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The squamation of the Eocene stem-basilisk *Geiseltaliellus maarius* (Squamata: Iguanidae: Corytophaninae) from Messel, Germany

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Abstract. An exceptional new specimen of the stem-basilisk *Geiseltaliellus maarius* from the middle Eocene of Messel, Germany, preserves details of the squamation of this extinct species. The dorsum and extremities were covered by small, rhomoidal scales, about 0.2 mm in size in most places; somewhat larger scales were present on the lower extremities and on the head. Scales of the venter were arranged in transverse rows, unlike in extant *Polychrus* and *Laemanctus*. There is some evidence that the scales on the extremities possessed keels, as in extant basilisks and *Polychrus*. Keratin appears to be preserved in places. The "Oberhäutchen" is nearly featureless, probably the result of postmortem microbial decomposition; scale organs were not observed. Overall, the body of *G. maarius* possessed a fine, homogeneous squamation most similar to *Basiliscus*. Possible sexual dimorphism in the form of the parietal crest raises the prospect of a projecting median keel composed of skin in male *G. maarius*, although direct evidence on this point is currently lacking. The squamation of the tail is discussed in light of the pseudoautotomy shown by this species.

Key words. Fossils, Corytophanidae, Eocene, scales, keratin.

Introduction

Extant squamate species are most commonly recognized and diagnosed on the basis of scale patterns, with other soft tissue structures like the hemipenes playing an important role in certain clades (e.g., Klaver & Böhme 1986, Köhler 2008, Schleich et al. 1996), but this is obviously not possible for most fossil species. Isolated epidermal scales known from late Pleistocene and Holocene packrat middens (Cole & Van Devender 1976), and specimens preserved in amber (Borsuk-Białynicka et al. 1999, Daza et al. 2016, de Queiroz et al. 1998, Polcyn et al. 2002) or as other external molds (Estes 1962), are rare exceptions. Occasionally, patches of scales or scale remnants are also preserved in squamate specimens from "Konservat-Lagerstätten" such as lakebeds (Conrad et al. 2014, Edwards et al. 2011, Rieppel & Grande 2007, Smith 2009) or anoxic marine basins (e.g., Gorjanović-Kramberger 1892, Ifrim et al. 2008, Kornhuber 1893, Lindgren et al. 2011, Reynoso 1997, Reynoso 1998, Reynoso 2000, Reynoso & Callison 2000, Smith & Buchy 2008).

The Messel Pit is a UNESCO World Heritage site located near the city of Darmstadt in Germany. This "Konservat-Lagerstätte" is well known for the exceptional preservational quality of its fossils (e.g., Behnke et al. 1986, Schaal & Ziegler1988). Recent work has shown that this exceptional preservation extends also to the cellular and subcellular levels. Structural coloration in insects (McNamara et al. 2011) as well as melanosomes (Colleary et al. 2015, Vinther et al. 2008, Vinther et al. 2010, Vitek et al. 2013), osteocyte-like structures and possible collagen fibers (Cadena 2016) in vertebrates have now been reported. Thus far, almost nothing has been reported on the preservation of epidermal structures in reptiles from Messel, apart from the hand scales of *Geiseltaliellus maarius*. This species is known from a dozen specimens, and detailed study of the skeleton of this pleurodont iguanian and phylogenetic analyses have shown it to lie on the stem of the Neotropical basilisks, Corytophaninae (Smith 2009).

Here I describe the squamation of a new specimen of *G. maarius* Smith, 2009, which preserves unprecedented details in this ~48 million year-old species (Lenz et al. 2015) and extends the observation of exceptional integumentary preservation at Messel to reptiles. Relevant observations on other specimens and extant taxa help to flesh out the portrait of the fossil species and the evolution of squamation in basilisks.

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Materials and methods

Preparation was conducted at the Messel Research Station of SMF by Bruno Behr. The scale remains were studied under a binocular dissecting microscope after preparation of the initially exposed sides of the part and counterpart (SMF ME 11380a and b, respectively). The specimen, submerged in water, was photographed. The program ImageJ was used to measure the scales in close-up (low field-of-view) photographs, which themselves were calibrated in ImageJ using photographs of the whole specimen. During preparation, scales of the foot, hand, and forearm were also removed for study under the SEM (now catalogued as SMF ME 11380c–e). The part and counterpart were then embedded in epoxy resin and prepared, exposing the other side.

Modern comparative specimens: *Polychrus gutturosus* (SMF 83422), *P. liogaster* (SMF 30122), *Basiliscus galeritus* (SMF 11029), *B. basiliscus* (SMF 71635), *Corytophanes hernandesii* (SMF 11015), *C. cristatus* (SMF 24876), *C. percarinatus* (SMF 82558), *Laemanctus longipes* (SMF 11017, 11018), *L. serratus* (SMF 11016).

Abbreviations: HLMD-Me, Messel collection, Hessisches Landesmuseum, Darmstadt, Germany; SMF, Herpetology collection, Senckenberg Research Institute, Frankfurt am Main, Germany; SMF ME, Messel collection, ditto; YPM R, Yale Peabody Museum of Natural History, New Haven, Connecticut, USA.

Results

Geiseltaliellus maarius SMF ME 11380 has a snout–vent length of 9.1 cm (Smith & Wuttke 2012). It shows a clear body outline everywhere except on the left lower leg (Figs 1A, 2A), where the skin may have been disrupted and pulled downwards. Remains of scales are preserved on significant portions of the body. On the temple, neck, and thigh these are visible as splotches of dark material, possibly melanosomes (cf. Colleary et al. 2015, Vinther et al. 2008, Vinther et al. 2010) or other organic compounds (Edwards et al. 2011). On the venter, the forearm and hand, and the lower leg and foot, however, the keratinous scales appear to be preserved. These are three-dimensional and flexible.

Where preserved whole, scales usually appear as rhombi, and 'scale length' refers to one side of such a rhombus as exposed (i.e., ignoring overlap, which cannot be corrected for, where appropriate). In other places, scales appear roughly circular, and 'scale size' refers to the diameter; in none of the places where 'circular' scales are found are they represented by original keratin, so it seems likely that rhomboidal scales were present everywhere, but where the keratin has decayed this is no longer apparent.

