), *Ameiva wetmorei* SDS 67842 (cast), *Callopiastes flavipunctatus* BMNH 1900.2.26.11 (cast), *Callopiastes maculatus* BMNH 1904.1.25.12 (cast), *Callopiastes maculatus* ZFMK 7828 (cast), *Callopiastes maculatus* BMNH 1904.1.25.12. (cast), *Callopiastes maculatus* ZFMK 7833 (cast), *Callopiastes maculatus* ZFMK 7854 (cast), *Callopiastes maculatus* ZFMK 7855 (cast), *Callopiastes maculatus* ZFMK 7858 (cast), *Cnemidophorus* sp. ZFMK 4129 (cast), *Cnemidophorus c. communis* SDS 60426 (cast), *Cnemidophorus exsanguis* SDS 63187 (cast), *Cnemidophorus exsanguis* SDS 63254 (cast), *Cnemidophorus exsanguis* SDS 64562 (cast), *Cnemidophorus exsanguis* USNM 161278 (cast), *Cnemidophorus gularis* SRK 00.063, *Cnemidophorus gularis* SRK 00.064, *Cnemidophorus gularis* SRK 00.102, *Cnemidophorus gularis* SRK 00.129, *Cnemidophorus gularis* SRK 00.130, *Cnemidophorus gularis* SRK 00.131, *Cnemidophorus guttatus immutabilis* SDS 48494 (cast), *Cnemidophorus hyperythrus* SDS 65041 (cast), *Cnemidophorus hyperythrus* SDS 65042 (cast), *Cnemidophorus hyperythrus beldingi* SDS 64563 (cast), *Cnemidophorus lemniscatus* SRK 00.023, *Cnemidophorus lemniscatus* SRK 00.100, *Cnemidophorus lemniscatus* SRK 00.128, *Cnemidophorus lemniscatus* SRK 00.226, *Cnemidophorus lemniscatus* USNM 313933 (cast), *Cnemidophorus lemniscatus* USNM 313934 (cast), *Cnemidophorus murinus* BMNH 91.11.4.-16. (cast), *Cnemidophorus sackii* USNM 165690 (cast), *Cnemidophorus sackii* USNM 165691 (cast), *Cnemidophorus sexlineatus* BMNH 96. (cast), *Cnemidophorus sexlineatus* USNM 220273 (cast), *Cnemidophorus sexlineatus* USNM 313461 (cast), *Cnemidophorus sexlineatus* USNM 525732 (cast), *Cnemidophorus sonora* Priv. Coll. EVANS, non cataloged (cast), *Cnemidophorus sonora* SDS 63225 (cast), *Cnemidophorus sonora* SDS 63246 (cast), *Cnemidophorus sonora* SDS 64564 (cast), *Cnemidophorus tessellatus* BMNH 1926.4.28.1. (cast), *Cnemidophorus tessellatus* USNM 17024 (cast), *Cnemidophorus tessellatus* USNM 220275 (cast), *Cnemidophorus tessellatus* USNM 220276 (cast), *Cnemidophorus tigris* Priv. Coll. EVANS, non cataloged (cast), *Cnemidophorus tigris* SDS 55285 (cast), *Cnemidophorus tigris* SDS 60422 (cast), *Cnemidophorus tigris* SDS 63129 (cast), *Cnemidophorus tigris* USNM 229863 (cast), *Cnemidophorus tigris* USNM 292549 (cast), *Cnemidophorus tigris undulatus* USNM 11808 (cast), *Cnemidophorus uniparens* Priv. Coll. EVANS, non cataloged (cast), *Cnemidophorus uniparens* SDS 66413 (cast), *Cnemidophorus uniparens* SDS 66596 (cast), *Cnemidophorus uniparens* USNM 320282 (cast), *Cnemidophorus vanzoi* SDS 65759 (cast), *Cnemidophorus vanzoi* SDS 65773 (cast), *Cnemidophorus vanzoi* SRK 00.101, *Cnemidophorus vanzoi* SRK 00.227, *Cnemidophorus vanzoi* SRK 00.234, *Cnemidophorus vanzoi* USNM 220277 (cast), *Crocodylus lacertinus* BMNH 1970.446-497 (cast), *Dicrodon guttulatatum* BMNH 1932.9.7.-8 (cast), *Dicrodon guttulatatum* IFSZ 13844 (cast), *Dicrodon guttulatatum* SDS 30842 (cast), *Dracaena guianensis* USNM 71729 (cast), *Dracaena guianensis* ZFMK 4132 (cast), *Kentropyx calcarata* BMNH 1902.5.29.91 (cast), *Neusticurus ecleopus* SDS 46994 (cast), *Pholidobolus montium* BMNH 1986-278-286 (cast), *Pholidobolus montium* SRK 348, *Teius teyou* BMNH 111.27.a (cast), *Teius teyou* BMNH 1910.12.16.4.-12. (cast), *Teius teyou* IFSZ 13845 (cast), *Teius teyou* IFSZ 16139 (cast), *Tejus teyou* IFSZ 25471 (cast), *Tupinambis* sp. IFSZ 35588 (cast), *Tupinambis* sp. IFSZ 61998 (cast), *Tupinambis merianae* IFSZ 19073 (cast), *Tupinambis merianae* IFSZ 19077 (cast), *Tupinambis merianae* SDS 65496 (cast), *Tupinambis merianae* ZFMK 4131 (cast), *Tupinambis merianae* ZFMK 21638 (cast), *Tupinambis merianae* ZFMK 53531 (cast), *Tupinambis merianae* ZFMK 53532 (cast), *Tupinambis merianae* IFSZ 19075 (cast), *Tupinambis teguixin* SDS 67087 (cast), *Tupinambis teguixin* SDS 64932 (cast), *Tupinambis teguixin* SRK 00.195

Xantusidae:

Cricosaura typica ZFMK 54260 (cast), *Lepidophyma flavimaculatum* SRK 00.068, *Lepidophyma flavimaculatum* SRK 00.078, *Lepidophyma flavimaculatum* SRK 00.098, *Lepidophyma flavimaculatum* SRK 00.338, *Xantusia henschawi* BMNH 1969.2961 (cast), *Xantusia henschawi* Priv. Coll. EVANS, non cataloged (cast), *Xantusia henschawi* SDS 63032 (cast), *Xantusia henschawi* SDS 63133 (cast), *Xantusia henschawi* SDS 63256 (cast), *Xantusia henschawi* SDS 64070 (cast), *Xantusia henschawi* SDS 64072 (cast), *Xantusia henschawi* SDS 65397 (cast), *Xantusia henschawi* SDS 67092 (cast), *Xantusia henschawi* SDS 67095 (cast), *Xantusia henschawi* USNM 161279 (cast), *Xantusia henschawi* ZFMK 7814 (cast), *Xantusia riversiana* SDS 48492 (cast), *Xantusia riversiana* USNM 220288 (cast), *Xantusia riversiana* USNM 313463 (cast), *Xantusia vigilis* SDS 66396 (cast), *Xantusia v. vigilis* Priv. Coll. EVANS, non cataloged (cast), *Xantusia v. vigilis* SDS 63113 (cast), *Xantusia v. vigilis* SDS 63158 (cast)

Specimens for comparison (non-Scincomorpha):

Agamidae:

Agama agama SRK 00.003, *Agama stellio* SRK 00.321, *Calotes versicolor* SRK 00.192, *Ceratophora aspera* SRK 00.203, *Chlamydosaurus kingii* SRK 00.021, *Chlamydosaurus kingii* SRK 00.328, *Goniocephalus chamaeleonides* SRK 00.008, *Goniocephalus chamaeleonides* SRK 00.309, *Hydrosaurus amboinensis* SRK 00.141, *Hydrosaurus amboinensis* SRK 00.152, *Hydrosaurus amboinensis* SRK 00.199, *Hydrosaurus weberi* SRK 00.288, *Leiolepis belliana* SRK 00.183, *Leiolepis belliana* SRK 00.299, *Physignathus concincinus* SRK 00.039, *Physignathus cocincinus* SRK 00.137, *Physignathus concincinus* SRK 00.153, *Physignathus lesueuri* SRK 00.233, *Physignathus lesueuri* SRK 00.329, *Pogona vitticeps* SRK 00.006, *Pogona vitticeps* SRK 00.007, *Uromastyx acanthinura* SRK 00.143, *Uromastyx hardwicki* SRK 00.310, *Uromastyx o. ocellata* SRK 00.010, *Uromastyx o. ocellata* SRK 00.296

Amphisbaenidae:

Blanus cinereus SRK 00.225

Anguidae:

Anguis fragilis SRK 00.235, *Anguis fragilis* SRK 00.276, *Anguis fragilis* SRK 00.294, *Anguis fragilis* SRK 00.320, *Anguis fragilis* SRK 00.323, *Anguis fragilis* SRK 00.334, *Gerrhonotus multicarinatus* SRK 00.132, *Mesaspis* sp. SRK 00.189, *Ophisaurus apodus* SRK 00.179, *Ophisaurus apodus* SRK 00.180, *Ophisaurus apodus* SRK 00.216, *Ophisaurus apodus* SRK 00.335

Chamaeleonidae:

Bradypodion damaranum SRK 00.286, *Bradypodion damaranum* SRK 00.315, *Bradypodion damaranum* SRK 00.340, *Bradypodion fischeri* SRK 00.314, *Bradypodion fischeri* SRK 00.342, *Bradypodion tavetanum* SRK 00.316, *Bradypodion thamnobates* SRK 00.301, *Brookesia* sp. SRK 00.343, *Brookesia stumpffii* SRK 00.313, *Chamaeleo calypttratus* SRK 00.011, *Chamaeleo dilepis* SRK 00.341, *Chamaeleo hoehnelii* SRK 00.300, *Chamaeleo hoehnelii* SRK 00.305, *Chamaeleo jacksoni* SRK 00.142, *Chamaeleo jacksonii* SRK 00.344, *Chamaeleo jacksonii* SRK 00.345, *Chamaeleo cf. johnstoni* SRK 00.339, *Chamaeleo (Triceros) montium* SRK 00.317, *Chamaeleo quadricornis* SRK 00.040, *Chamaeleo quadricornis* SRK 00.318, *Chamaeleo quilensis* SRK 00.291, *Rhampholeon spectrum* SRK 00.302

Gekkonidae:

Aristelliger georgeensis SRK 00.026, *Cyrtodactylus louisianensis* SRK 00.134, *Eublepharus macularius* SRK 00.013, *Gecko gecko* SRK 00.012, *Gekko gecko* SRK 00.140, *Hemitheconyx caudicinctus* SRK 00.017, *Phelsuma madagascariensis grandis* SRK 00.004, *Phelsuma madagascariensis grandis* SRK 00.014, *Phelsuma madagascariensis grandis* SRK 00.133, *Phelsuma madagascariensis grandis* SRK 00.289, *Phelsuma madagascariensis grandis* SRK 00.290, *Teratoscincus scincus* SRK 00.185, *Uroplatus* sp. SRK 00.330

Iguanidae:

Anolis ocularis winstoni SRK 00.005, *Basiliscus basiliscus* SRK 00.167, *Basiliscus basiliscus* SRK 00.224, *Basiliscus plumifrons* SRK 00.009, *Basiliscus plumifrons* SRK 00.166, *Callisaurus draconoides* SRK 00.165, *Corytophanes cristatus* SRK 00.135, *Corytophanes cristatus* SRK 00.196, *Crotaphytus collaris* SRK 00.020, *Iguana iguana* SRK 00.181, *Iguana iguana* SRK 00.284, *Iguana iguana* SRK 00.298, *Iguana iguana* SRK 00.304, *Laemantius serratus* SRK 00.205, *Leiocephalus* sp. SRK 00.322, *Liolaemus* sp. SRK 00.287, *Oplurus cyclurus* SRK 00.308, *Phrynosoma cornutum* SRK 00.072, *Phrynosoma coronatum* SRK 00.319, *Sceloporus malachiticus* SRK 00.158, *Sceloporus malachiticus* SRK 00.169, *Sceloporus malachiticus* SRK 00.307

Shinisauridae:

Shinisaurus crocodilurus SRK 00.015, *Shinisaurus crocodilurus* SRK 00.016

Varanidae:

Varanus exanthematicus SRK 00.121, *Varanus niloticus* SRK 00.099, *Varanus prasinus* SRK 00.331

Fossil Taxa:

Bavarian Freshwater-Molasse:

Möhren 12 (MP 21): 6 specimens
Nideraichbach (M. SCHÖTZ, Nr. 1980 IX): 27 specimens
Gisseltshausen 1a: 17 specimens
Schönenberg (Bayer. Schwaben, Sandgrube NE d. Ortes, 1966 IX): 7 specimens
Dieshof b. Pöttmes (Unterer Mergel): 3 specimens
Adelschlag (Untermiozän): 3 specimens
Gisseltshausen 1b: 12 specimens
Unterempfenbach 1b: 9 specimens
Gallenbach 2b: 14 specimens
Laimering 3: 10 specimens
Langenmoosen: 6 specimens
Walda 1: 27 specimens
Merkur Nord: 3 specimens
Petersbuch 2 (Scincidae): 2 specimens
Petersbuch 2 (Cordylidae): 1 specimen
Rembach (Scincidae): 1 specimen
Unterhausen: 16 specimens
Altburdig, Wintershof-West (R. DEHM 1937, Mittelmiozän): 12 specimens
Montaigu le Blin (Allier): 3 specimens
Goldberg 2 b. Pflaumloch (Obermiozäne Spaltenfüllung): 6 specimens
Ronheim 1 b. Harburg (Mitteloligozän): 7 specimens
Gaimersheim (Oberoligozän, Chattium; 1952 II): 15 specimens
Floersheim (R. ESTES; z VIII 65): 1 specimen
Goldberg b. Pflaumloch (Obermiozän, Süßwasserkalk): 7 specimens

Guimarota (Kimmeridgium):

Saurillodon:

Gui. Squ. 31, Gui. Squ. 36, Gui. Squ. 43, Gui. Squ. 44, Gui. Squ. 45, Gui. Squ. 48, Gui. Squ. 49

Paramacellodus:

Gui. Squ. 54, Gui. Squ. 55, Gui. Squ. 58

Becklesius:

Gui. Squ. 63, Gui. Squ. 64, Gui. Squ. 65, Gui. Squ. 66, Gui. Squ. 70, Gui. Squ. 71, Gui. Squ. 72, Gui. Squ. 74, Gui. Squ. 76

Paramacellodidae sensu lato:

Gui. Squ. 121, Gui. Squ. 122, Gui. Squ. 124, Gui. Squ. 126, Gui. Squ. 133, Gui. Squ. 136, Gui. Squ. 139, Gui. Squ. 142, Gui. Squ. 144, Gui. Squ. 145, Gui. Squ. 148, Gui. Squ. 161, Gui. Squ. 163, Gui. Squ. 164, Gui. Squ. 169, Gui. Squ. 171, Gui. Squ. 172, Gui. Squ. 174, Gui. Squ. 179, Gui. Squ. 180, Gui. Squ. 189, Gui. Squ. 190, Gui. Squ. 200, Gui. Squ. 204, Gui. Squ. 206, Gui. Squ. 208, Gui. Squ. 212, Gui. Squ. 227, Gui. Squ. 231, Gui. Squ. 234, Gui. Squ. 239, Gui. Squ. 277, Gui. Squ. 340

Paramacelodidae *sensu lato* (Collection SEIFFERT):

Gui. Squ. 532, Gui. Squ. 573, Gui. Squ. 656, Gui. Squ. 698, Gui. Squ. 699, Gui. Squ. 709, Gui. Squ. 712, Gui. Squ. 715, Gui. Squ. 717, Gui. Squ. 720, Gui. Squ. 781, Gui. Squ. 782, Gui. Squ. 783, Gui. Squ. 793, Gui. Squ. 794, Gui. Squ. 801

II Plates

Plate I

Recent Cordylidae:

Chamaesaurinae:

Figs. 1-3: *Chamaesaura macrolepis* (COPE, 1862); (SDS 59535)

- 1: teeth from the central portion of the tooth row; right mandible; lingual view
- 2: isolated tooth from the central portion of the tooth row; right mandible; lingual view
- 3: tooth from the central portion of the tooth row; right mandible; occlusal view

Cordylinae:

Fig. 4: *Cordylus cataphractus* BOIE, 1828; (specimen SDS 68129)

isolated tooth crown from the central portion of the tooth row; right mandible; lingual view

Figs. 5-6: *Cordylus cataphractus* BOIE, 1828; (specimen ZFMK 7808)

- 5: teeth from the central portion of the tooth row; right mandible; lingual view
- 6: isolated tooth crown from the central portion of the tooth row; right mandible; lingual view

Figs. 7-8: *Cordylus peersi* (HEWITT, 1932); (specimen ZFMK 29406)

- 7: tooth from the central portion of the tooth row; right mandible; occlusal view
- 8: tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 9: *Platysaurus capensis* SMITH, 1844; (specimen ZFMK 14833)

tooth from the central portion of the tooth row; left mandible; lingual view

Fig. 10: *Pseudocordylus microlepidotus* (CUVIER, 1829); (specimen BMNII 64.2.21.27)

tooth from the central portion of the tooth row; right mandible; occlusal view

Recent Gerrhosauridae:

Gerrhosaurinae:

Figs. 11-12: *Angolosaurus skoogi* (ANDERSSON, 1916); (specimen ZFMK 7819)

- 11: tooth from the central portion of the tooth row; right mandible; lingual view
- 12: tooth from the central portion of the tooth row; right mandible; occlusal view