Frontal table

Rossmann (2000) and Smith (2009) described grooves on the frontal table in what is now the holotype (Fig. 3A), which they interpreted as demarcating polygonal epidermal scales. Along the margin these scales therefore correspond to the supraorbital semicircles. With a length tangential to the orbital margin of 0.9–1.5 mm, these are the largest documented scales on the body of *G. maarius*. Their orbital margin is nearly straight, and the interscale boundaries are roughly orthogonal to the orbital tangent (Smith 2009: fig. 2).

Parietal crest

Although osseous in nature, the median crest on the parietal is potentially relevant to the squamation. In SMF ME 11380 it has a uniform height from its origin where the adductor crests meet until the posterior end of the parietal (Fig. 3B). This is also true of SMF ME 2 and 1769, but not of two other specimens of the species. In the holotype, HLMD-Me 10207, the anterior portion of the median parietal crest is expanded and sinuous (Fig. 3A; see also Smith 2009: fig. 5). The parietal of SMF ME 11304 shows an even more marked expansion in the same position, although it is not sinuous.

Sexual dimorphism is common in members of some iguanid groups like *Anolis*, *Polychrus*, and *Basiliscus* (Butler et al. 2007, Garda et al. 2012, Lang 1989b). The last taxon is notable in that the parietal blade is strongly developed in males but virtually absent in females (Lang 1989b). Thus, we have in *G. maarius* two morphotypes that differ clearly from one another, and the manner in which they differ corresponds to sexual dimorphism in a close living relative (*Basiliscus*). This suggests that varying development of the parietal crest in *G. maarius* might be a sexually dimorphic character, in which case the the specimens with an expanded parietal crest (incipient bony blade) are presumably males (HLMD-Me 10207 and SMF ME 11304) and the others females (SMF ME 2, 1769 and 11380). Conceivably the expanded parietal crest was associated with an elaboration of the skin, but there are no data bearing on the question at present. Further specimens with the head preserved in lateral profile will be necessary to test this hypothesis.

Temple

In the left supratemporal fossa there is a regular array of small (0.45 mm), dark greenish splotches that appear to be arrayed in oblique rows (Fig. 2). The splotches – interpreted as scales – are more clearly individuated on the counterpart, SMF ME 11380b, but also seen on the part (Fig. 1A). Similar splotches occur irregularly and more widely spaced on other parts of the head. Little can be said about interscale relations in this area.

Throat or shoulder

A patch of organic material immediately between the proximal end of the right arm and the posterior end of the right

mandible represents portions of the shoulder or throat squamation (Fig. 1B, 2A). Scale boundaries are not always clearly discerned on the part, but enough is preserved to show that the scales are small (0.16 mm) and apparently nearly uniform in size. Once again, individuation of scales is clearer on the counterpart, but the area clearly covered by scales is smaller. There is some suggestion of tiny scales located at the triple-junctions of the main scales. The scales are arranged in oblique rows, as previously determined for the nape of *G. maarius* SMF ME 2 (Smith 2009), but the scales are distinctly larger than reported for that specimen. Inter-scale relations cannot be determined here.

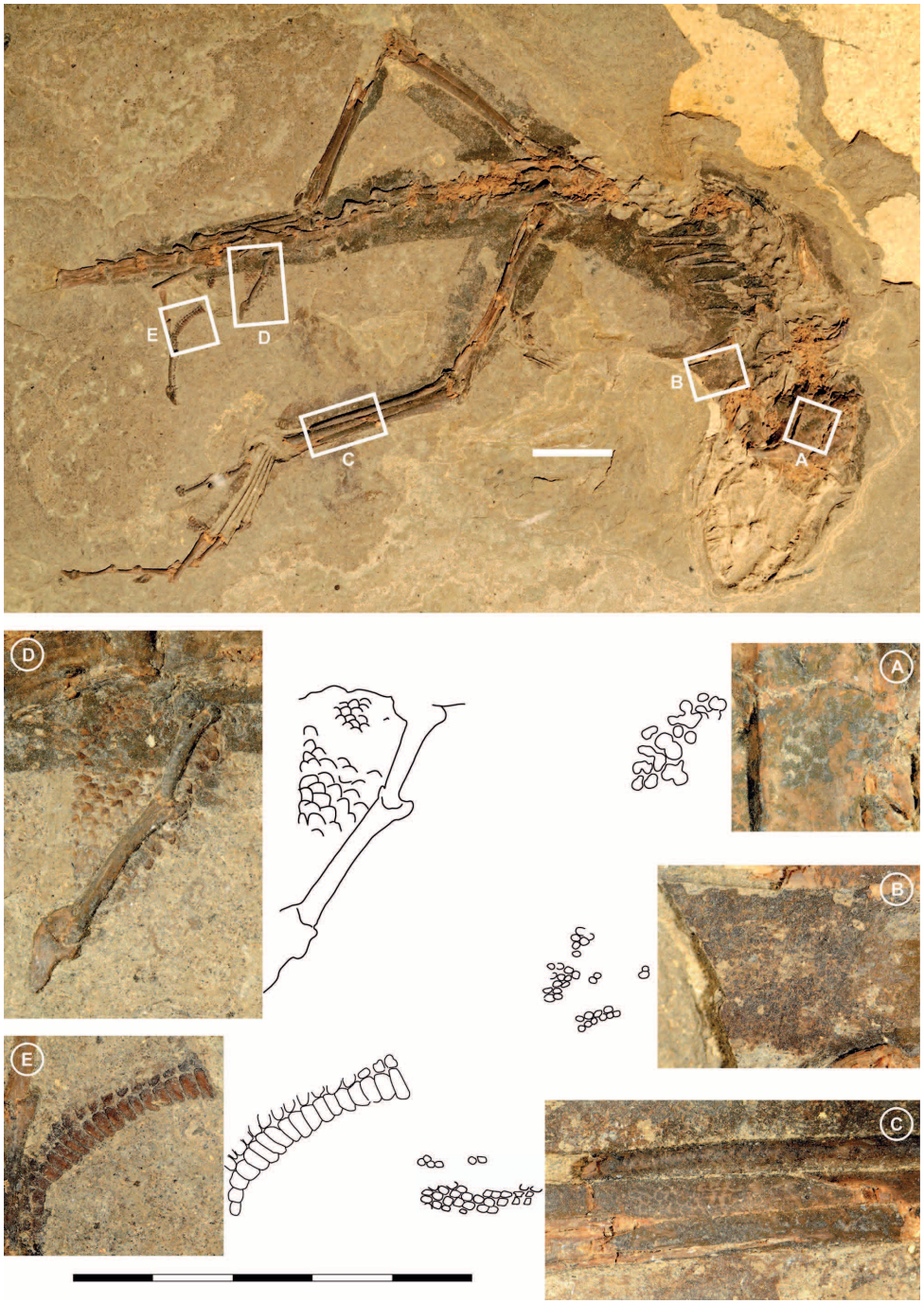


Figure 1. Skeleton with skin shadows of *Geiseltaliellus maarius*, SMF ME 11380a (part). (A) Detail of temple region of head. (B) Detail of throat or shoulder region. (C) Detail of right lower leg scales (over tibia and fibula). (D) Detail of left lower leg scales (torn downward and preserved around toe). (E) Detail of digit IV of left pes. Scale bar is 5 mm.