Figs. 13-15: *Gerrhosaurus flavigularis fitzsimonsi* LOVERIDGE, 1942; (specimen ZFMK 7813)

- 13: isolated tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- 14: tooth from the anterior portion of the tooth row; right mandible; lingual view
- 15: tooth from the anterior portion of the tooth row; right mandible; occlusal view
- 16: tooth from the posterior portion of the tooth row; right mandible; occlusal view

Zonosaurinae:

Fig. 17: *Tracheloptychus petersi* GRANDIDIER, 1869; (specimen ZFMK 8903)

teeth from the posterior portion of the tooth row; right mandible; lingual view

Fig. 18: *Zonosaurus laticaudatus* (GRANDIDIER, 1869); (specimen ZFMK 7256)

teeth from the central portion of the tooth row; right mandible; lingual view

Fig. 19: *Zonosaurus madagascariensis* (GRAY, 1831); (specimen BMNH 63.5.14)

tooth from the posterior portion of the tooth row; left mandible; lingual view

Fig. 20: *Zonosaurus maximus* BOULENGER, 1896; (specimen ZFMK 7802)

tooth from the central portion of the tooth row; right mandible; lingual view

Plate I

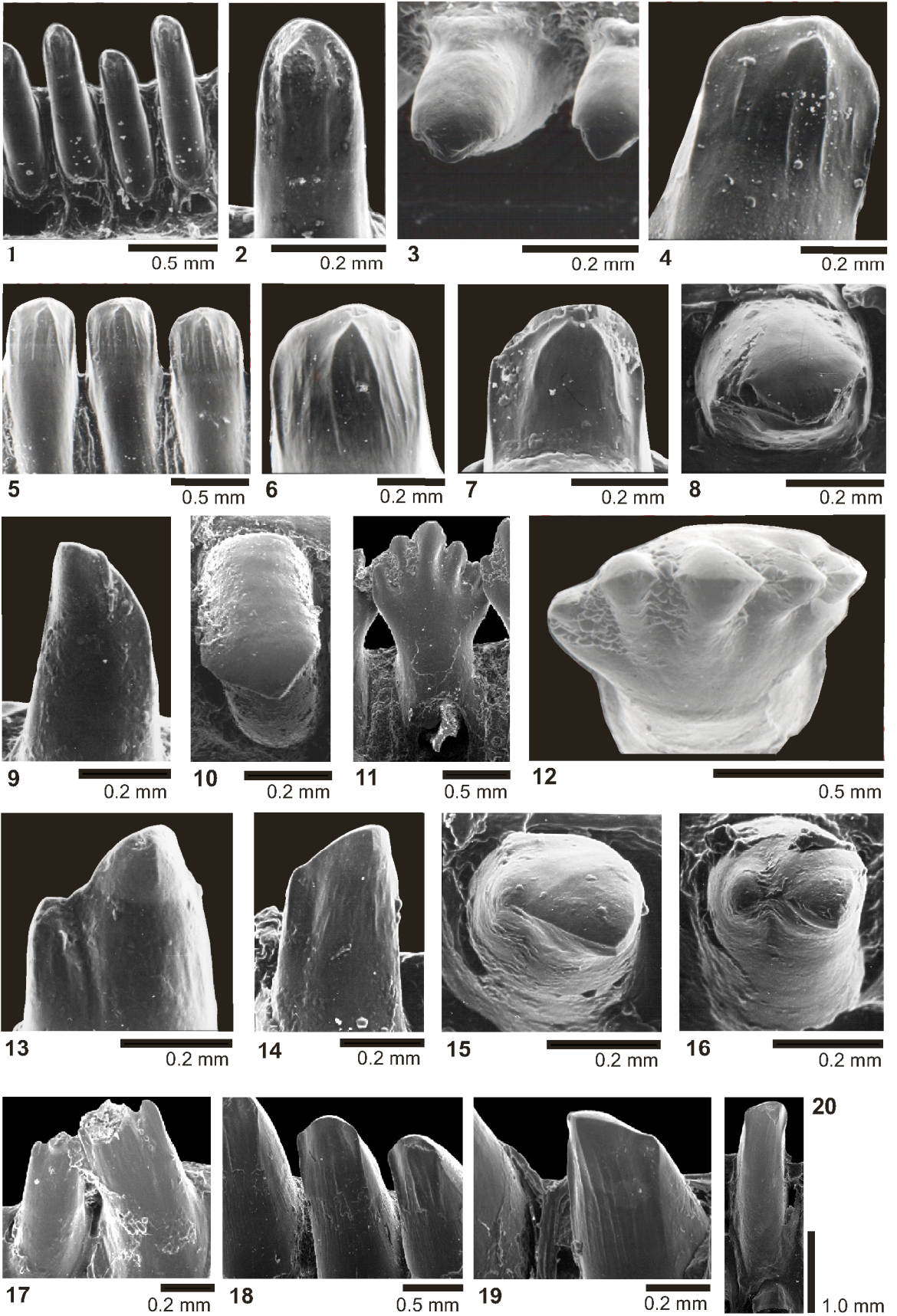


Plate II

Recent Gerrhosauridae (continued):

Figs. 1-2: *Zonosaurus maximus* BOULENGER, 1896; (specimen ZFMK 7825)

- 1: isolated tooth crown from the central portion of the tooth row; right mandible; occlusal view
- 2: isolated tooth crown from the central portion of the tooth row; right mandible; lingual view

Fig. 3: *Zonosaurus quadrilineatus* (GRANDIDIER, 1867); (specimen ZFMK 7804)

- tooth from the central portion of the tooth row; right mandible; lingual view

Recent Lacertidae:

Gallotiinae:

Fig. 4: *Gallotia atlantica* (PETERS & DORIA, 1882); (specimen ZFMK 34964)

- isolated tooth crown from the central portion of the tooth row; right mandible; lingual view

Figs. 5-6: *Gallotia caesaris gomeræ* BOETTGER & MÜLLER, 1914; (specimen ZFMK 4108)

- 5: tooth crown from the central portion of the tooth row; right mandible; lingual view
- 6: tooth crown from the central portion of the tooth row; right mandible; occlusal view

Fig. 7: *Gallotia caesaris gomeræ* BOETTGER & MÜLLER, 1914; (specimen ZFMK 4110)

- tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 8: *Gallotia caesaris* (LEHRS, 1914); (specimen ZFMK 4114)

- tooth from the posterior portion of the tooth row; right mandible; lingual view

Fig. 9: *Gallotia g. galloti* (OUDART, 1839); (specimen ZFMK 4102)

- tooth crown from the posterior portion of the tooth row; right mandible; lingual view

Figs. 10-11: *Gallotia stehlini* (SCHENKEL, 1901); (specimen ZFMK 7876)

- 10: tooth crown from the central portion of the tooth row; right mandible; lingual view
- 11: tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 12: *Psammodromus algirus* (LINNAEUS, 1758); (specimen USNM 199210)

- tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 13: *Psammodromus algirus* (LINNAEUS, 1758); (specimen ZFMK 7864)

- tooth crown from the anterior portion of the tooth row; right mandible; lingual view

Fig. 14: *Psammodromus algirus* (LINNAEUS, 1758); (specimen ZFMK 4086)

- tooth crown from the posterior portion of the tooth row; right mandible; lingual view

Fig. 15: *Psammodromus hispanicus* FITZINGER, 1826; (specimen BMNH 120.1.20.1159)

- tooth from the posterior portion of the tooth row; right mandible; lingual view

Lacertinae:

Fig. 16: *Acanthodactylus pardalis latastasii* (LICHTENSTEIN, 1823); (specimen BMNH 1920.1.20.2715)

- (= *Acanthodactylus maculatus latastasii* (LICHTENSTEIN, 1823))
- tooth crown from the central portion of the tooth row; right mandible; lingual view

Fig. 17: *Darevskia chlorogaster* (BOULENGER, 1908); (BMNH; non cataloged specimen)

- tooth from the posterior portion of the tooth row; right mandible; occlusal view

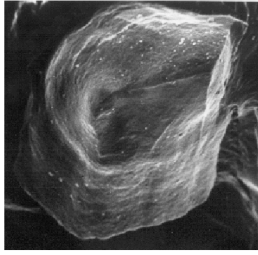
Figs. 18-19: *Gastropholis echinata* (COPE, 1862); (specimen BMNH 1903.7.28.4)

- 18: tooth crown from the central portion of the tooth row; right mandible; lingual view
- 19: tooth from the central portion of the tooth row; right mandible; occlusal view

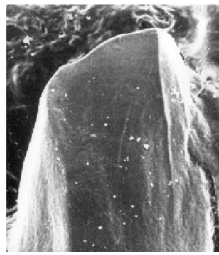
Fig. 20: *Ichnotropis capensis* (SMITH, 1838); (specimen USNM 058611)

- tooth from the central portion of the tooth row; right mandible; occlusal view

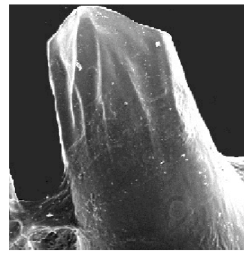
Plate II



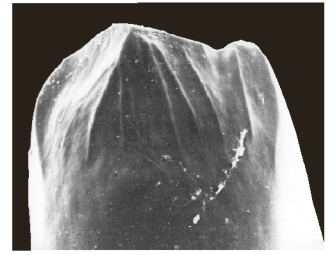
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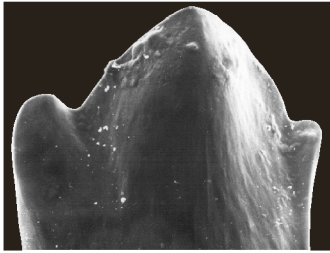
2 0.3 mm



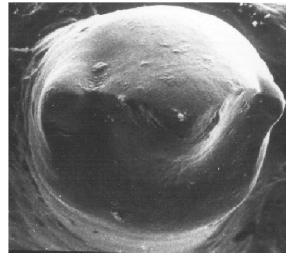
3 0.5 mm



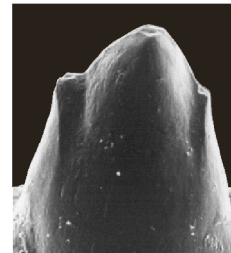
4 0.2 mm



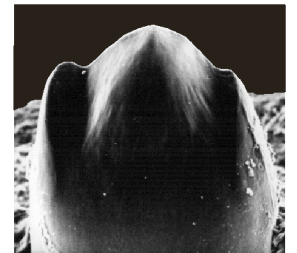
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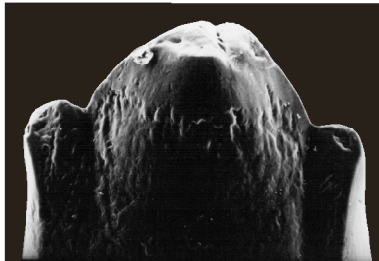
6 0.2 mm



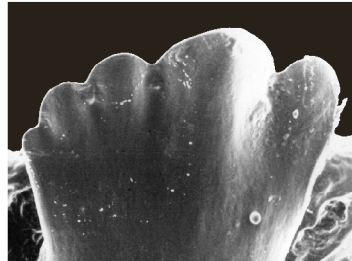
7 0.5 mm



8 0.2 mm



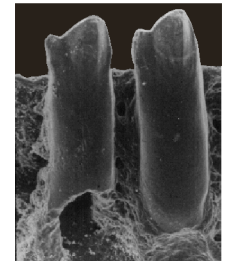
9 0.2 mm



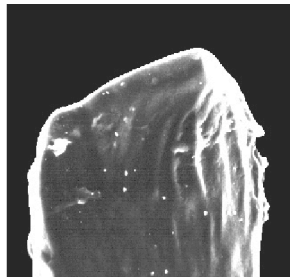
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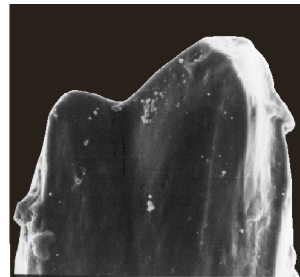
11 1.0 mm



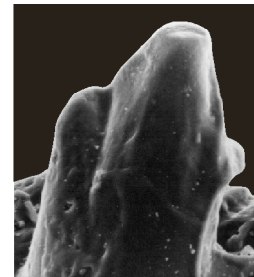
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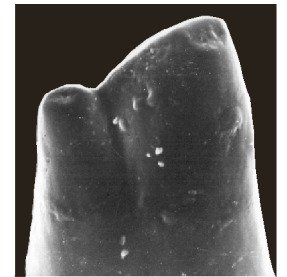
13 0.2 mm



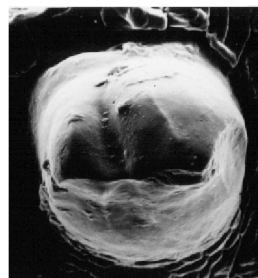
14 0.1 mm



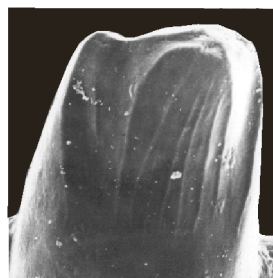
15 0.1 mm



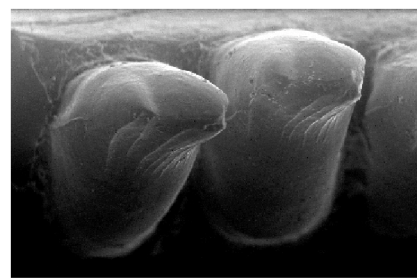
16 0.1 mm



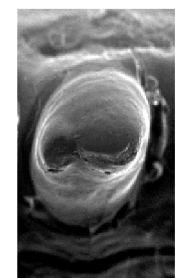
17 0.2 mm



18 0.2 mm



19 0.5 mm



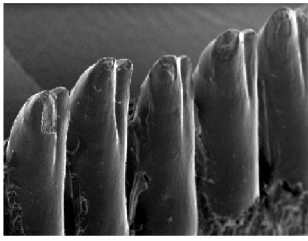
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Plate III

Recent Lacertidae (continued):

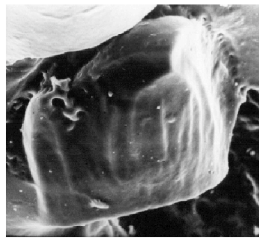
- Fig. 1: *Ichnotropis squamulosa* PETERS, 1854; (BMNH; non cataloged specimen)
teeth from the central portion of the tooth row; left mandible; lingual view
- Fig. 2: *Lacerta agilis* LINNAEUS, 1758; (specimen ZFMK 4090)
replacement tooth in resorption pit; right mandible; lingual view
- Fig. 3: *Lacerta cappadocica urmiana* WERNER, 1902; (specimen ZFMK 4065)
teeth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 4: *Lacerta schreiberi* BEDRIAGA, 1878; (specimen S7, Priv. Coll. EVANS)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 5: *Lacerta trilineata gica* (BEDRIAGA, 1886); (specimen ZFMK 4059)
tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 6: *Lacerta trilineata* (BEDRIAGA, 1886); (specimen ZFMK 7869)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 7: *Lacerta v. viridis* (LAURENTI, 1768); (specimen BMNH 1920.1.20.725)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 8: *Lacerta viridis* (LAURENTI, 1768); (Priv. Coll. EVANS; non cataloged specimen)
teeth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 9: *Meroles suborbitalis* (PETERS, 1869); (specimen USNM 292594)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 10: *Philochortus hardeggeri* (STEINDACHNER, 1891); (specimen BMNH 1905.10.58.9)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 11: *Podarcis bocagei* (SEOANE, 1885); (specimen PB57, Priv. Coll. EVANS)
teeth from the anterior portion of the tooth row; right mandible; dorsolingual view
- Fig. 12: *Podarcis filfolensis* (BEDRIAGA, 1876); (specimen BMNH 1909.10.30.56)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 13: *Podarcis hispanica* (STEINDACHNER, 1870); (specimen H-5, Priv. Coll. EVANS)
teeth from the central portion of the tooth row; right mandible; lingual view
- Fig. 14: *Podarcis muralis liolepis* (LAURENTI, 1768); (specimen USNM 220261)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 15: *Podarcis peloponnesiaca* (BIBRON & BORY, 1833); (specimen ZFMK 4095)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 16: *Podarcis sicula* (RAFINESQUE-SCHMALTZ, 1810); (specimen ZFMK 1729)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 17: *Podarcis taurica* (PALLAS, 1814); (specimen ZFMK 7865)
tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 18: *Takydromus formosanus* (BOULENGER, 1894); (specimen BMNH 18231)
tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 19: *Takydromus septentrionalis* (GÜNTHER, 1864); (specimen ZFMK 14830)
teeth from the central portion of the tooth row; right mandible; dorsolingual view
- Fig. 20: *Takydromus sexlineatus* DAUDIN, 1802; (specimen SRK 00.269)
tooth from the central portion of the tooth row; right mandible; lingual view