Venter

Scales of the venter are well preserved in the belly region on the counterpart (Fig. 2B). They appear to be nearly complete on the anteriorly on the venter. Posteriorly, in the belly region, the keratinous material forms tiny, transversely elongate structures; as in the previously described SMF ME 2 (Smith 2009) these are aligned with one another transversely and are exceedingly small. Transverse rows appear to have behaved as units during deformation; in particular, many rows appear to have been drawn backward around the distal end of the posterior-most ribs. Posterior to this point, the rows all remain parallel with one another. Smith (2009) interpreted the wide separation of these rows in SMF ME 2 as an indication that the belly of that animal may have been bloated prior to final collapse. SMF

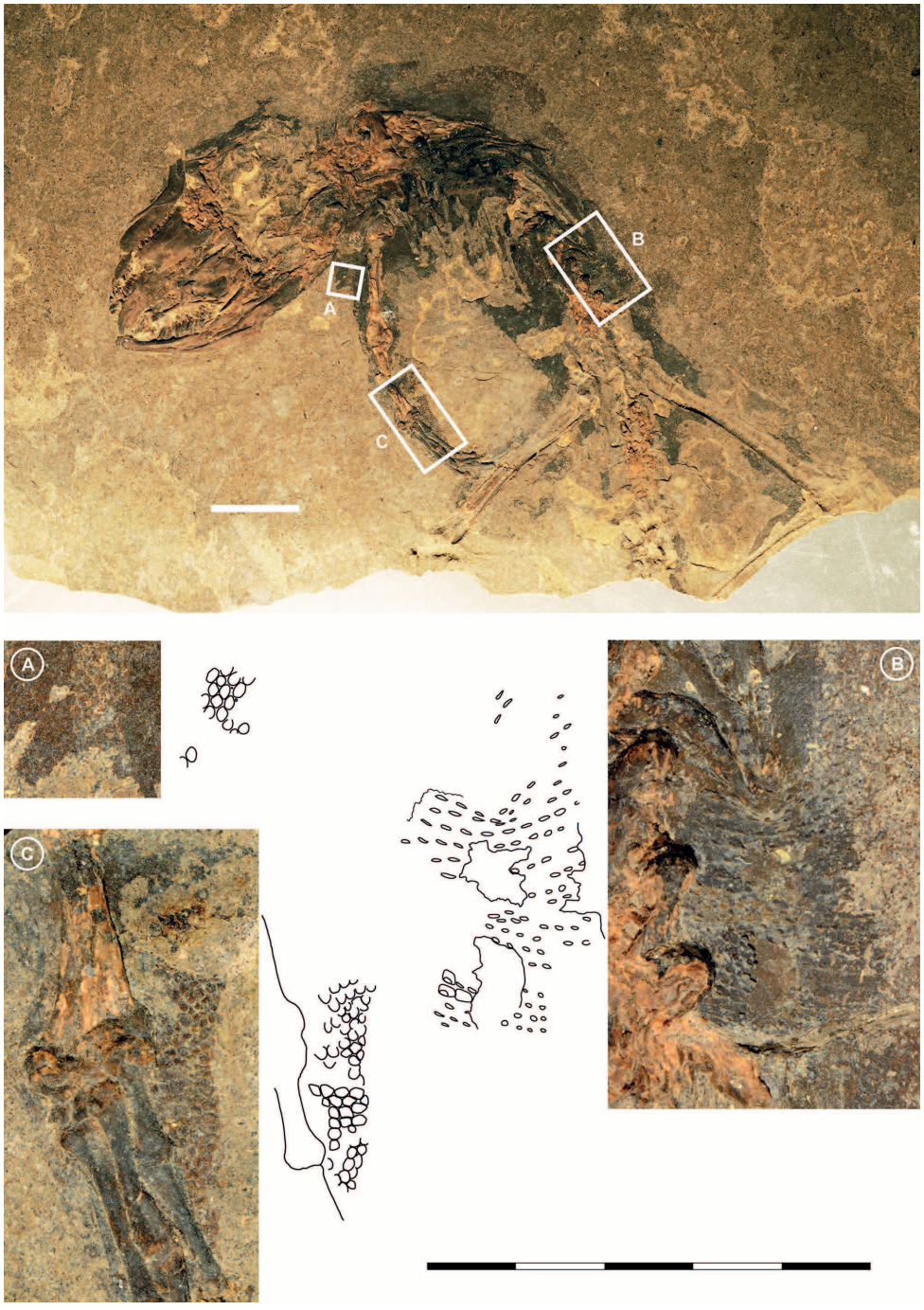


Figure 2. Skeleton with skin shadows of *Geiseltaliellus maarius*, SMF ME 11380b (counterpart). (A) Detail of throat/shoulder. (B) Detail of belly. (C) Detail of right forearm and wrist. Scale bar is 5 mm.

ME 11380 suggests a different interpretation. Near the posterior end of the belly region with preserved scales there is an area where each elongate keratinized mass is associated with the distal edge of a larger, nearly rectangular structure. It is probably that degradation of the ventral scales destroyed most of their keratin (like most scales on the body), which once were considerably larger (rectangles to lower left in Fig. 2B); only their presumably thicker distal edg-