Plate III



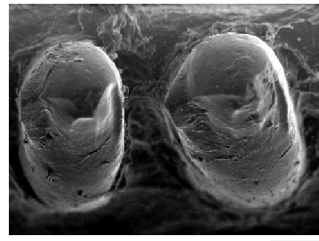
1

0.5 mm



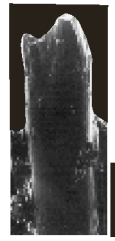
2

0.1 mm



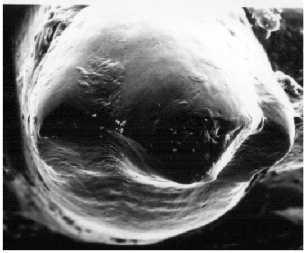
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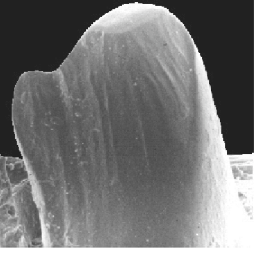
4

0.5 mm



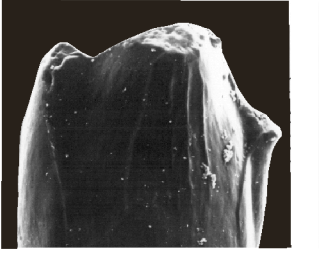
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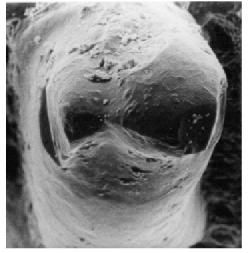
6

0.5 mm



7

0.2 mm



8

0.2 mm



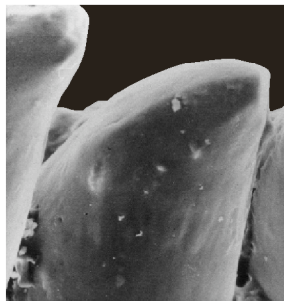
9

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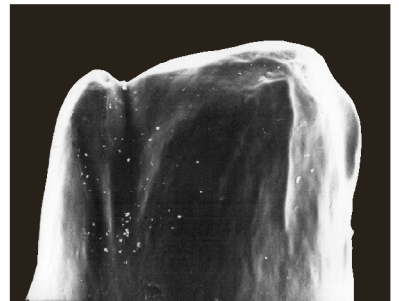
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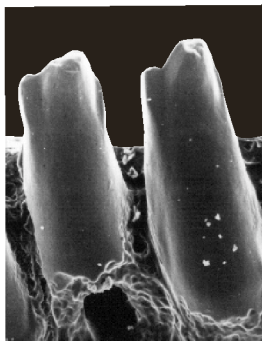
11

0.1 mm



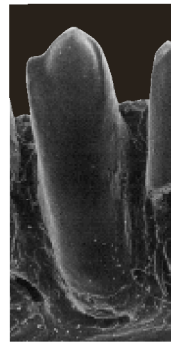
12

0.2 mm



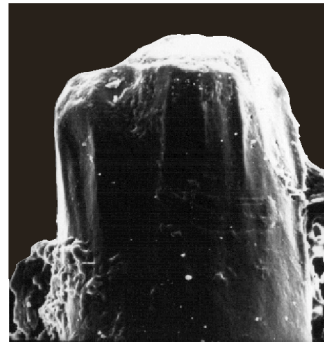
13

0.5 mm



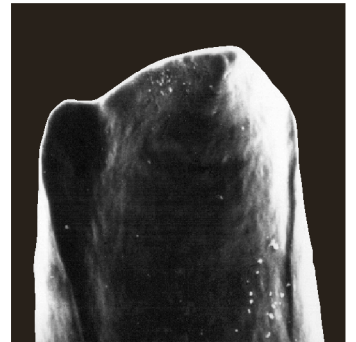
14

0.5 mm



15

0.2 mm



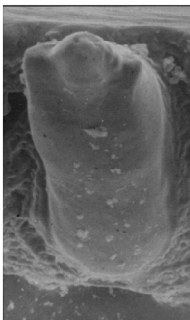
16

0.2 mm



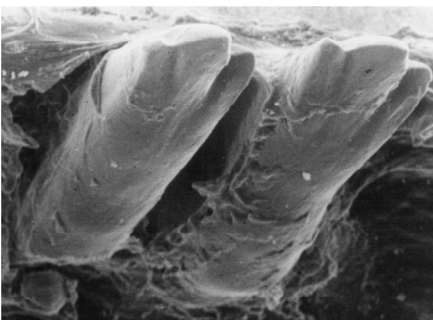
17

0.2 mm



18

0.2 mm



19

0.5 mm



20

0.2 mm

Plate IV

Recent Lacertidae (continued):

- Fig. 1: *Takydromus sexlineatus* DAUDIN, 1802; (specimen SRK 00.269)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Figs. 2-3: *Teira d. dugesii* (MILNE-EDWARDS, 1829); (specimen ZFMK 4079)
2: tooth from the central portion of the tooth row; right mandible; lingual view
3: isolated tooth crown from the central portion of the tooth row; right mandible; lingual view
- Figs. 4-5: *Timon lepidus* (DAUDIN, 1802); (specimen K-37, Priv. Coll. EVANS)
4: tooth from the central portion of the tooth row; right mandible; lingual view
5: tooth from the posterior portion of the tooth row; right mandible; lingual view
- Figs. 6-7: *Timon lepidus* (DAUDIN, 1802); (specimen ZFMK 7800)
6: tooth from the posterior portion of the tooth row; right mandible; lingual view
7: tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 8: *Timon pater* (LATASTE, 1880); (specimen ZFMK 7870)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Figs. 9-11: *Timon pater* (LATASTE, 1880); (specimen BMNH 1974.24.91)
9: tooth from the central portion of the tooth row; right mandible; lingual view
10: tooth from the central portion of the tooth row; right mandible; lingual view
11: tooth from the anterior portion of the tooth row; right mandible; lingual view
- Figs. 12-13: *Timon princeps* (BLANFORD, 1874); (specimen ZFMK 7877)
12: tooth from the anterior portion of the tooth row; right mandible; lingual view
13: tooth from the anterior portion of the tooth row; right mandible; occlusal view
- Fig. 14: *Zootoca vivipara* (VON JACQUIN, 1787); (specimen ZFMK 4063)
tooth from the central portion of the tooth row; right mandible; lingual view

Recent Scincidae:

Acontinae :

- Fig. 15: *Acontias g. gracilicauda* (ESSEX, 1925); (specimen AMNH 48507)
tooth from the anterior portion of the tooth row; right mandible; lingual view
- Fig. 16: *Acontias meleagris* LINNAEUS, 1758; (specimen SRK 00.055)
teeth from the anterior portion of the tooth row; right mandible; lingual view
- Figs. 17-20: *Acontias plumbeus* BIANCONI, 1849; (specimen BMNH 49.6.29.-38)
17: tooth position 1; right mandible; lingual view
18: tooth from the anterior portion of the tooth row; right mandible; lingual view
19: tooth from the posterior portion of the tooth row; right mandible; lingual view
20: posteriormost tooth (tooth position 13); right mandible; lingual view

Plate IV

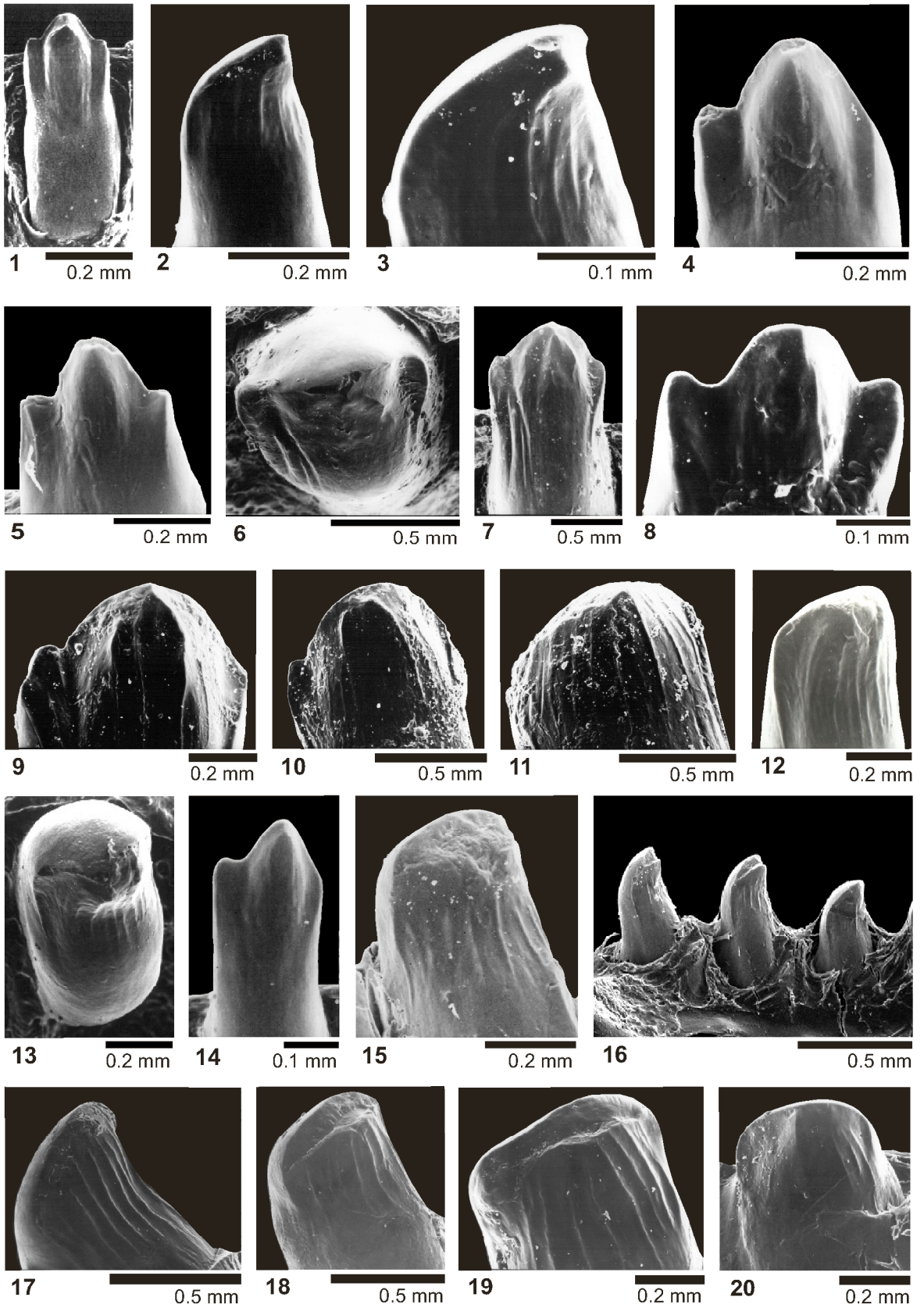


Plate V

Recent Scincidae (continued):

Feylininae:

Fig. 1: *Feylinia currori* GRAY, 1845; (specimen IFSZ 14562)
tooth crown from the central portion of the tooth row; right mandible; lingual view

Lygosominae:

Fig. 2: *Ablepharus grayanus* BOULENGER, 1887; (specimen BMNH 91.9.14.8)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 3: *Ablepharus lineo-ocellatus* nomen dubium; (specimen BMNH XI.4A)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 4: *Carlia fusca* (DUMÉRIL & BIBRON, 1839); (specimen USNM 323696)
tooth from the anterior portion of the tooth row; right mandible; lingual view

Figs. 5-6: *Corucia zebrata* GRAY, 1855; (specimen SDS 62346)
5: tooth from the central portion of the tooth row; right mandible; lingual view
6: tooth from the central portion of the tooth row; right mandible; occlusal view

Fig. 7: *Cryptoblepharus boutoni* MERTENS, 1928; (specimen BMNH 1947.3.3.34)
tooth from the central portion of the tooth row; right mandible; occlusal view

Fig. 8: *Cryptoblepharus poecilopleurus* WIEGMANN, 1836; (specimen USNM 337782)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 9: *Dasia olivacea* GRAY, 1839; (specimen ZFMK 14828)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 10: *Egernia dorsalis* nomen dubium; (specimen BMNH 1908.2.25.9)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 11: *Egernia stokesii* (GRAY, 1838); (specimen ZFMK 14820)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 12: *Egernia striolata* (PETERS, 1870); (specimen ZFMK 1482)
tooth from the central portion of the tooth row; right mandible; dorsolingual view

Fig. 13: *Egernia whitii* (LACÉPÈDE, 1804); (specimen IFSZ 14262)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 14: *Emoia caeruleocauda* (DE VIES, 1892); (specimen USNM 323699)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 15: *Emoia caeruleocauda* (DE VIES, 1892); (specimen USNM 122578)
tooth from the central portion of the tooth row; right mandible; dorsolingual view

Fig. 16: *Emoia cyanura* (LESSON, 1826/1830); (specimen USNM 249750)
tooth from the central portion of the tooth row; right mandible; dorsolingual view

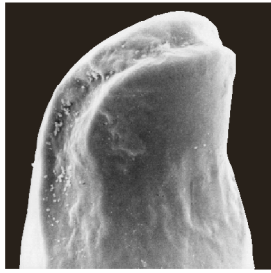
Fig. 17: *Emoia jakati* (KOPSTEIN, 1926); (specimen USNM 512284)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 18: *Emoia nigromarginata* (ROUX, 1913); (specimen USNM 334060)
tooth from the central portion of the tooth row; right mandible; lingual view

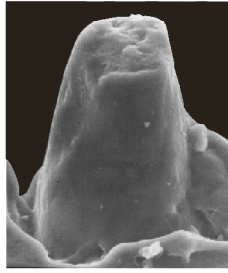
Fig. 19: *Emoia sanfordi* SCHMIDT & BURT, 1930; (specimen AMNH R40169)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 20: *Emoia slevini* BROWN & FALANRUW, 1972; (specimen USNM 536082)
tooth from the central portion of the tooth row; right mandible; lingual view

Plate V



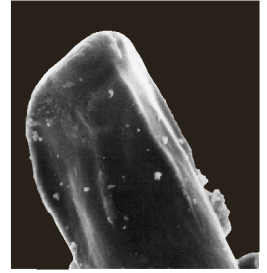
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2 0.05 mm



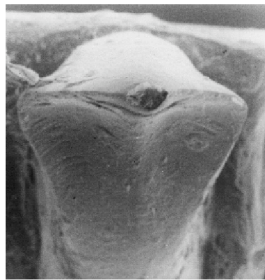
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4 0.1 mm



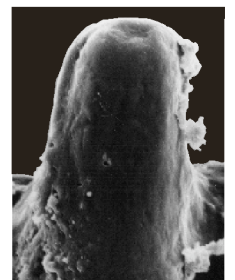
5 1.0 mm



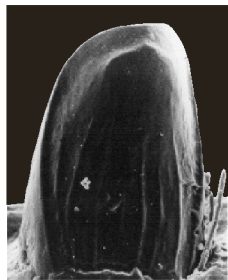
6 1.0 mm



7 0.1 mm



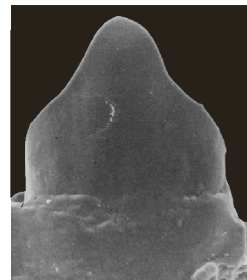
8 0.1 mm



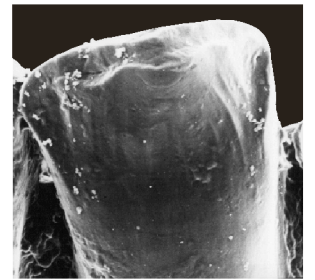
9 0.2 mm



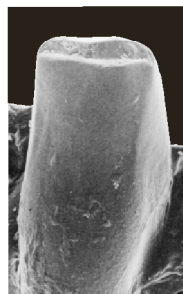
10 0.5 mm



11 0.2 mm



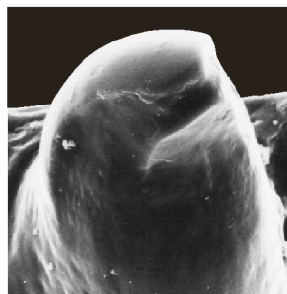
12 0.2 mm



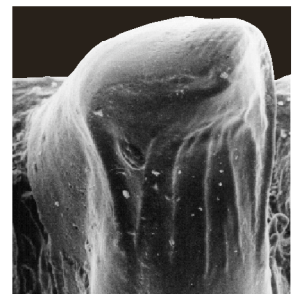
13 0.1 mm



14 0.1 mm



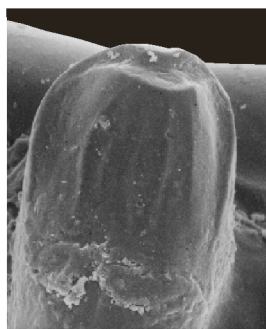
15 0.1 mm



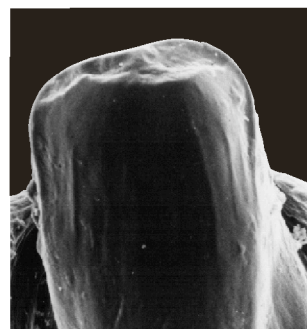
16 0.2 mm



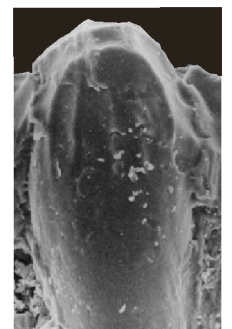
17 0.05 mm



18 0.2 mm



19 0.2 mm



20 0.2 mm

Plate VI

Recent Scincidae (continued):

- Fig. 1: *Emoia trossula* BROWN & GIBBONS, 1986; (specimen USNM 249745)
teeth from the central portion of the tooth row; right mandible; lingual view
- Fig. 2: *Eugongylus albifasciolatus* (GÜNTHER, 1872); (specimen BMNH 98.5.27.-13)
teeth from the central portion of the tooth row; right mandible; lingual view
- Figs. 3-4: *Eugongylus rufescens* (SHAW, 1802); (specimen BMNH 97.12.10.73)
3: teeth from the central portion of the tooth row; left mandible; lingual view
4: teeth from the central portion of the tooth row; left mandible; occlusal view
- Figs. 5-7: *Eumecia anchietae* BOCAGE, 1870; (specimen BMNH 1906.7.6.4.)
5: tooth from the anterior portion of the tooth row; right mandible; lingual view
6: tooth from the central portion of the tooth row; right mandible; lingual view
7: tooth from the anterior portion of the tooth row; right mandible; occlusal view
- Fig. 8: *Hemiergis decresiensis* (CUVIER, 1829); (specimen SRK 00.261)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 9: *Hemiergis peronii* (GRAY, 1831); (specimen SRK 00.282)
tooth from the anterior portion of the tooth row; right mandible; lingual view
- Figs. 10-12: *Hemisphaeriodon gerrardi* (GRAY, 1845); (specimen BMNH 1882.210)
10: tooth from the anterior portion of the tooth row; right mandible; dorsolingual view
11: tooth from the central portion of the tooth row; right mandible; dorsolingual view
12: tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 13: *Lamprolepis smaragdina* (LESSON, 1826); (specimen USNM 340061)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 14: *Lamprolepis smaragdina* (LESSON, 1826); (specimen ZFMK 14825)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 15: *Lamprolepis smaragdina* (LESSON, 1826); (specimen USNM 340061)
tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 16: *Lampropholis delicata* (DE VIES, 1888); (specimen SDS 63231)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 17: *Leiolepisma austracaledonicum* nomen dubium; (specimen ZFMK 14826)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 18: *Lerista planiventralis* (LUCAS & FROST, 1902); (specimen BMNH 1954.1-2.21)
tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 19: *Lipinia leptosoma* (BROWN & FEHLMANN, 1958); (specimen USNM 507554)
tooth from the central portion of the tooth row; right mandible; occlusal view

Plate VI

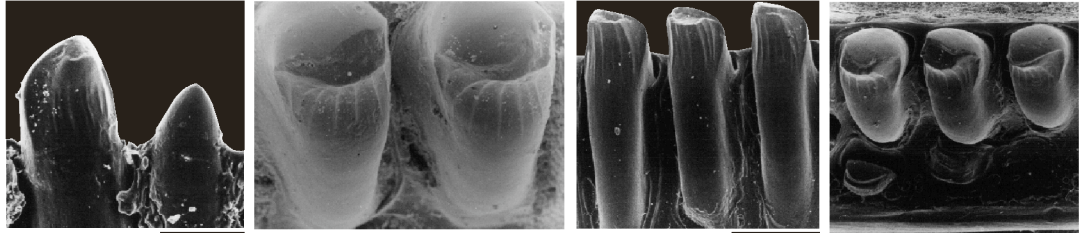


Fig. 1 0.2 mm Fig. 2 0.5 mm Fig. 4 0.5 mm Fig. 3 0.5 mm

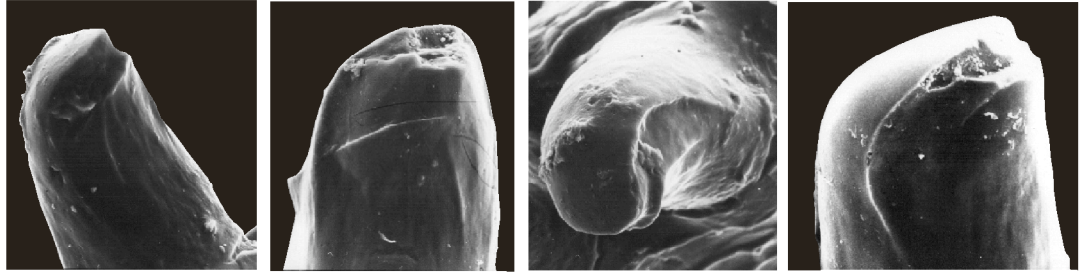


Fig. 5 0.1 mm Fig. 6 0.1 mm Fig. 7 0.1 mm Fig. 8 0.05 mm

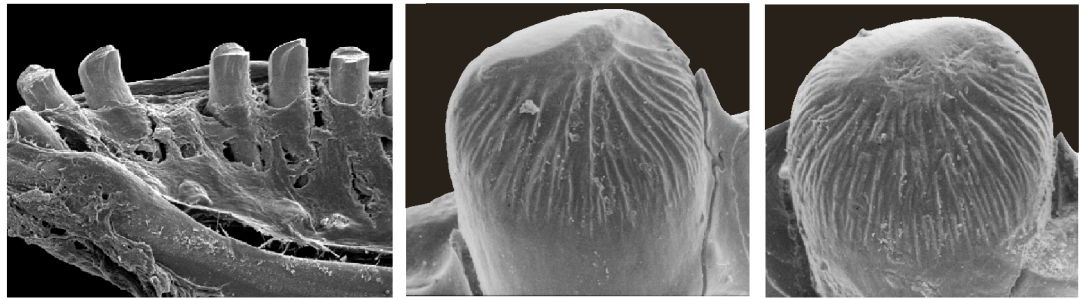


Fig. 9 0.5 mm Fig. 10 0.5 mm Fig. 11 0.5 mm

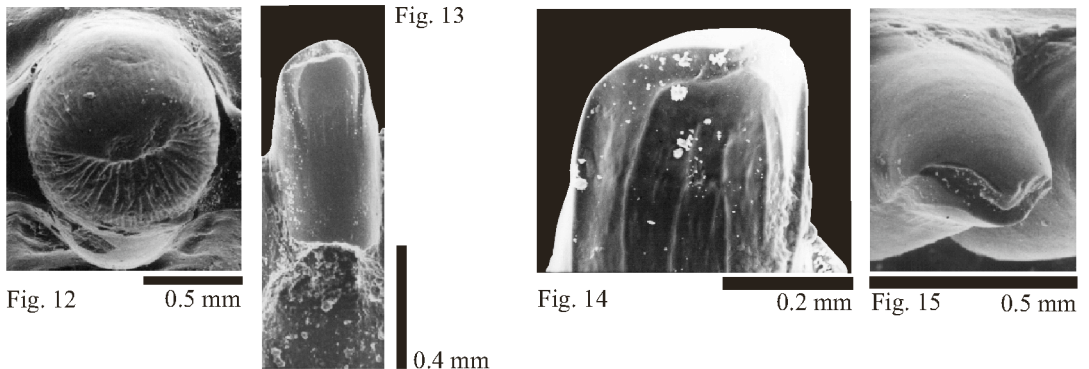


Fig. 12 0.5 mm Fig. 13 0.4 mm Fig. 14 0.2 mm Fig. 15 0.5 mm

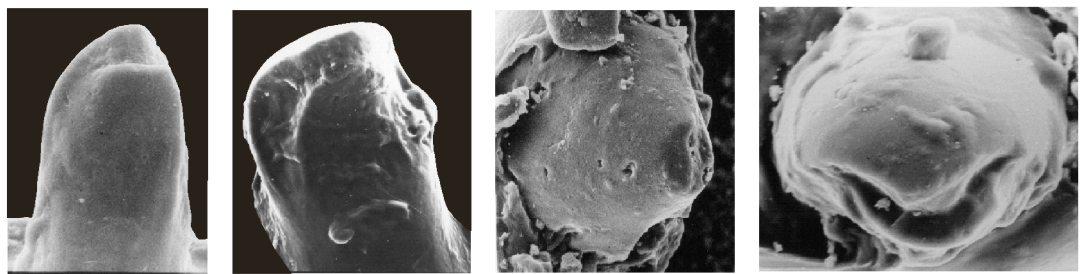


Fig. 16 0.05 mm Fig. 17 0.1 mm Fig. 18 0.1 mm Fig. 19 0.1 mm

Plate VII

Recent Scincidae (continued):

- Fig. 1: *Lipinia noctua* (LESSON, 1826); (specimen SDS 18018)
teeth from the central portion of the tooth row; right mandible; lingual view
- Fig. 2: *Lipinia pulchella* (GRAY, 1845); (specimen USNM 509419)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 3: *Lygosoma afra* (PETERS, 1854); (specimen SRK 00.293)
teeth from the anterior portion of the tooth row; right mandible; lingual view
- Fig. 4: *Mabuya affinis* (GRAY, 1838); (specimen ZFMK 9196)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 5: *Mabuya bistriata* (SPLX, 1825); (specimen USNM 292410)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 6: *Mabuya gravenhorstii* (DUMÉRIL & BIBRON, 1839); (specimen USNM 336440)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 7: *Mabuya macularis comorensis* nomen dubium; (specimen BMNH 77.8.9.8)
tooth from the anterior portion of the tooth row; right mandible; lingual view
- Fig. 8: *Mabuya vittata* (OLIVIER, 1804); (specimen ZFMK 9194)
tooth from the anterior portion of the tooth row; left mandible; lingual view
- Fig. 9: *Mabuya wrightii* BOULENGER, 1887; (specimen BMNH 1956.1.15.60)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 10: *Mochlus fernandi* (BURTON, 1836); (specimen BMNH 88.829.-3)
tooth from the central portion of the tooth row; right mandible; lingual view
- Figs. 11-12: *Mochlus s. sundevalli* (SMITH, 1849); (specimen AMNH 40723)
11: tooth from the anterior portion of the tooth row; right mandible; lingual view
12: tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 13: *Panaspis africana* (GRAY, 1845); (specimen BMNH 1906.3.30.54)
tooth from the central portion of the tooth row; right mandible; lingual view
- Figs. 14-15: *Saprosincus mustelinus* (O'SHAUGHNESSY, 1874); (specimen SRK 00.260)
14: tooth from the anterior portion of the tooth row; right mandible; lingual view
15: tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 16: *Scincella lateralis* (SAY, 1823); (specimen USNM 332758)
tooth from the anterior portion of the tooth row; right mandible; lingual view
- Fig. 17: *Scincella lateralis* (SAY, 1823); (specimen AMNH R-16974)
teeth from the central portion of the tooth row; right mandible; lingual view
- Fig. 18: *Sphenomorphus aignanus* nomen dubium; (specimen BMNH 1946.8.15.48)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 19: *Sphenomorphus dussumieri* (DUMÉRIL & BIBRON, 1839); (specimen BMNH 1946.8.15.42)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 20: *Sphenomorphus indicus* (GRAY, 1853); (specimen BMNH 1965.1064)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Figs. 21-22: *Sphenomorphus muelleri* (SCHLEGEL, 1834); (specimen BMNH 88.3.21.-5.)
21: tooth from the central portion of the tooth row; right mandible; lingual view
22: tooth from the central portion of the tooth row; right mandible; occlusal view

Plate VII

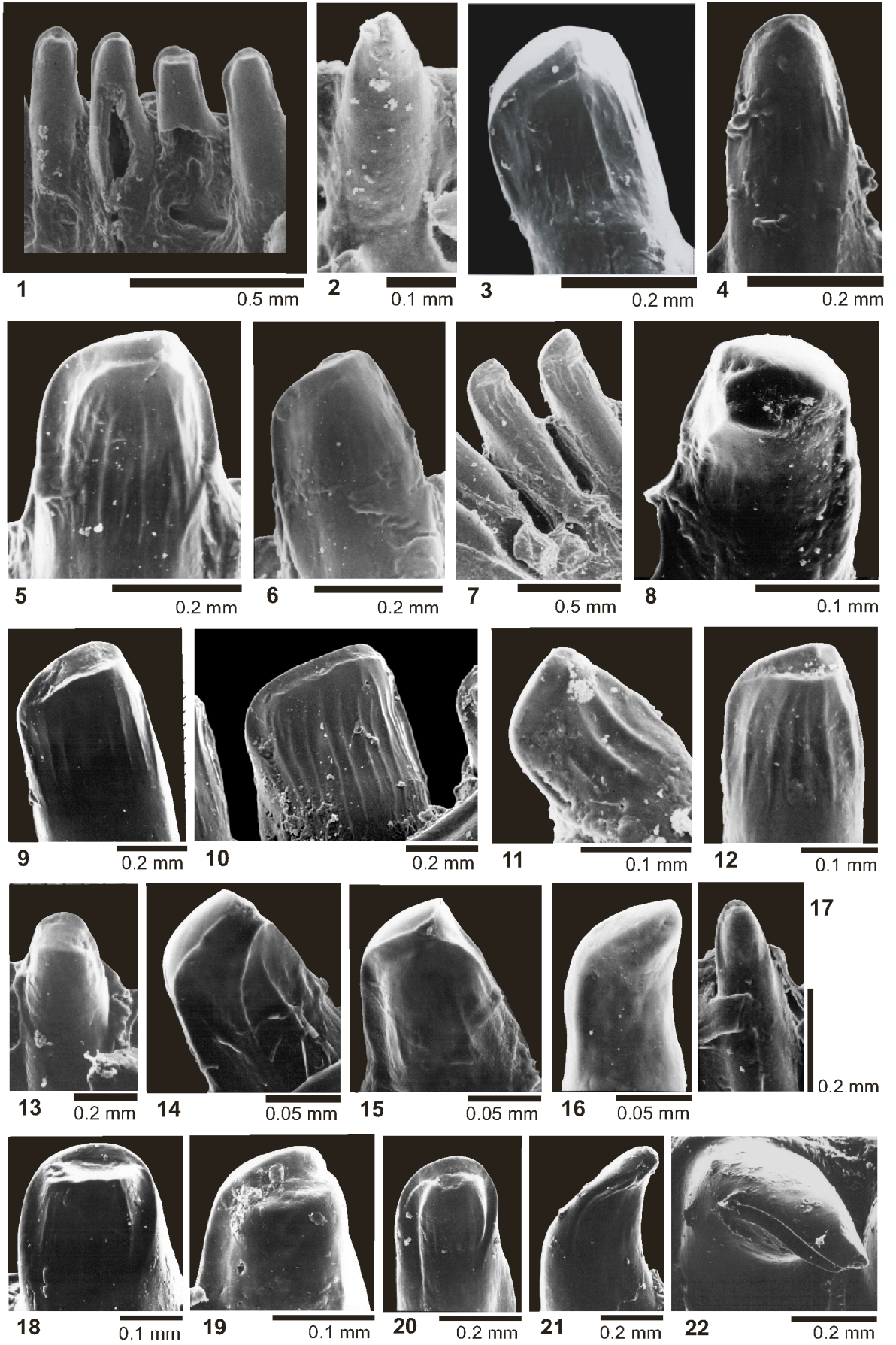


Plate VIII

Recent Scincidae (continued):

Fig. 1: *Sphenomorphus striatopunctatus* (BOULENGER, 1907); (specimen BMNH 1948.1.7.60)
tooth from the anterior portion of the tooth row; right mandible; lingual view

Figs. 2-7: *Sphenomorphus variegatus* (PETERS, 1867); (specimen SRK 00.297)
2: tooth crown from the anterior portion of the tooth row; right mandible; lingual view
3: tooth crown from the central portion of the tooth row; right mandible; lingual view
4: anterior portion of the tooth row; right mandible; lingual view (“multiple tooth replacement”)
5: anterior portion of the tooth row; right mandible; occlusal view (“multiple tooth replacement”)
6: central portion of the tooth row; right mandible; lingual view (“multiple tooth replacement”)
7: anterior portion of the tooth row; right mandible; occlusal view (“multiple tooth replacement”)

Fig. 8: *Tiliqua gigas* (SCHNEIDER, 1801); (specimen ZFMK 7852)
tooth from the central portion of the tooth row; right mandible; dorsolingual view

Figs. 9-11: *Tiliqua gigas* (SCHNEIDER, 1801); (specimen ZFMK 14829)
(neonate specimen)
9: tooth from the central portion of the tooth row; right mandible; lingual view
10: tooth from the posterior portion of the tooth row; right mandible; lingual view
11: posteriormost tooth of the tooth row; right mandible; lingual view

Fig. 12: *Tiliqua rugosa* (GRAY, 1825); (specimen SDS 68063)
tooth from the anterior portion of the tooth row; right mandible; occlusal view

Figs. 13-14: *Tiliqua rugosa* (GRAY, 1825); (specimen ZFMK 5235)
13: tooth from the central portion of the tooth row; right mandible; lingual view
14: tooth from the central portion of the tooth row; right mandible; occlusal view

Fig. 15: *Tiliqua rugosa* (GRAY, 1825); (specimen SDS 68064)
(embryo of specimen SDS 68063)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 16: *Tiliqua scincoides* (WHITE, 1790); (specimen IFSZ 27821)
tooth from the anterior portion of the tooth row; right mandible; lingual view