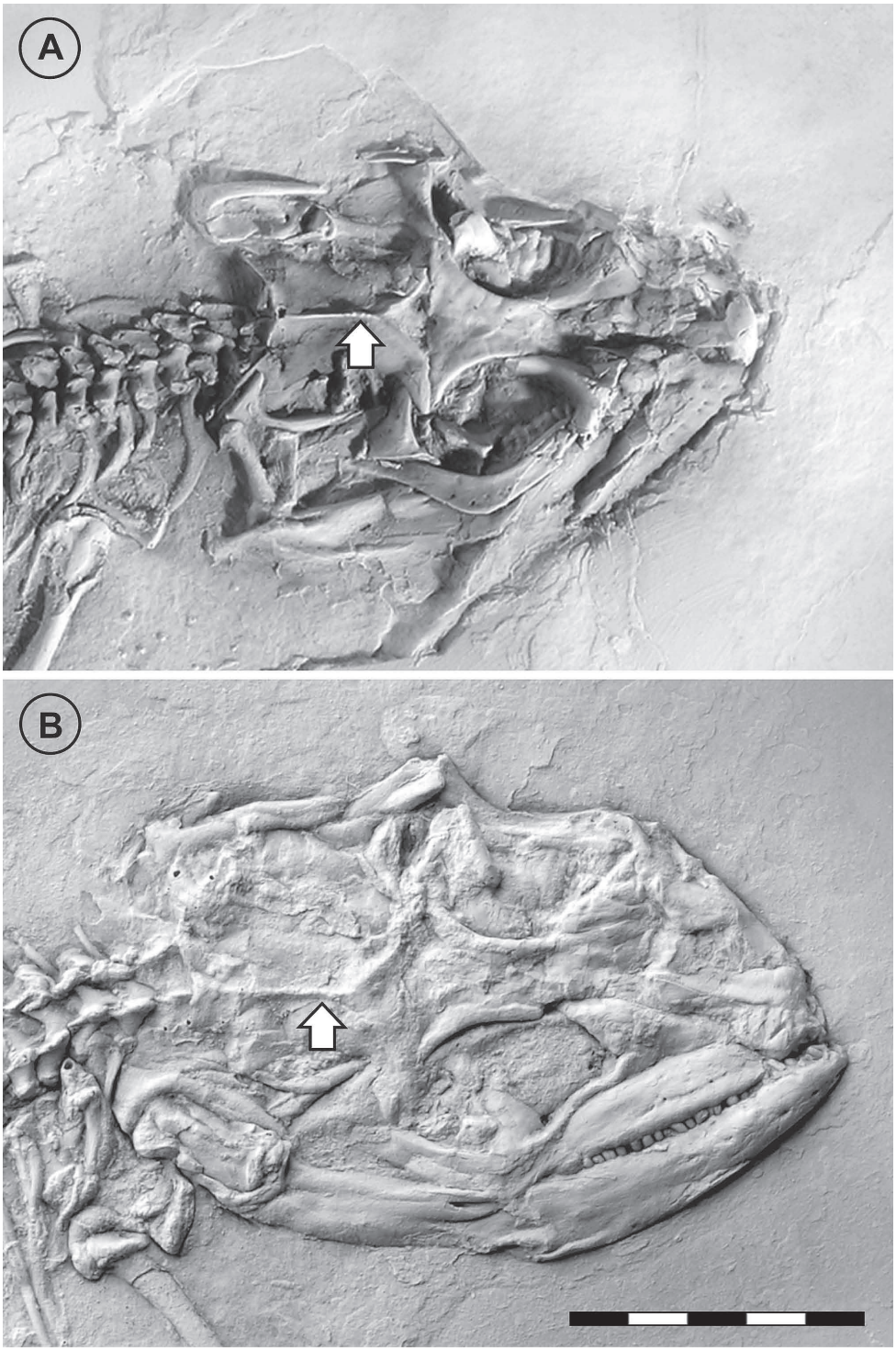


Figure 3. Two parietal morphotypes, possibly representing different sexes, compared. (A) Holotype (HLMD-Me 10207), showing expanded and sinuous anterior portion of parietal crest (arrow). Interpreted as male. (B) SMF ME 11380, lacking any such expansion (arrow). Interpreted as female. Scale bar is 5 mm.

es retain keratin. However, the relative shape and orientation – nearly rectangular and transverse, respectively – is as previously interpreted. Anteriorly on the venter the scales measure about 0.38 x 0.54 mm; posteriorly, they appear to be slightly smaller: 0.32 x 0.46 mm.

Forearm and manus

Keratinous scales are preserved on the distal right forearm and preaxial side of the right hand on the counterpart (Fig. 2C). On the distal forearm the scales are rhomboidal and overlapping, about 0.38 mm in length. They decrease in length to about 0.3 mm toward the preaxial edge of the distal forearm (Fig. 4). The scales on the wrist are around 0.28 mm in size as well, but they do not appear to overlap strongly and are irregularly polygonal in shape, rather than rhomboidal. Those on the hand are again smaller, about 0.25 mm in size, and also do not appear to overlap. These observations are consistent with Smith's (2009) observations on the manual scales of a specimen attributed to *G. maarius*, SMF ME 2684. On several of the scales, most prominently on those marked with arrows in Figure 4, there are longitudinal folds, which might indicate the presence of keels on these scales.

The subdigital scales, best preserved adjacent to the (non-preserved) second phalanx of the third digit of the right manus, are about 0.2–0.3 mm in length (Fig. 5). They grow narrower from the interphalangeal articular region proximally to the middle of the phalanx distally. They are smooth and generally flat, but on the postaxial side each scale bears a very strong keel, forming an acute V in cross-section. These scales were pressed closely against the dorsal side of the third phalanx of the fourth digit, and it is possible that this keel is an artifact.

Thigh

Scales are represented by semi-regular dark splotches only proximally on the left thigh. Scales appear to be arranged diagonally and are 0.25 mm in size here.

Leg and pes

The legs of the counterpart are missing. Actual scale material is preserved of the lower left leg and foot, with a few subdigital lamellae on the right foot. Scales are represented by regular arrays of dark splotches over the lower half of the right tibia and fibula (Fig. 1C).