Plate VIII

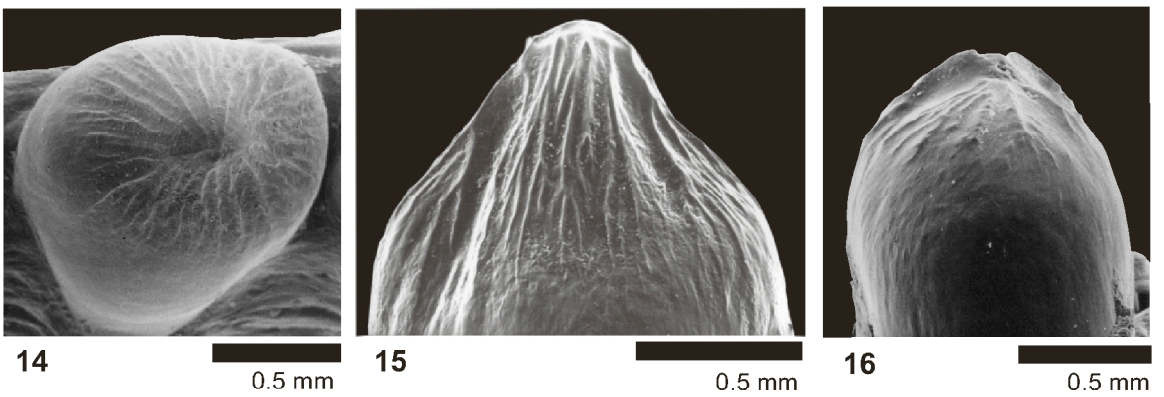
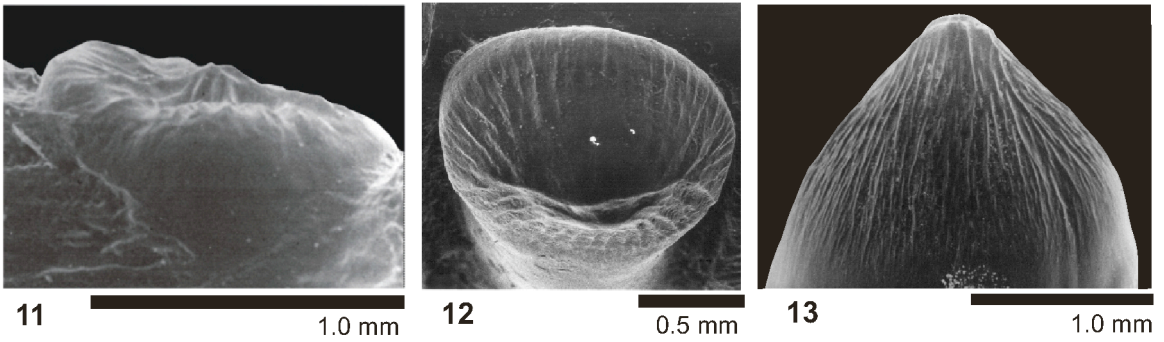
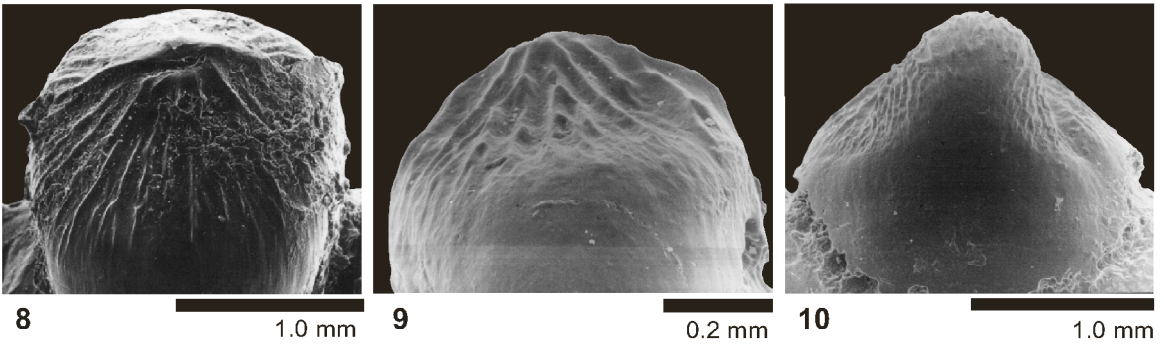
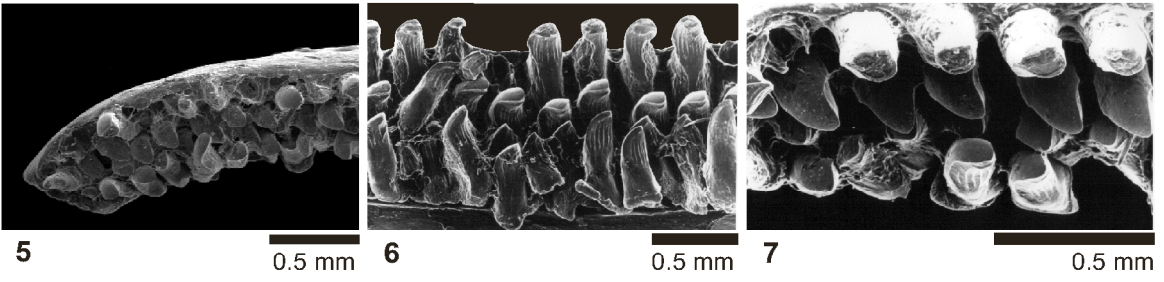
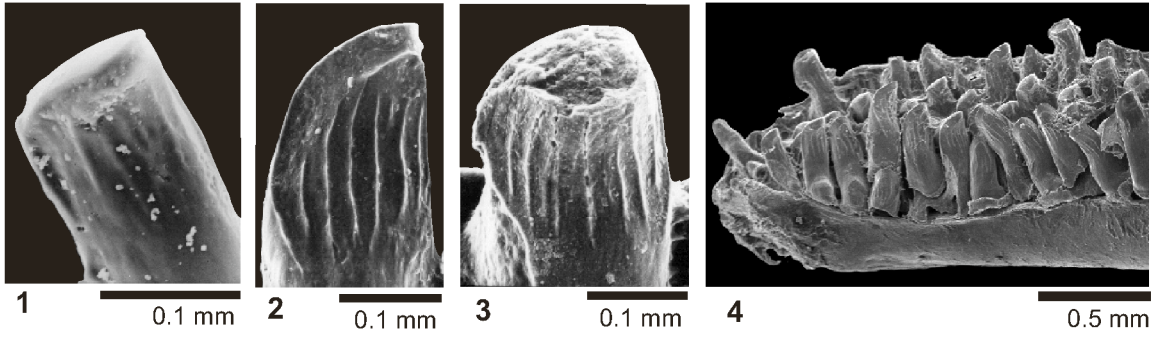


Plate IX

Recent Scincidae (continued):

Figs. 1-2: *Tiliqua scincoides* (WHITE, 1790); (specimen IFSZ 27821)
1: tooth from the central portion of the tooth row; right mandible; lingual view
2: tooth from the central portion of the tooth row; right mandible; occlusal view

Fig. 3: *Tribolonotus novaeguineae* (SCHLEGEL, 1834); (specimen BMNH 1905.11.29.10)
tooth from the central portion of the tooth row; right mandible; lingual view

Figs. 4-5: *Tropidophorus beccarii* PETERS, 1871; (specimen BMNH 1929.12.22.103)
4: teeth from the central portion of the tooth row; right mandible; lingual view
5: teeth from the central portion of the tooth row; right mandible; occlusal view

Figs. 6-7: *Tropidophorus herdmorei* (BLYTH, 1853); (specimen BMNH 1964.964)
6: tooth from the central portion of the tooth row; right mandible; lingual view
7: tooth from the posterior portion of the tooth row; right mandible; lingual view

Fig. 8: *Tropidophorus robinsoni* SMITH, 1919; (specimen BMNH 1933.5.13.27)
tooth from the central portion of the tooth row; right mandible; lingual view

Scincinae:

Fig. 9: *Brachymeles boulengeri taylori* TAYLOR, 1922; (specimen USNM 305968)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 10: *Brachymeles tridactylus* BROWN, 1956; (specimen USNM 229623)
tooth crown from the central portion of the tooth row; right mandible; dorsolingual view

Fig. 11: *Chalcides bedriagai* (BOSCA, 1880); (specimen ZFMK 14823)
tooth crown from the anterior portion of the tooth row; right mandible; lingual view

Fig. 12: *Chalcides chalcides* (LINNAEUS, 1758); (specimen SRK 00.277)
tooth crown from the anterior portion of the tooth row; right mandible; lingual view

Fig. 13: *Chalcides ocellatus* (FORSKAL, 1775); (specimen USNM 313453)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 14: *Chalcides viridanus* (GRAVENHORST, 1851); (specimen ZFMK 49964)
central portion of the tooth row; right mandible; anterolabial view

Fig. 15: *Eumeces fasciatus* (LINNAEUS, 1758); (specimen USNM 220267)
tooth crown from the central portion of the tooth row; right mandible; lingual view

Fig. 16: *Eumeces gilberti* VAN DENBURGH, 1896; (specimen USNM 5310)
tooth crown from the central portion of the tooth row; right mandible; lingual view

Fig. 17: *Eumeces gilberti rubricaudatus* VAN DENBURGH, 1896; (specimen SDS 63125)
tooth crown from the central portion of the tooth row; right mandible; lingual view

Fig. 18: *Eumeces inexpectatus* TAYLOR, 1932; (specimen USNM 332755)
tooth from the central portion of the tooth row; right mandible; occlusal view

Fig. 19: *Eumeces laticeps* (SCHNEIDER, 1801); (specimen AMNH R-110724)
tooth from the anterior portion of the tooth row; right mandible; lingual view

Fig. 20: *Eumeces laticeps* (SCHNEIDER, 1801); (specimen USNM 525729)
tooth from the central portion of the tooth row; right mandible; lingual view

Fig. 21: *Eumeces longirostris* (COPE, 1861); (specimen USNM 217505)
tooth crown from the central portion of the tooth row; right mandible; lingual view

Fig. 22: *Eumeces marginatus* (HALLOWELL, 1861); (specimen USNM 17853)
tooth from the central portion of the tooth row; right mandible; lingual view

Plate IX

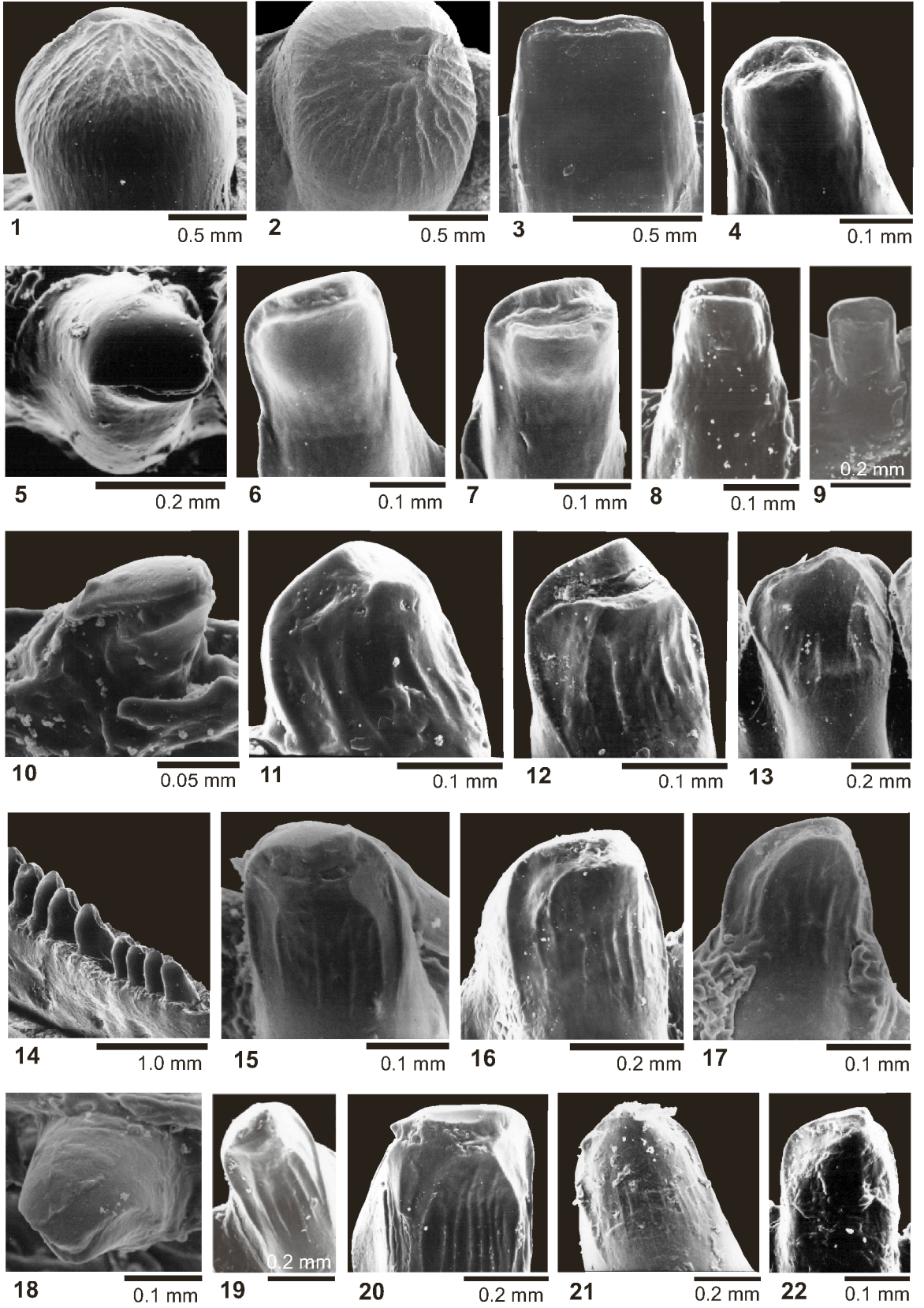


Plate X

Recent Scincidae (continued):

- Fig. 1: *Eumeces obsoletus* (BAIRD & GIRARD, 1852); (AMNH; non cataloged specimen)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 2: *Eumeces schwarzei* nomen dubium; (specimen USNM 113603)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 3: *Eumeces skiltonianus* (BAIRD & GIRARD, 1852); (specimen SDS 63107)
tooth from the central portion of the tooth row; right mandible; dorsolingual view
- Fig. 4: *Eumeces tunganus* STEJNEGER, 1924; (specimen USNM 82751)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 5: *Eurylepis taeniolatus* BLYTH, 1854; (specimen AMNH 110170)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 6: *Janetaescincus braueri* (BOETTGER, 1896); (specimen BMNH 1910.3.18.33)
tooth from the anterior portion of the tooth row; right mandible; lingual view
- Fig. 7: *Melanoseps occidentalis* (PETERS, 1877); (specimen BMNH 1907.5.22.6A)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 8: *Neoseps reynoldsi* STEJNEGER, 1910; (specimen USNM 48762)
tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 9: *Novoeumeces schneideri* (DAUDIN, 1802); (specimen BMNH 1920.1.20.2702)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 10: *Novoeumeces schneideri* (DAUDIN, 1802); (specimen BMNH 1920.1.20.2702)
teeth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 11: *Scelotes gronovii* (DAUDIN, 1802); (specimen BMNH 97.5.15.8)
central portion of the tooth row; right mandible; lingual view
- Fig. 12: *Scincopus fasciatus* PETERS, 1864; (specimen BMNH 1906.5.7.5)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 13: *Scincus mitranus* ANDERSON, 1871; (specimen BMNH 1973.405)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 14: *Scincus scincus* (LINNAEUS, 1758); (specimen IFSZ 19107)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 15: *Scincus scincus* (LINNAEUS, 1758); (specimen SDS 65230)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 16: *Typhlacontias gracilis* ROUX, 1907; (specimen USNM 159338)
teeth from the central portion of the tooth row; right mandible; lingual view

Recent Teiidae:

Teiinae:

- Fig. 17: *Ameiva auberi sabulicolor* COCTEAU, 1838; (specimen USNM 220669)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 18: *Ameiva bifrontata* COPE, 1862; (specimen ZFMK 21640)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 19: *Ameiva chrysoleama* COPE, 1868; (specimen SDS 64800)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 20: *Ameiva chrysoleama boekeri* MERTENS, 1938; (specimen USNM 259527)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 21: *Ameiva chrysoleama parvovis* SCHWARTZ & KLINIKOWSKI, 1966; (specimen USNM 259532)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 22: *Ameiva corax* CENSKY & PAULSON, 1992; (specimen SDS 64800)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 23: *Ameiva exsul desechensis* HEATWOLE & TORRES, 1967; (specimen USNM 221745)
tooth crowns from the posterior portion of the tooth row; right mandible; lingual view

Plate X

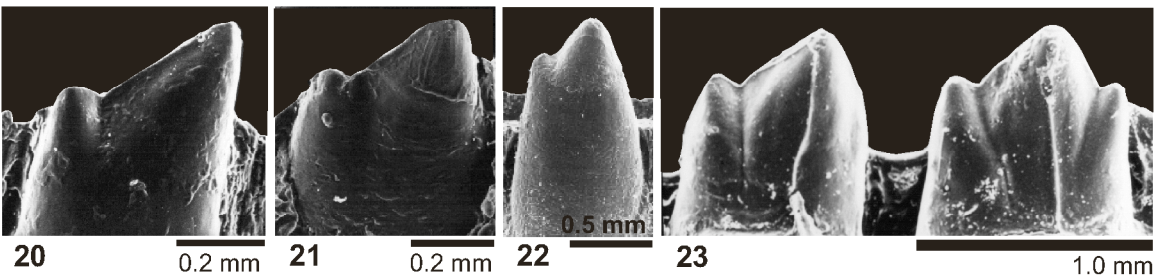
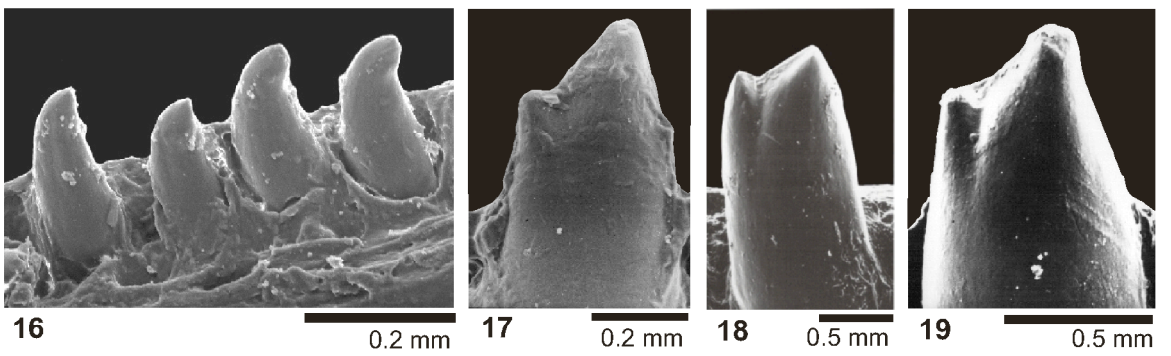
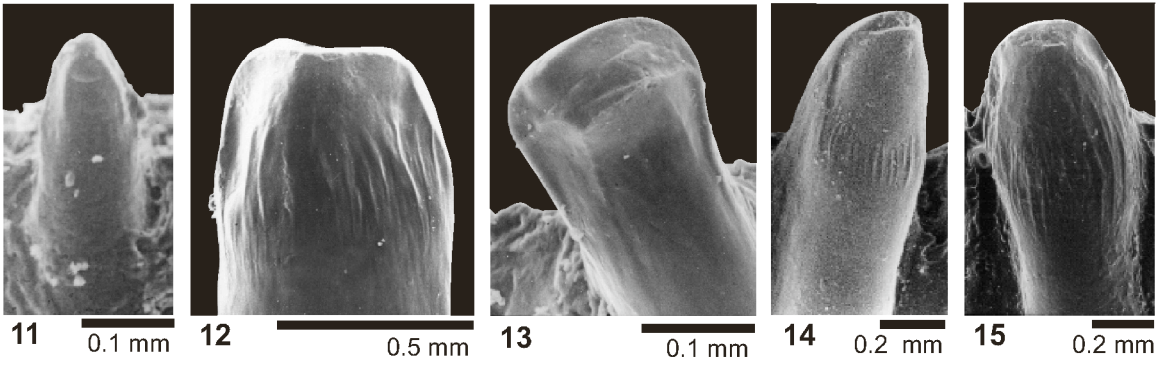
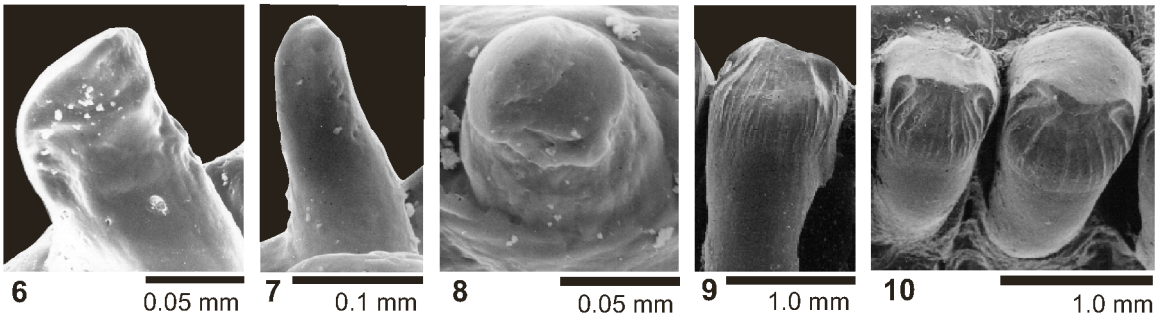
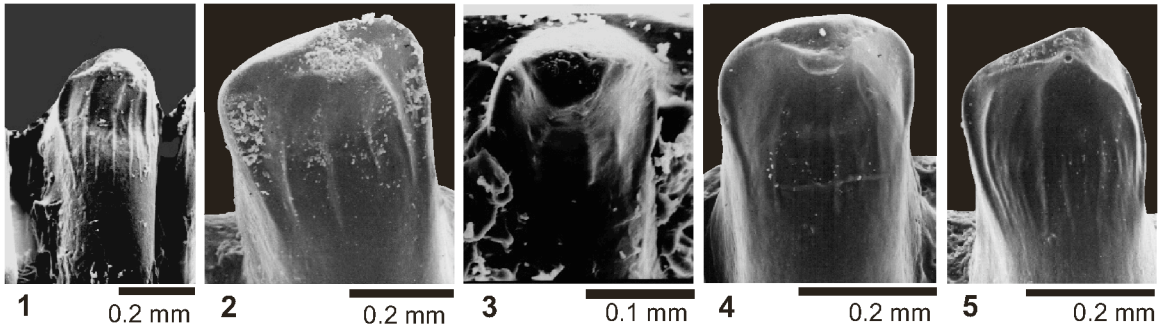


Plate XI

Recent Teiidae (continued):

- Fig. 1: *Ameiva exsul* (COPE, 1862); (specimen USNM 314244)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 2: *Ameiva festiva* (LICHTENSTEIN, 1856); (specimen USNM 313854)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 3: *Ameiva fuscata* GARMAN, 1887; (specimen USNM 158908)
crushing tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 4: *Ameiva griseivittata* BARBOUR, 1916; (specimen USNM 218353)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Figs. 5-6: *Ameiva plei* (DUMÉRIL & BIBRON, 1839); (specimen USNM 236394)
5: crushing tooth with tricuspid replacement tooth from the posterior portion of the tooth row; right mandible; lingual view
6: tooth crown of posterior crushing tooth; right mandible; lingual view
- Fig. 7: *Ameiva plei* (DUMÉRIL & BIBRON, 1839); (specimen SDS 63976)
crushing tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 8: *Ameiva plei* (DUMÉRIL & BIBRON, 1839); (specimen USNM 236379); juvenile specimen
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 9: *Ameiva pluvianotata* GARMAN, 1887; (specimen SDS 64014)
tooth from the central portion of the tooth row; right mandible; anterolingual view
- Fig. 10: *Ameiva p. pluvianotata* GARMAN, 1887; (specimen SDS 64011)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 11: *Ameiva quadrilineata* (HALLOWELL, 1861); (specimen SDS 46993A)
teeth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 12: *Ameiva taeniura* COPE, 1862; (specimen USNM 55053)
teeth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 13: *Ameiva wetmorei* STEJNEGER, 1913; (specimen SDS 67839)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 14: *Callopiastes flavipunctatus* (DUMÉRIL & BIBRON, 1839); (specimen BMNH 1900.2.26.11)
tooth crown from the central portion of the tooth row; right mandible; lingual view
- Fig. 15: *Callopiastes maculatus* GRAVENHORST, 1838; (specimen ZFMK 7858)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 16: *Cnemidophorus exsanguis* LOWE, 1956; (specimen SDS 64562)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 17: *Cnemidophorus hyperythrus beldingi* (STEJNEGER, 1894); (specimen SDS 64563)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 18: *Cnemidophorus lemniscatus* (LINNAEUS, 1758); (specimen USNM 313933)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 19: *Cnemidophorus murinus* (LAURENTI, 1768); (specimen BMNH 91.11.4.-16.)
enamel striations on the lingual surface of a tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 20: *Cnemidophorus sackii* WIEGMANN, 1834; (specimen USNM 165690)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 21: *Cnemidophorus sexlineatus* (LINNAEUS, 1766); (specimen USNM 220273)
tooth from the posterior portion of the tooth row; left mandible; lingual view
- Fig. 22: *Cnemidophorus sonorae* LOWE & WRIGHT, 1964; (specimen SDS 64564)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 23: *Cnemidophorus tessellatus* (SAY, 1823); (specimen USNM 220276)
tooth from the posterior portion of the tooth row; right mandible; lingual view

Plate XI

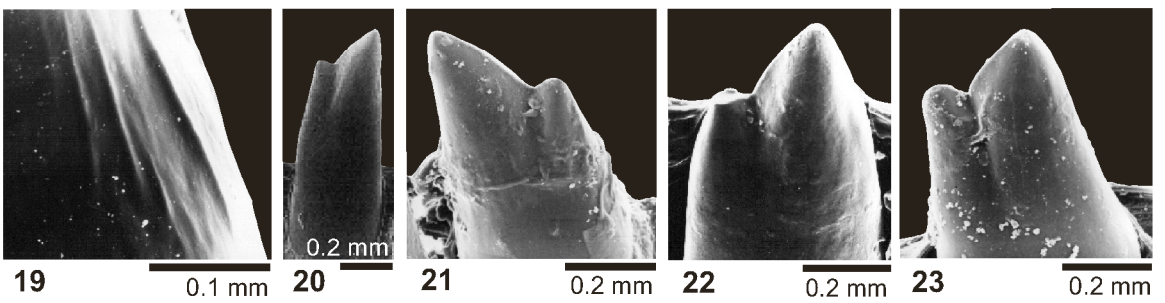
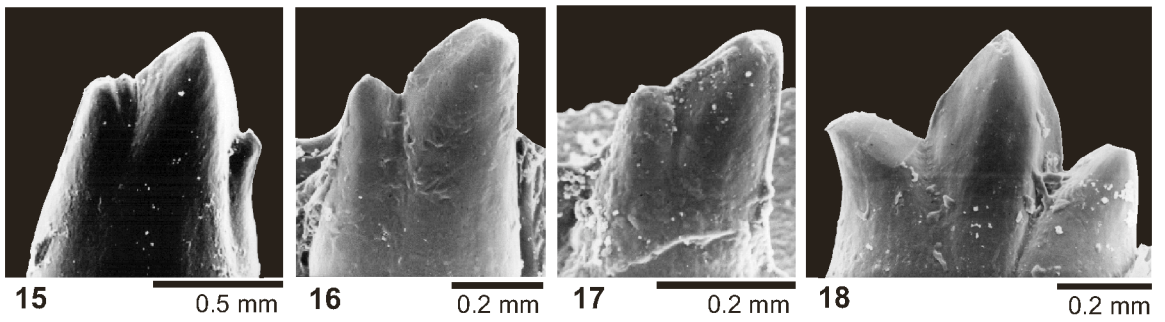
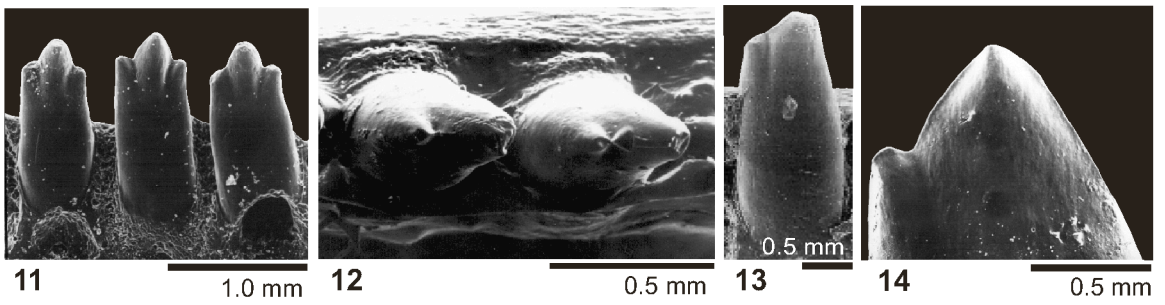
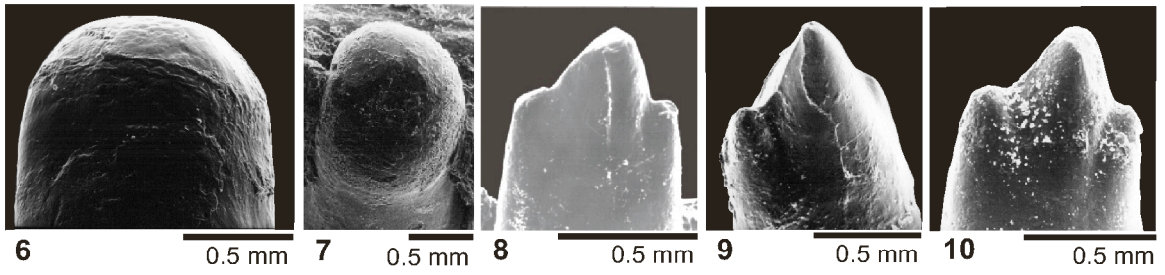
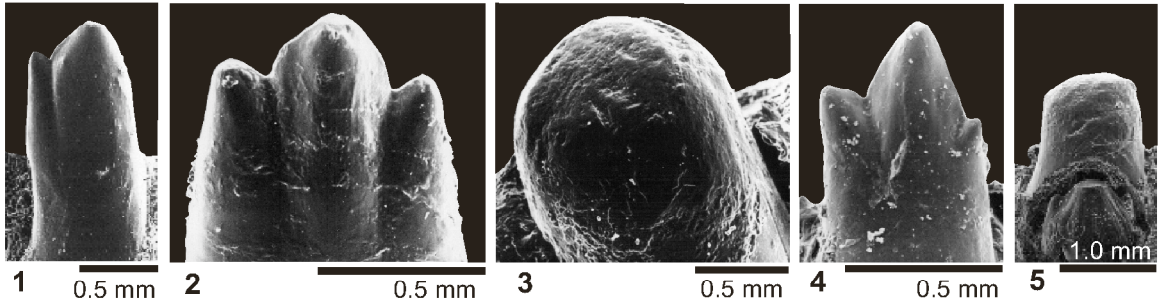


Plate XII

Recent Teiidae (continued):

- Fig. 1: *Cnemidophorus tigris* BAIRD & GIRARD, 1852; (specimen SDS 63129)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 2: *Cnemidophorus uniparens* WRIGHT & LOWE, 1965; (Priv. Coll. EVANS; non cataloged specimen)
tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 3: *Cnemidophorus vanzoi* (BASKIN & WILLIAMS, 1966); (specimen SDS 65759)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 4: *Crocodylus lacertinus* (DAUDIN, 1802); (specimen BMNH 1970.446-497)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 5: *Dicrodon guttulatum* DUMÉRIL & BIBRON, 1839; (specimen BMNH 1932.9.7.-8)
tooth from the anterior portion of the tooth row; right mandible; lingual view
- Fig. 6: *Dicrodon guttulatum* DUMÉRIL & BIBRON, 1839; (specimen SDS 30842)
tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Figs. 7-8: *Dicrodon guttulatum* DUMÉRIL & BIBRON, 1839; (specimen BMNH 1932.9.7.-8)
7: tooth crown from the posterior portion of the tooth row; right mandible; lingual view
8: enamel striations at the surface of labial side cusp (posterior tooth); right mandible; lingual view
- Figs. 9-10: *Dracaena guianensis* (LACÉPÈDE, 1788); (specimen USNM 71729)
9: enamel surface of posterior crushing tooth; right mandible; lingual view
10: enamel surface of posterior crushing tooth; right mandible; occlusal view
- Figs. 11-13: *Kentropyx calcarata* (SPIX, 1825); (specimen BMNH 1902.5.29.91)
11: tooth from the posterior portion of the tooth row; right mandible; lingual view
12: tooth crown from the anterior portion of the tooth row; right mandible; lingual view
13: tooth crown from the posterior portion of the tooth row; right mandible; lingual view
- Figs. 14-15: *Teius teyou* (DAUDIN, 1802); (specimen BMNH III.27a)
14: tooth from the posterior portion of the tooth row; right mandible; lingual view
15: tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 16: *Teius teyou* (DAUDIN, 1802); (specimen BMNH 1910.12.16.4.-12.)
tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Figs. 17-18: *Teius teyou* (DAUDIN, 1802); (specimen IFSZ 25471); this specimen probably belongs to *Tupinambis* sp.
17: tooth from the anterior portion of the tooth row; right mandible; lingual view
18: crushing tooth from the posterior portion of the tooth row; right mandible; lingual view