Near the left foot is a patch of keratinous scales whose overlapping relations and orientation – opposite the expected direction in this extremity – indicate that this is a patch of skin torn from the lower leg and folded downward around the ankle (Fig. 1D). This interpretation is supported by the lack of a body outline on the left lower leg (Fig. 1). However, the exact place from which this patch of skin derives cannot be determined. The scales here are rhomboidal and form regular diagonal rows. They vary in size along the patch. More proximally these scales are comparatively large (0.46 mm long), whereas more distally

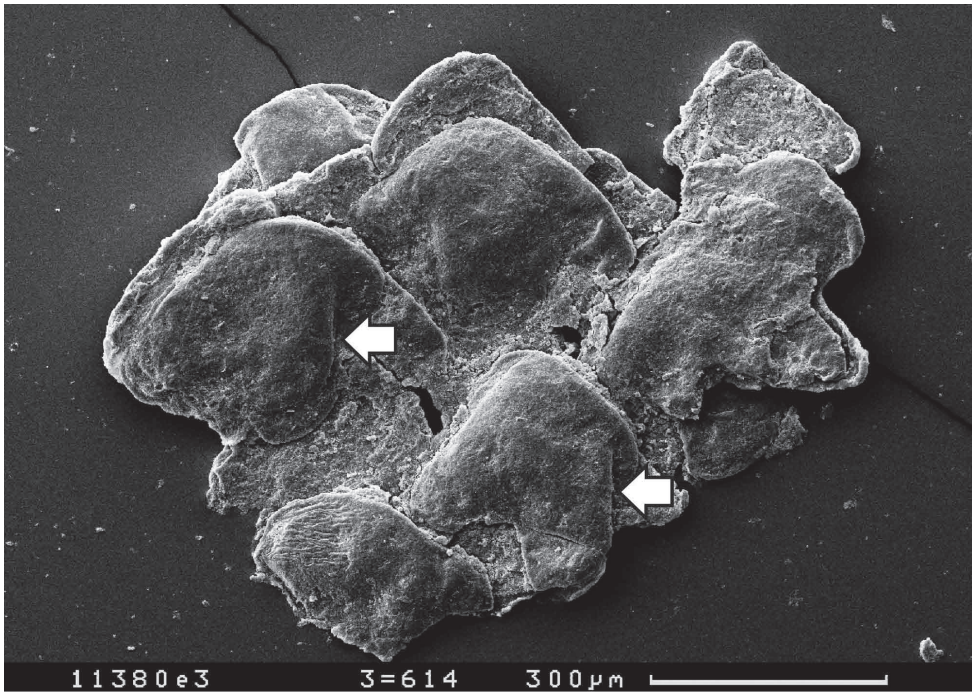


Figure 4. Scanning electron micrograph of scales of right forearm (taken from part). Catalogued as SMF ME 11380e.

they decrease in length to 0.31 mm. On the right lower leg, scales in the middle of the lower leg are about 0.30 mm in size. These data indicate that enlarged scales as big as those on the temples and venter were common on the lower leg near the calf or knee, and scale size diminished again distally on the leg.

The subdigital lamellae of the toes are rectangular in shape and vary in preaxial–postaxial width along the length of the toe (Fig. 1E). Near the interphalangeal joints, where the bony framework is greater, the scales are wider, up to 0.96 mm; they become narrow, as little as 0.66 mm, toward mid-length along a phalanx. The scales vary from about 0.29–0.42 mm in proximodistal length (i.e., somewhat longer than the corresponding scales of the manus). The subdigital lamellae are accompanied by smaller scales on the preaxial side. These smaller scales are often located at the same transverse level as a lamella but are sometimes staggered.

Like those of the manus, the subdigital lamellae of the pes are smooth and flat, but they are without keels or eminences (Fig. 6A). The postaxial edges of these scales preserve grooves (Fig. 6A), presumably facets for interlocking with the adjacent scales (Fig. 6B). There is no evidence of the expansions of the skin of the toes known in extant *Basiliscus* as 'rectangular fringes' (Luke 1986) or 'fringe scales' (Laerm 1973).

Microstructure

In several places (forearm, lower leg, subdigital lamellae) the flexibility and form of the scales suggest they represent keratin, although how and to what degree it may have been altered is unknown. On the forearm, the distal tip of the proximal-most examined scale exposes what appears to be a thick beta-layer (see Klein & Gorb 2012) with clearly recognizable microstructure (Fig. 4). Fine-scale ornamentation (microstructure or microarchitecture) of the "Oberhäutchen" – the uppermost layer of the outer (beta) keratinized stratum – is not preserved on any of the scales examined closely by scanning electron microscopy. In particular, there was little indication of a honeycomb pattern (Peterson 1984), which Etheridge & de Queiroz (1988) took to be the primitive condition in Iguanidae and which is present in living Corytophaninae (Lang 1989a, Peterson 1984) and *Polychrus* (Peterson 1984). Only in a few places, for instance on the distal-most subdigital scale in Figure 5, are there small (about 10 μm), closely spaced pits that possibly represent the remnants of a honeycomb-like ornamentation. Neither round nor funnel scale organs (Lang 1989a) were observed on the scales whose substance was preserved.

Discussion

Comparisons with extant taxa

Comparisons with extant taxa focus on members of Corytophaninae and of *Anolis* (sensu Poe 2004, rather than Nicholson et al. 2012) and *Polychrus*, which are frequently considered to be close relatives (e.g., Pyron et al. 2013, Smith 2009). Furthermore, phylogenetic analyses that have included *Geiseltaliellus maarius* have shown without exception that it is in the total clade of Corytophaninae (Smith 2009, Conrad 2015). Given this agreement, a new phylogenetic analysis incorporating the scale characters discussed here was not conducted.

In examined members of *Polychrus*, *Basiliscus* and *Laemanctus* the scales of the dorsum are generally rhomboidal in shape and obliquely arranged, but they are relatively large with respect to head scales in *Laemanctus*, interme-

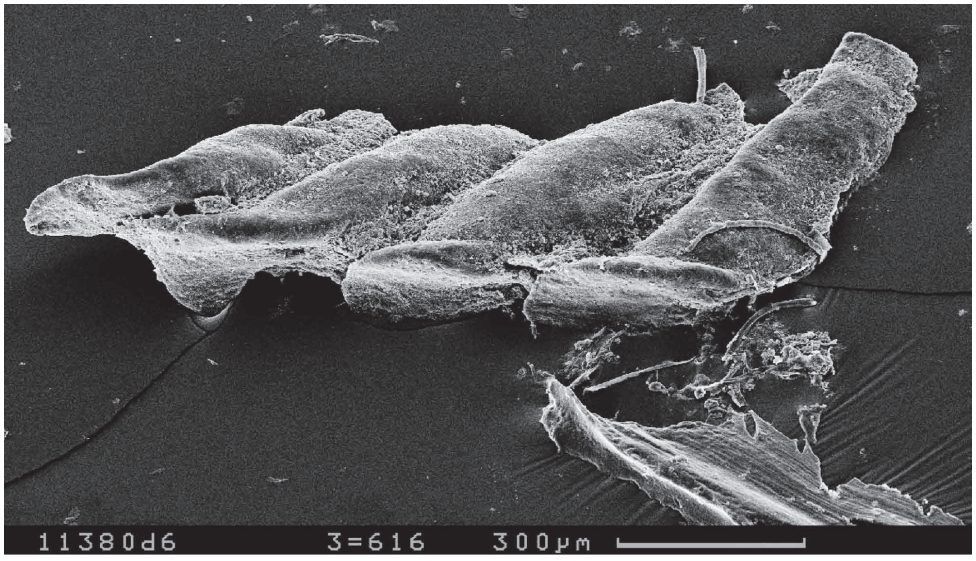


Figure 5. Scanning electron micrograph of lamellae beneath phalanx 2 of digit III of right manus. Catalogued as SMF ME 11380d.