Plate XII

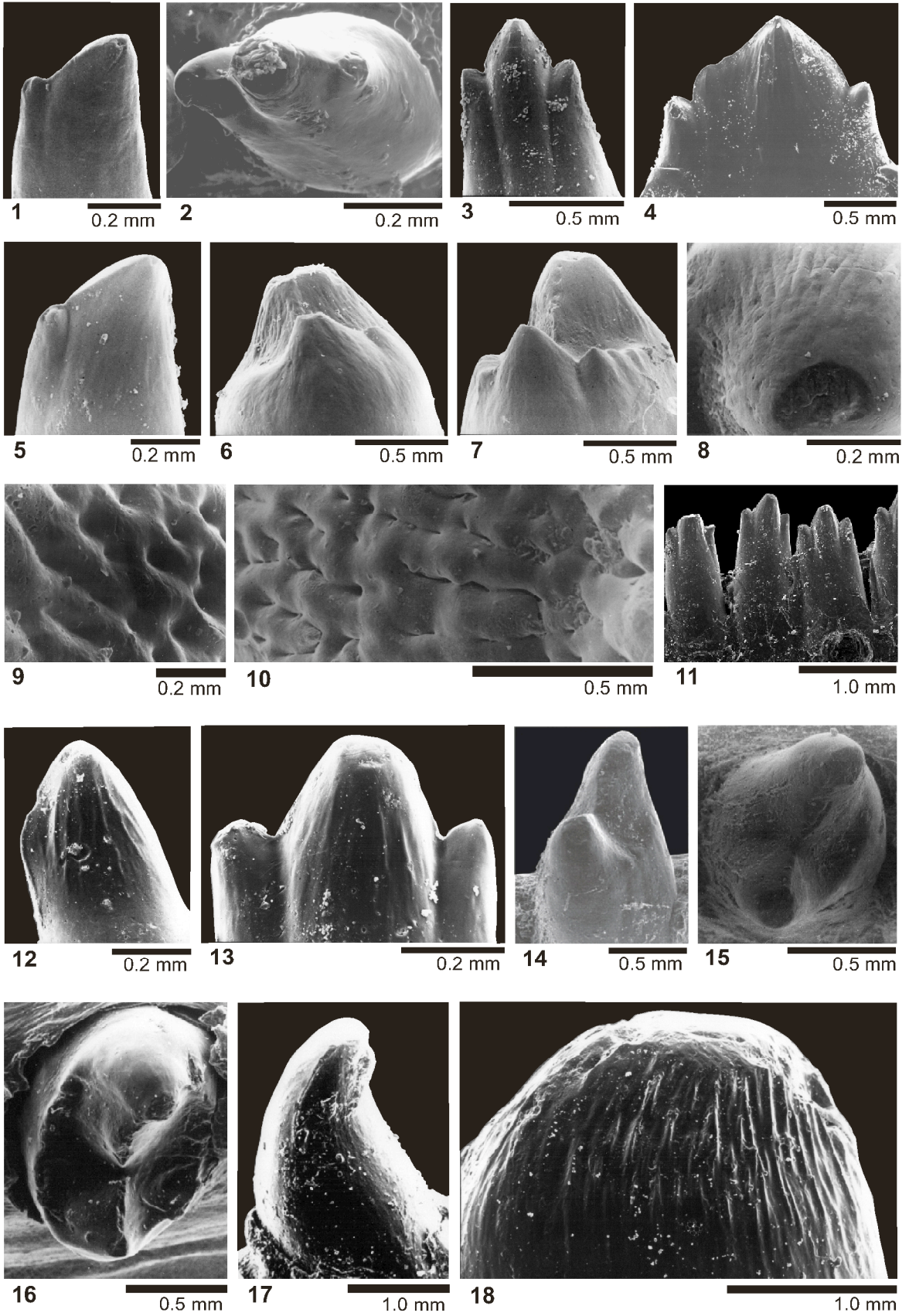


Plate XIII

Recent Teiidae (continued):

- Fig. 1: *Tupinambis merianae* (DUMÉRIL & BIBRON, 1839); (specimen IFSZ 19073)
crushing tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 2: *Tupinambis merianae* (DUMÉRIL & BIBRON, 1839); (specimen ZFMK 53532)
tooth (with minute mesial side cusp) from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 3: *Tupinambis merianae* (DUMÉRIL & BIBRON, 1839); (specimen ZFMK 21638)
tooth crown of posterior crushing tooth with minute mesial side cusp; right mandible; lingual view
- Fig. 4: *Tupinambis merianae* (DUMÉRIL & BIBRON, 1839); (specimen IFSZ 19073)
tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 5: *Tupinambis* sp.; (specimen IFSZ 35588)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 6: *Tupinambis* sp.; (specimen IFSZ 35588)
tooth from the posterior portion of the tooth row; right mandible; occlusal view
- Fig. 7: *Tupinambis teguixin* (LINNAEUS, 1758); (specimen SDS 64932)
tooth from the posterior portion of the tooth row; right mandible; lingual view

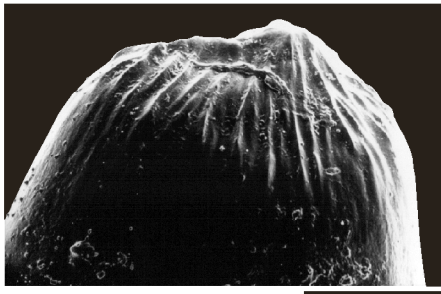
Gymnophthalminae:

- Fig. 8: *Neusticurus epleopus* COPE, 1876; (specimen SDS 46994)
tooth crown from the anterior portion of the tooth row; right mandible; lingual view
- Figs. 9-10: *Pholidobolus montium* (PETERS, 1863); (specimen BMNH 1986-278-286)
9: tooth crown from the central portion of the tooth row; right mandible; lingual view
10: tooth crown from the posterior portion of the tooth row; right mandible; lingual view

Recent Xantusiidae:

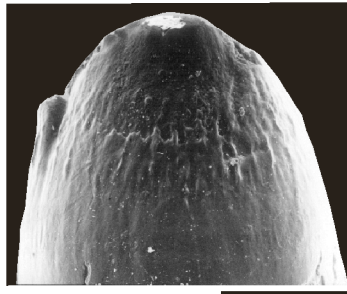
- Fig. 11: *Cricosaura typica* GRUNDLACH & PETERS, 1863; (specimen ZFMK 54260)
tooth from the central portion of the tooth row; right mandible; lingual view
- Fig. 12: *Xantusia henschawi* STEJNEGER, 1893; (specimen SDS 65397)
tooth from the central portion of the tooth row; right mandible; occlusal view
- Figs. 13-14: *Xantusia riversiana* (COPE, 1884); (specimen USNM 220288)
13: tooth crown from the central portion of the tooth row; right mandible; lingual view
14: tooth from the central portion of the tooth row; right mandible; occlusal view
- Fig. 15: *Xantusia* v. *vigilis* BAIRD, 1859; (specimen SDS 63158)
tooth from the posterior portion of the tooth row; right mandible; lingual view
- Fig. 16: *Xantusia* v. *vigilis* BAIRD, 1859; (Priv. Coll. EVANS; non cataloged specimen)
tooth from the central portion of the tooth row; right mandible; occlusal view

Plate XIII



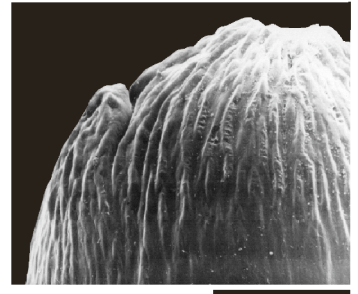
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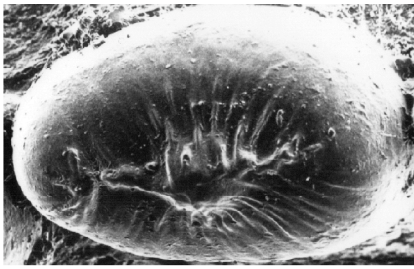
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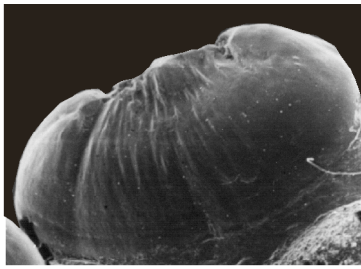
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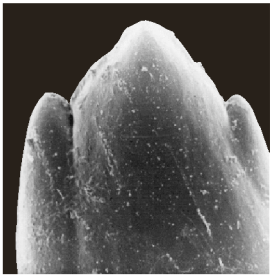
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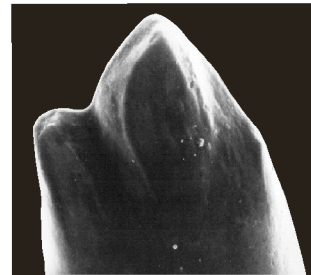
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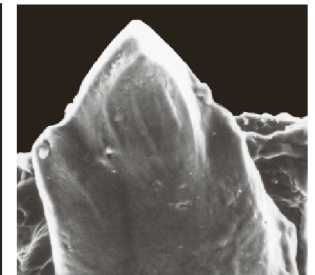
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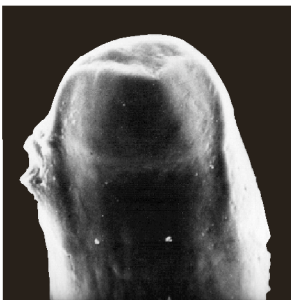
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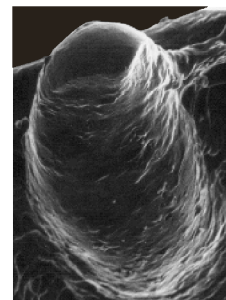
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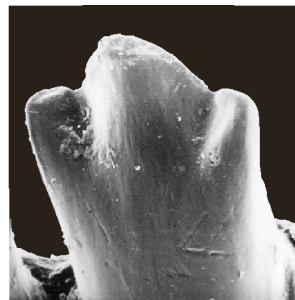
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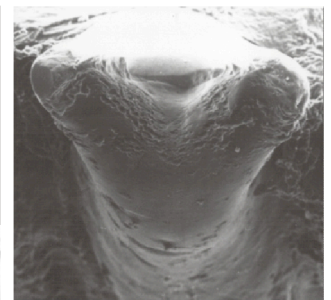
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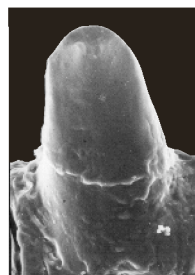
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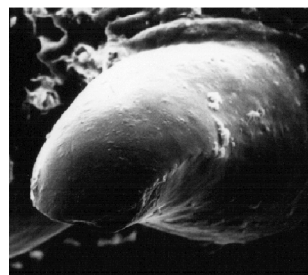
14

0.2 mm



15

0.1 mm



16

0.1 mm

Plate XIV

Upper Jurassic Paramacellodidae from the Guimarota mine:

- Fig. 1: *Becklesius hoffstetteri* (SEIFFERT, 1973); (specimen Gui. Squ. 70)
tooth crown (with characteristic pattern of striations) from the central portion of the tooth row; fragment of a right dentary; lingual view
- Fig. 2: *Becklesius hoffstetteri* (SEIFFERT, 1973); (specimen Gui. Squ. 171)
three teeth (with complex tooth crown morphologies) from the posterior portion of the tooth row; fragment of a left dentary; lingual view
Comment: The mesially expanded tooth crowns of this specimen resemble similar tooth crowns found in recent *Egernia* species (Scincidae).
- Fig. 3: *Becklesius hoffstetteri* (SEIFFERT, 1973); (specimen Gui. Squ. 208)
tooth crown (with characteristic pattern of striations) from the posterior portion of the tooth row; badly preserved left dentary; lingual view
- Fig. 4: *Becklesius hoffstetteri* (SEIFFERT, 1973); (specimen Gui. Squ. 717)
tooth crown of an isolated tooth with pronounced culmen lateris anterior; fragmentary left dentary; anterolingual view
- Fig. 5: *Becklesius hoffstetteri* (SEIFFERT, 1973); (specimen Gui. Squ. 782)
central portion of the tooth row; complete right dentary; lingual view
- Fig. 6: *Becklesius hoffstetteri* (SEIFFERT, 1973); (specimen Gui. Squ. 794)
tooth crown from the posterior portion of the tooth row; almost complete left dentary with narrow spaced teeth; lingual view
- Fig. 7: *Becklesius* sp.; (specimen Gui. Squ. 698)
isolated tooth with pronounced lingual ornamentation of the apex; right dentary; the angulus mesialis and the angulus distalis are sinus-shaped in this individual; lingual view
- Fig. 8: *Becklesius* sp.; (specimen Gui. Squ. 709)
tooth crown (with pronounced lingual ornamentation) from the posterior portion of the tooth row; right dentary; like in specimen Gui. Squ. 698, the angulus mesialis and the angulus distalis are sinus-shaped in this individual; lingual view
- Fig. 9: *Paramacellodus oweni* HOFFSTETTER, 1967; (specimen Gui. Squ. 699)
three teeth from the central portion of a fragmentary right dentary; lingual view
- Fig. 10: *Paramacellodus oweni* HOFFSTETTER, 1967; (specimen Gui. Squ. 163)
section of a complete left dentary (24 tooth positions) with two slender teeth from the central portion of the tooth row; the characteristic pattern of striations is developed on the lingual surfaces of the apices; lingual view
- Fig. 11: *Paramacellodus oweni* HOFFSTETTER, 1967; (specimen Gui. Squ. 54)
tooth crown of a posterior tooth with lingual striations; almost complete left dentary (symphysic region lost) with cylindrical, narrow spaced teeth, and tooth size reduction in posterior direction; lingual view
- Fig. 12: specimen Gui. Squ. 781
Isolated?paramacellodid teeth with extremely pointed apices showing distinct striations; ?conspecific with specimen Gui. Squ. 801 (see below); lingual view
- Fig. 13: specimen Gui. Squ. 801
isolated?paramacellodid teeth with extremely pointed apices showing distinct striations; ?conspecific with specimen Gui. Squ. 781 (see above); lingual view
- ### Upper Jurassic ?Scincidae from the Guimarota mine:
- Fig. 14: *Chalcidosaurus guimarotensis* gen. et sp. nov.; (specimen Gui. Squ. 212)
two preserved teeth from the central portion of the tooth row showing unwrinkled enamel surfaces; right dentary; lingual view
- Fig. 15: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 139)
sympysic region of a complete right dentary (14 tooth positions) representing an individual with robust and relatively long teeth which lack basal expansions; lingual view
- Fig. 16: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 204)
sympysic region of a fragmentary right dentary representing an individual with robust and relatively short teeth; replacement tooth present at the basis of the tooth occupying tooth position 6; lingual view

Plate XIV

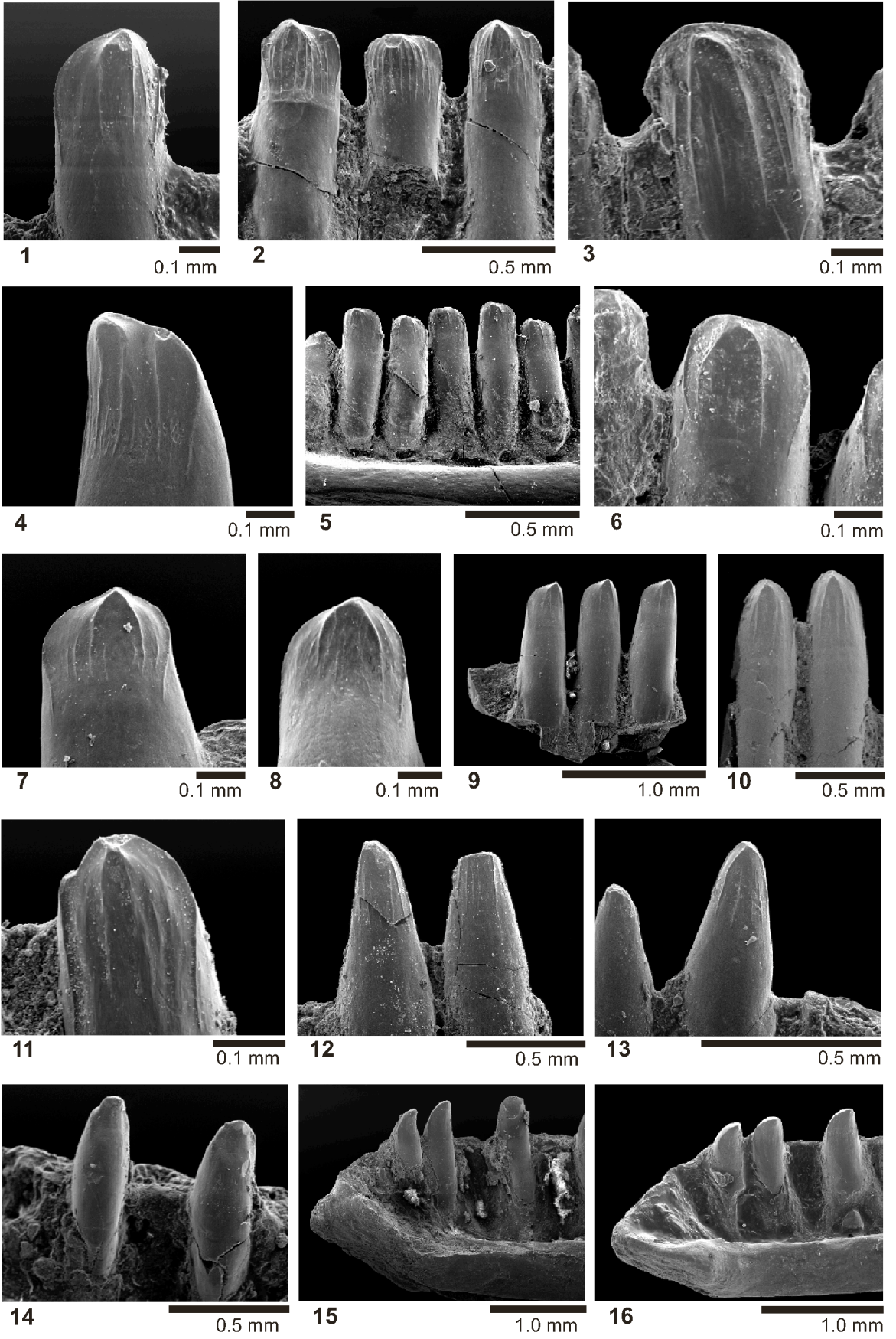


Plate XV

Upper Jurassic ?Scincidae from the Guimarota mine (continued):

- Fig. 1: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 234)
anterior tooth, showing faint lingual striae; fragment of a right dentary; lingual view
- Fig. 2: *Saurillodon* sp.; (specimen Gui. Squ. 231 (neonate))
anterior tooth, showing pronounced lingual striae; complete right dentary (16 tooth positions); lingual view
Comment: The anterior teeth of the two *Saurillodon* specimens illustrated in Fig. 1 and Fig. 2 represent two different patterns of striations which evolved within the genus *Saurillodon*.
- Fig. 3: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 31)
strongly recurved and mesially flattened teeth from the central portion of the tooth row; complete left dentary (14 tooth positions); lingual view
- Fig. 4: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 122)
tooth positions 7 and 8 with pronounced culmines lateres; teeth are slightly stout and show expanded bases; complete right dentary (14 tooth positions); lingual view
- Fig. 5: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 179)
distinctly rounded posterior teeth; complete right dentary (16 tooth positions); lingual view
- Fig. 6: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 277)
short rounded teeth with smooth enamel surfaces from the posterior portion of the tooth row; almost complete left dentary (21 tooth positions); lingual view
Comment: The abraded teeth probably indicate a specimen of high individual age.
- Fig. 7: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 36)
anterior teeth with prominent culmines lateres and slightly pronounced carina intercuspidalis; complete right dentary (16 tooth positions); lingual view
- Fig. 8: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 36)
posterior tooth and stump of a broken tooth making visible the large lumen; complete right dentary (16 tooth positions); lingual view
- Fig. 9: *Saurillodon henkeli* (SEIFFERT, 1973); (specimen Gui. Squ. 793)
posterior portion of a fragmentary right dentary, showing an abrupt reduction in tooth size; lingual view

Caenozoic Scincomorpha from the Bavarian Freshwater Molasse:

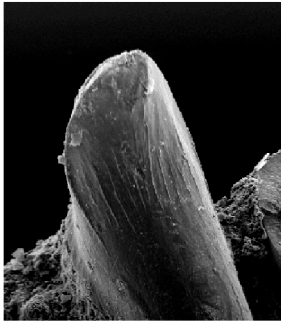
Caenozoic Cordylidae:

- Figs. 10-13: *Bavaricordylus ornatus* gen. et sp. nov. (specimen M 16; Holotype) from the Lower Miocene (lower MN4) fissure filling Petersbuch 2, South Germany
10: fragment of a left dentary with 3 preserved teeth representing the central portion of the tooth row; lingual view
11: isolated tooth crown with pronounced lingual striations and a prominent culmen lateris anterior; lingual view
12: isolated tooth crown with complex lingual striations; lingual view
13: isolated tooth crown with complex lingual striations; lingual view
Comment: The number and arrangement of the striae vary within the tooth row of a single individual.