diate in *Polychrus* and small in *Basiliscus*. In all taxa the scales of the head and limbs are larger than those of the dorsum, as in SMF ME 11380, but the degree varies (extremely enlarged in *C. cristatus*, but in *B. basiliscus* more comparable to SMF ME 11380). In all taxa the scales around the joints (axilla, elbow, groin, knee) are smaller than scales elsewhere on the limb, presumably to maintain flexibility. The heterogeneous dorsal squamation in *Corytophanes* is obviously an autapomorphy of the clade. Keels on at least some scales are well developed in all taxa. *Polychrus gutturosus* has keels everywhere, but in *P. liogaster* they are lacking on most of the dorsum (except near the midline) and venter. Keels are absent on the dorsum in *Basiliscus*, and in *Corytophanes* they are only found on the enlarged scales of the dorsum; in *Laemanctus* keels on the dorsum are only found on the flanks. However, in *Laemanctus* and *Corytophanes* keels are present on all scales of the venter. Keeled scales are present on at least the dorsal surface of the extremities in all taxa, although keels on ventral scales are less prevalent. The scales of the venter are rhomboidal in all taxa, and because the two sides are mirror symmetric, it is clear that the scale rows must meet in some kind of V-shape. In *Basiliscus* and *Corytophanes* the scales of the venter are arranged such that they formed transverse rows, the V only apparent at the midline. But in *Polychrus* and *Laemanctus* the scale rows are oblique on the venter. The scales of the tail are arranged in transverse rows near the autotomy planes on the proximal part of the tail in *Basiliscus*. In *Polychrus*, *Corytophanes* and *Laemanctus*, however, they form oblique rows everywhere.

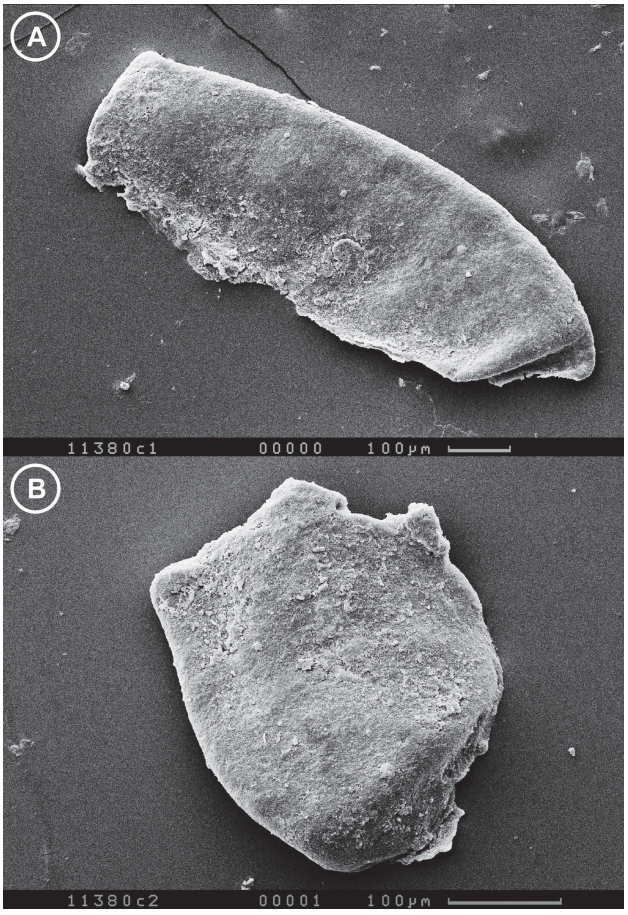


Figure 6. Scanning electron micrographs of subdigital scales beneath digit IV of left pes. (A) Subdigital lamella. (B) Adjacent postaxial scale.

The subdigital lamellae of *Polychrus* (Smith 2009: fig. 14D), *Corytophanes* (Smith 2009: fig. 14B) and *Laemanctus* (Smith 2009: fig. 14A) are similar in having a low aspect ratio: their length is not much greater than their width. The lamellae are also keeled in some fashion in all three taxa. In contrast, the subdigital lamellae of *Basiliscus* (Smith 2009: fig. 14C) and *Anolis* (e.g., Peterson 1983) are notable for their smoothness (macroscopically) and great width. SMF ME 11380 shows that *Geiseltaliellus maarius* is similar to the latter taxa in this character, raising the prospect that wide lamellae are primitive for a larger group and transformed in *Polychrus* and *Corytophanes* + *Laemanctus* independently. Only on subdigital lamellae of digits III–IV of the right hand of *B. basiliscus* SMF 71635 was there any indication of the asymmetry and keel seen in *G. maarius* SMF ME 11380; it may be an artifact.

In summary, *Geiseltaliellus maarius* was similar to *Basiliscus* in many respects: very small scales on the body; slightly larger scales on head and lower limbs; broad, smooth subdigital lamellae; and possibly keeled scales on the extremities and a projecting median head crest in male individuals. However, *G. maarius* differs from *Basiliscus* in having even smaller body scales. If the strongly asymmetrical subdigital lamellae of the manus are not artifactual, this may be a further autapomorphy of *G. maarius*; that the strong keels are developed on the postaxial side suggests they could be an adaptation for maintaining grip on a vertical substrate.

Caudal scales

A majority of specimens of *G. maarius*, including the young individual SMF ME 902 (SVL ~ 5.2 cm), are lacking the distal tail after vertebra 12–19. The last vertebra is invariably whole, and no structure similar to a cartilage tube (Fisher et al. 2012) indicates regrowth, unlike in autotomic lizards from Messel like *Eolacerta robusta* (Müller 2001). These facts led Smith & Wuttke (2012) to conclude that *G. maarius* showed intervertebral urotomy, or pseudoautotomy (Slowinski & Savage 1995). No very small specimens of *G. maarius* are known, but ones ('*Capitolacerta dubia*', SVL ~ 3.0 cm; Smith 2009) assigned to *G. longicauda* (Estes 1983) lack autotomy planes (Smith 2009). *Geiseltaliellus longicauda* and *G. maarius* probably both lacked autotomy planes early in postembryonic ontogeny.

No specimen of *G. maarius* in which the tail is whole has details of the squamation preserved (in SMF ME 11380 only the outline is visible). Thus, examination of the caudal scales of *G. maarius* must await a conjunction of two cir-

cumstances: tail extensive and scale structures preserved. Yet it may be possible to predict the scale pattern that will be found in *G. maarius* by considering scalation in extant lizards. As Alibardi (2010) noted, the caudal scales of autotomic lizards are frequently arranged in whorls, where the boundaries between adjacent whorls correspond to autotomic planes in the vertebrae. In some taxa these whorls are extremely well defined (although it is in such cases not uncommon that autotomy is lost, e.g., *Uracentron*; Etheridge & de Queiroz 1988), whereas in others they are more subtle. In *Anolis cuvieri*, for instance, the caudal scales are generally hexagonal and form oblique and longitudinal rows, but not transverse ones (Fig. 7A). At the autotomic planes, however, the posterior margins of all pre-autotomic scales tend be transverse and aligned; they are also more widely separated from post-autotomic scales, such that the autotomic plane is clearly marked in the skin (Fig. 7B). This clear marking is maintained in the distal tail of ontogenetically advanced individuals of *Basiliscus*, where the autotomy planes are presumably all fused (cf. Etheridge 1967). This pattern is disrupted on the regrown tail immediately behind to the plane of autotomy (Fig. 7B), but more distally the scale pattern and keeling become highly regular again (Fig. 7C). Here, the scales form elongate rhombi, and their posterior margins do not align. Notably, there is no discernible pattern of segmentation in the regenerated axial skeleton of lizards; the blood vessels that penetrate the cartilage tube are not segmentally arranged, nor are the nerves (Fisher et al. 2012). In living *Corytophanes* and *Laemanctus*, where autotomy does not occur (Etheridge 1967, Lang 1989b), the scales of the tail form oblique rows along the entire length of the tail. This suggests that there is tissue interaction along the sclerotomal boundaries between the axial skeleton and the developing scales. Werner (1896) also noted differences between the squamation of the whole and regenerated tail in some lizards. In particular, he attributed this to degeneration to the primitive state in the 'family' among lizard species with a scale pattern (e.g., whorls proximally in *Stellagama stellio*), and indeed his example of *Gymnophthalmus quadrilineatus* regenerating whorls where the original pattern consisted of oblique rows is suggestive. To my knowledge, the mechanisms underlying caudal scale patterns have not been examined in detail. For the present purposes, it may suffice to note that: (i) oblique rows are widespread in Iguanidae and in Agamidae, even among pseudoautotomic forms; (ii) where caudal autotomy planes are absent post-embryonically in closely related taxa (*Polychrus, Corytophanes, Laemanctus*), oblique rows are present; and (iii) where the tail regrows in other closely related taxa (*Anolis, Basiliscus*), oblique rows are present. I predict, therefore, that the caudal scales of *G. maarius* are rhomboidal and arranged in oblique rows (Fig. 8).

Rectangular fringes

The 'rectangular flaps' are greatly expanded fringes on the postaxial side of the pedal digits, separated from the subdigital lamellae by one or several scale rows (Laerm 1973; pers. obs.), which in extant *Basiliscus* help its members run over bodies of water (Hallinan 1920, Luke 1986). They are accompanied by strongly and asymmetrically keeled subdigital lamellae, the steep side directed postaxially; the keels grow in prominence from digit I to IV, and on the last digit (V) they are so extensive that they form an additional preaxial fringe. These fringes are unique to *Basiliscus* among extant basilisks and so probably arose along the stem. Thus, if *Geiseltaliellus* is on the stem of Corytophaninae (Smith 2009; see also Conrad 2015), it should lack them. Only the scales immediately adjacent to the subdigital scales on the postaxial side are preserved in *G. maarius*

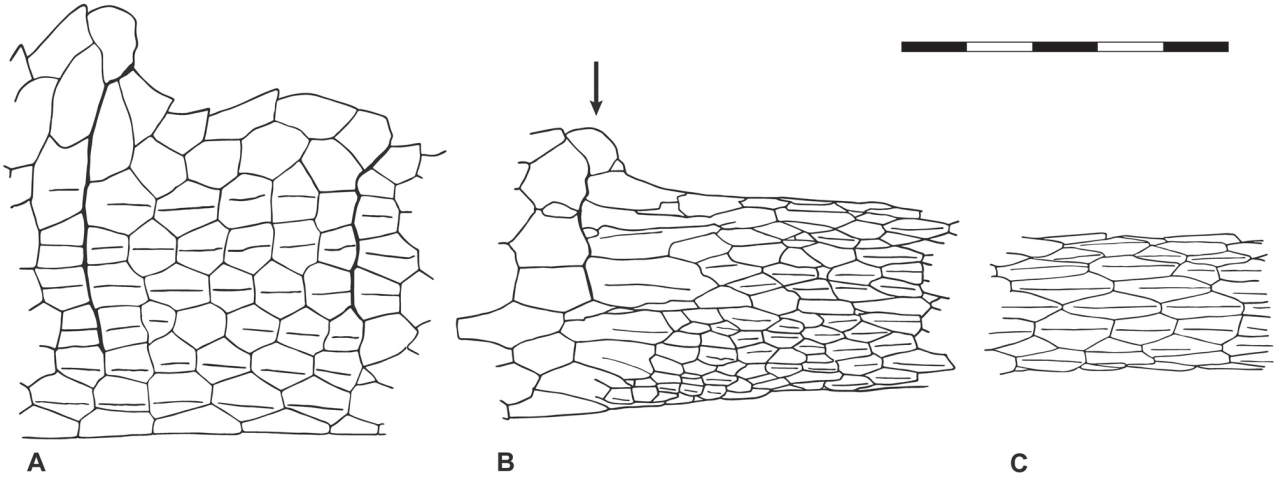


Figure 7. Squamation of tail in *Anolis cuvieri* in relation to autotomy. All figures are of the right side of the tail. (A) Position of autotomy planes visible externally, where pre-plane caudal scales form transverse line well separated from post-plane scales (YPM R12066). (B) Chaotic squamation immediately after tail loss (YPM R12065). (C) Well-developed oblique rows more distally after break, where a regular pattern has been re-established (YPM R12065). Scale bar is 5 mm.