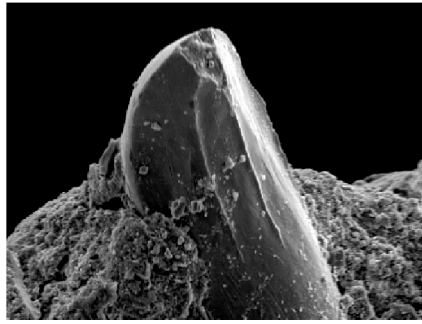
Caenozoic ?Scincidae:

- Figs. 14-15: *Bavariascincus mabuyiformis* gen. et sp. nov. (specimen M 15b; Holotype) from the Lower Miocene (lower MN4) fissure filling Petersbuch, South Germany
14: central portion of the almost complete right dentary (the tip of the dentary is lost), presenting slender teeth with striae on the lingual surfaces of the apices; lingual view
15: tooth crown with distinct striations, wide antrum intercristatum, and pronounced culmines lateres; lingual view

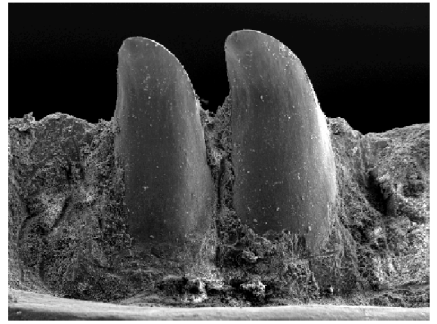
Plate XV



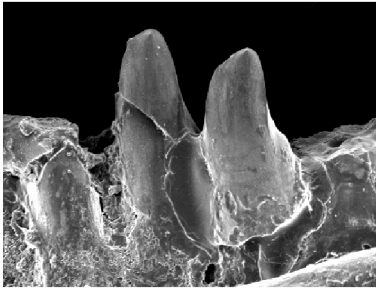
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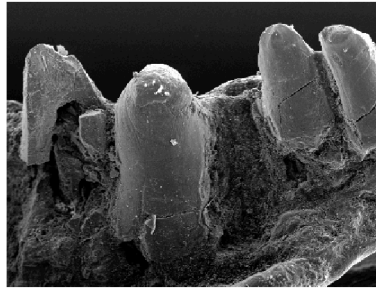
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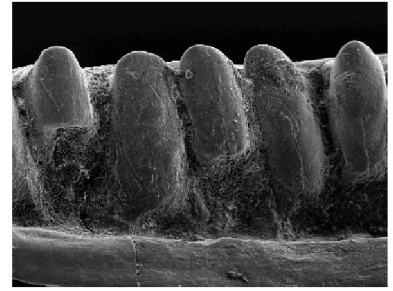
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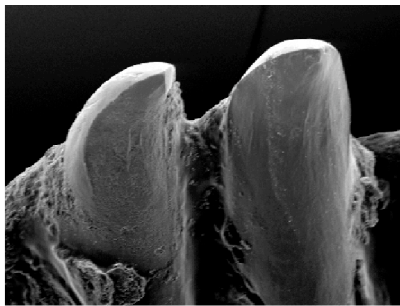
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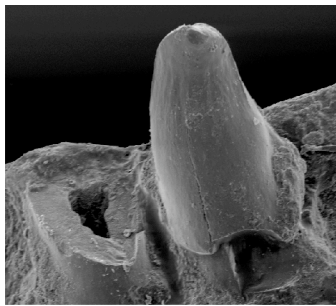
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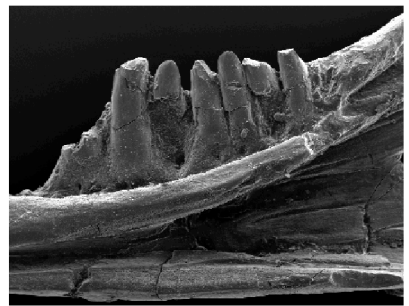
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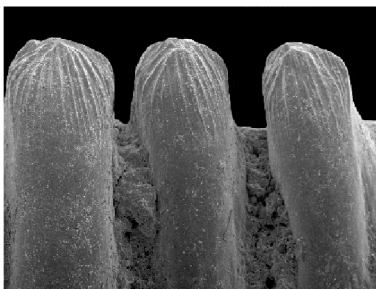
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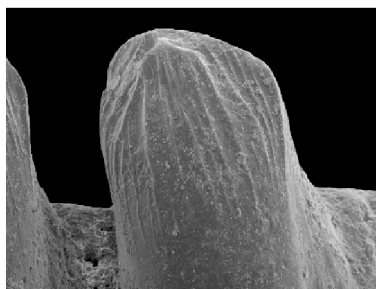
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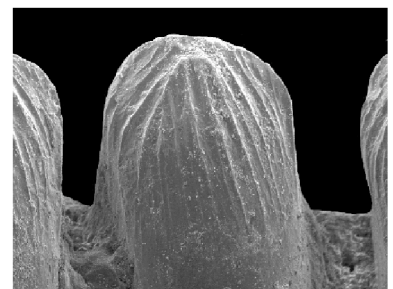
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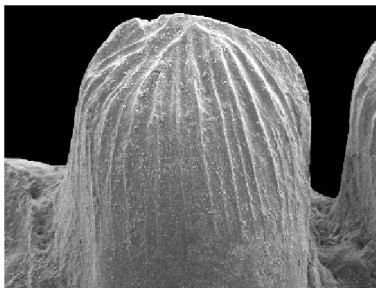
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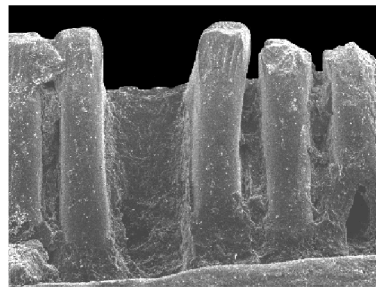
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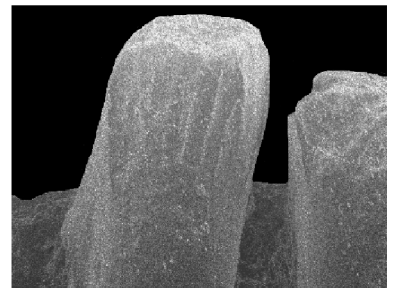
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0.5 mm



1.0 mm



0.2 mm

Plate XVI

Caenozoic ?Scincidae (continued):

- Fig. 1: *Bavariascincus mabuyaformis* gen. et sp. nov. (specimen M 17; Paratype) from the Lower Miocene (upper MN4) floodplain deposits/ paleosoil of Rembach in Bavaria, Germany.
M 17 is a fragment of the anterior portion of a right dentary with 6 preserved teeth; the tooth crowns show pronounced striae and long culmines lateres

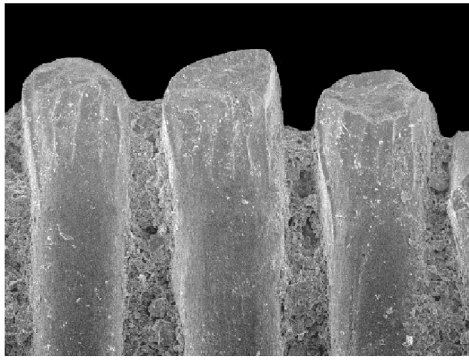
Caenozoic Lacertidae:

- Fig. 2: lacertid tooth from the central portion of a left dentary; (specimen M 9b) from the excavation site Gallenbach 2b (lower MN6; floodplain deposits and paleosoils)
- the tooth tip is divided into a cuspis labialis and a cuspis lingualis, and an additional side cusp is found anteriorly; the tooth crown morphology of this specimen strongly resembles the tooth crown morphologies of the Mesozoic Paramacellodidae; lingual view
- Fig. 3: lacertid tooth from the central portion of a left dentary; (specimen M 9a) from the excavation site Gallenbach 2b (lower MN6; floodplain deposits and paleosoils)
- the lingual surface of this bicuspid tooth crown is heavily striated (approximately 12 parallel striae); lingual view
- Fig. 4: lacertid tooth from the posterior portion of a left dentary; (specimen M 13c) from the excavation site Merkur Nord (lower MN3; palustric)
- the striations are separated into two striae dominantes and several subordinate striae; lingual surfaces of two bicuspid tooth crowns; lingual view
- Fig. 5: lacertid tooth from the central portion of a left dentary; (specimen M 4b) from the excavation site Schönenberg (Bayrisch Schwaben) (lower MN5; fluvial channel filling)
- in this individual the lingual surface of the tooth crowns are heavily striated with wide spaced and apically converging striae; lingual view
- Fig. 6: lacertid tooth from the posterior portion of a right dentary; (specimen M 12d) from the excavation site Walda 1 (middle MN5; fluvial channel filling)
- the lingual surface of this tooth crown is heavily striated with numerous parallel striae; striae dominantes are not developed; lingual view
- Fig. 7: lacertid tooth from the posterior portion of a left dentary; (specimen M 1a) from the excavation site Möhren 12 (MP21; fissure filling)
- the dental morphology of this individual strongly resembles the tooth crown morphology found in the recent lacertid genus *Timon*; lingual view

Caenozoic Anguimorpha:

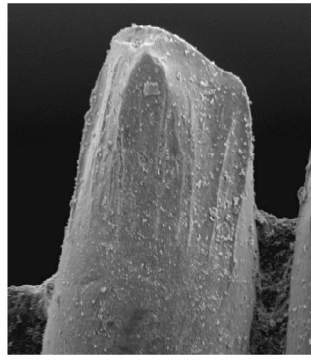
- Fig. 8: durophagous anguimorphan teeth (? *Ophisaurus* sp.) (specimen M8a) from the posterior portion of a right dentary; excavation site Unterempfenbach 1b (middle MN5; floodplain deposits, paleosoils)
- the enlarged posterior tooth represents a tooth crown morphology that is convergent to the recent scincid *Tiliqua scincoides*, which is highly adapted to a molluscivorous diet; lingual view
- Fig. 9: anguimorphan tooth (? *Ophisaurus* sp.) (specimen M8a) from the central portion of a right dentary; excavation site Unterempfenbach 1b (middle MN5; floodplain deposits, paleosoils)
- this occlusally flattened tooth represents a tooth crown morphology that is convergent to the recent teiid *Tupinambis merianae*, in which a comparable crushing dentition was found; even the small central uplift of the apex is present in the teeth of *T. merianae*; lingual view

Plate XVI



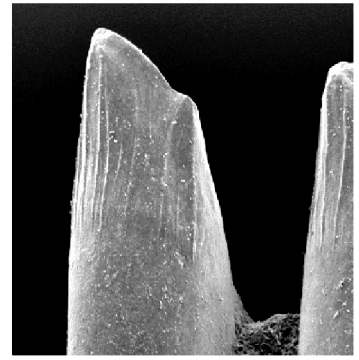
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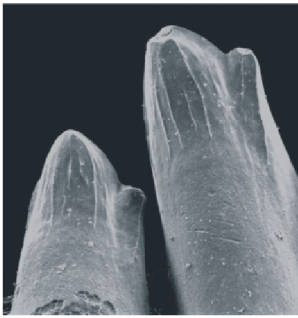
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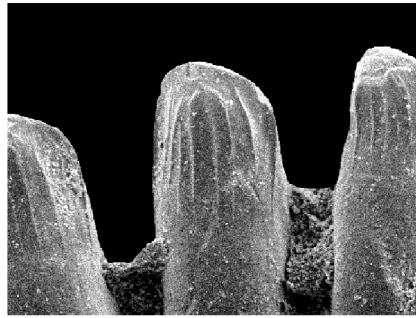
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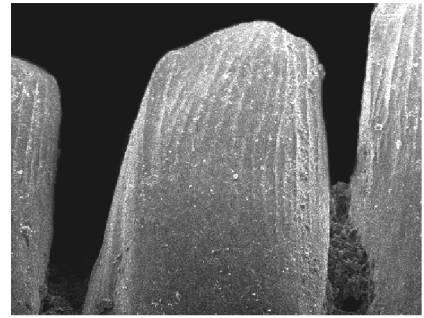
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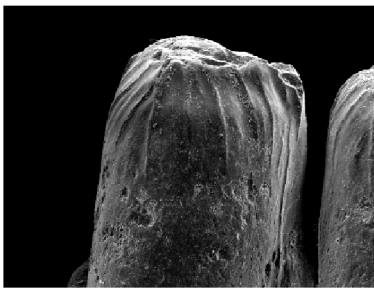
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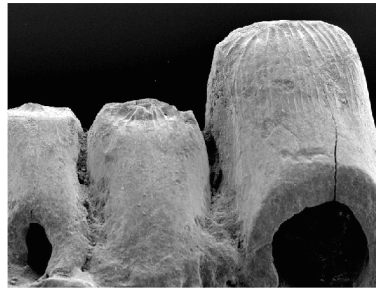
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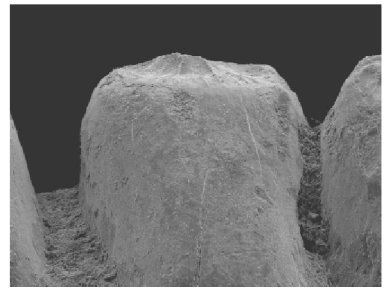
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9

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Lebenslauf

(curriculum vitae)

Ralf Kosma

Diplom-Geologe

Persönliche Angaben

Geburtsdatum: 30.06.1970
Geburtsort: Braunschweig
Staatsangehörigkeit: deutsch
Familienstand: verheiratet, zwei Kinder

Schulbildung

1977-1981 Grundschole Comeniusstraße, Braunschweig
1981-1983 Orientierungsstufe Georg-Eckert-Straße, Braunschweig
1983-1990 Gymnasium Neue Oberschule, Braunschweig
Abschluss: Allg. Hochschulreife (Abitur)

Wehr- und Ersatzdienst

1990-1992 Zivildienst (MSH)

Studium

1992-1999 Studiengang Geologie / Paläontologie
Technische Universität Carolo Wilhelmina, Braunschweig
04/1995 Vordiplom (Nebenfach Zoologie)
10/1999 Diplom bei Prof. Dr. P. Carls, TU Braunschweig
Diplom-Kartierung: „Die paläozoischen Schichten südlich von Wernigerode“
Diplom-Arbeit: „Die Sphenodontiden aus dem Kimmeridgium Norddeutschlands“
ab 11/1999 Tätigkeit als wissenschaftlicher Mitarbeiter am Projekt „Squamatenbezahnungen“ am Institut für Geologie und Paläontologie der Universität Hannover, zeitgleich Beginn der Vorarbeiten für die Promotion bei Prof. Dr. D. Thies an europäischen und US-amerikanischen Museen.

Praktika

09-10/1995 Geophysikalisches Praktikum, Tönder, Dänemark
07/1997 Mikropaläontologisches Laborpraktikum, Geomar, Kiel
ab 11/1999 Naturwissenschaftliches Zeichnen und Illustrieren, Niedersächsisches Landesmuseum Hannover

Große Exkursionen

07/1994 Südwestdeutschland
07/1995 Irland
07/1996 Aragon, Spanien

Mitgliedschaften

Deutsche Gesellschaft für Herpetologie und Terrarienkunde, Paläontologische Gesellschaft