Figure 8. Reconstruction of the squamation of male *Geiseltaliellus maarius* from Messel.

SMF ME 11380. Yet, the fringe scales are so large in comparison with the adjacent scales that it is difficult to imagine that such fringes were present in *G. maarius*. Moreover, the subdigital lamellae of the SMF ME 11380 are smooth and flat, rather than strongly keeled and asymmetric. SMF ME 11380 provides support for the phylogenetic inference that fringes were absent in *G. maarius*.

A life reconstruction of the squamation of *G. maarius* is presented in Figure 8.

Microstructure

The (beta) keratin matrix of some bird feathers from Messel is degraded (Vinther et al. 2010), as is the keratin of a shed skin from the Green River Formation (Edwards et al. 2011). Yet in some places in SMF ME 11380 and other Messel squamate specimens, as well as the stem pangolin *Eomanis waldi* (von Koenigswald et al. 1981), it appears that original keratin is preserved. The near-absence of surface microstructure may be due to microbial decomposition (von Holstein et al. 2014, Wilson et al. 2007). Keratins are well known for their great chemical and mechanical stability. Differences in scale structure as a function of body position are to be expected, although the matter has received comparably little attention (Klein & Gorb 2012). Possibly the scales of the lower limbs and especially the subdigital lamellae are thicker than elsewhere on the body because this is where they are most heavily abraded.

Biochemical, immunological and spectrometric studies to ascertain the actual composition of these apparent scales (Schweitzer et al. 1999) will be important. If confirmed, this leaves open the possibility that future Messel specimens that were exposed to more salubrious postmortem conditions might yet retain the original microstructure of the "Oberhäutchen" or scale organs. Moreover, the amino acid sequences of the keratin proteins (Schweitzer et al. 1999) might be determined and used in phylogenetic or other studies.

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References

Alibardi, L. (2010): Morphological and Cellular Aspects of Tail and Limb Regeneration in Lizards: A Model System with Implications for Tissue Regeneration in Mammals. – Springer, Heidelberg.

Behnke, C., H. Eikamp & M. Zollweg (1986): Die Grube Messel: Paläontologische Schatzkammer und unersetzliches Archiv für die Geschichte des Lebens; Geologie, Bergbaugeschichte, Fossilien. – Goldschneck, Korb, Germany.

Borsuk-Białynicka, M., M. Lubka & W. Böhme (1999): A lizard from Baltic amber (Eocene) and the ancestry of the crown group lacertids. – Acta Palaeontologica Polonica, **44**: 349–382.

Butler, M. A., S. A. Sawyer & J. B. Losos (2007): Sexual dimorphism and adaptive radiation in *Anolis* lizards. – Nature, **447**: 202–205.

Cadena, E. A. (2016): Microscopical and elemental FESEM and Phenom ProX-SEM-EDS analysis of osteocyte- and blood vessel-like microsctructures obtained from fossil vertebrates of the Eocene Messel Pit, Germany. – PeerJ, **4**: e1618.

Cole, C. J. & T. R. Van Devender (1976): Surface structure of fossil and Recent epidermal scales from North American lizards of the genus *Sceloporus* (Reptilia, Iguanidae). – Bulletin of the American Museum of Natural History, **156**: 455–513.

Colleary, C., A. Dolocan, J. D. Gardner, S. Singh, M. Wuttke, R. Rabenstein, J. Habersetzer, S. Schaal, M. Feseha, M. Clemens, B. F. Jacobs, E. D. Currano, L. L. Jacobs, R. L. Sylvestersen, S. E. Gabbott & J. Vinther (2015): Chemical, experimental, and morphological evidence for diagenetically altered melanin in exceptionally preserved fossils. – Proceedings of the National Academy of Sciences of the United States of America, **112**: 12592–12597.

Conrad, J. L. (2015): A new Eocene casquehead lizard (Reptilia, Corytophanidae) from North America. – PLoS One, **10**: e0127900.

Conrad, J. L., J. J. Head & M. T. Carrano (2014): Unusual soft-tissue preservation of a crocodile lizard (Squamata, Shinisauria) from the Green River Formation (Eocene) and shinisaur relationships. – Anatomical Record, **297**: 545–559.

Daza, J. D., E. L. Stanley, P. Wagner, A. M. Bauer & D. A. Grimaldi (2016): Mid-Cretaceous amber fossils illuminate the past diversity of tropical lizards. – Science Advances, **2**: e1501080.

de Queiroz, K., L.-R. Chu & J. B. Losos (1998): A second *Anolis* lizard in Dominican amber and the systematics and ecological morphology of Dominican amber anoles. – American Museum Novitates, **3249**: 1–23.

Edwards, N. P., H. E. Barden, B. E. van Dongen, P. L. Manning, P. L. Larson, U. Bergmann, W. I. Sellers & R. A. Wogelius (2011): Infrared mapping resolves soft tissue preservation in 50 million year-old reptile skin. – Proceedings of the Royal Society of London, Series B,

Estes, R. (1962): A fossil gerrhosaur from the Miocene of Kenya (Reptilia: Cordylidae). – Breviora, Museum of Comparative Zoology, **158**: 1–10.

Estes, R. (1983): Sauria Terrestria, Amphisbaenia (Handbuch der Paläoherpetologie, v. 10A). – Gustav Fischer Verlag, Stuttgart.

Etheridge, R. (1967): Lizard caudal vertebrae. – Copeia, **1967**: 699–721.

Etheridge, R. & K. de Queiroz (1988): A phylogeny of Iguanidae. – pp. 283–367 in: R. Estes & G. K. Pregill (eds): Phylogenetic Relationships of the Lizard Families. – Stanford University Press, Stanford.

Fisher, R. E., L. A. Geiger, L. K. Stroik, E. D. Hutchins, R. M. George, D. F. DeNardo, K. Kusumi, J. A. Rawls & J. Wilson-Rawls (2012): A histological comparison of the original and regenerated tail in the green anole, *Anolis carolinensis*. – Anatomical Record, **295**: 1609–1619.

Garda, A. A., G. C. Costa, F. G. R. França, L. G. Giugliano, G. S. Leite, D. O. Mesquita, C. Nogueira, L. Tavares-Bastos, M. M. Vasconcellos, G. H. C. Vieira, L. J. Vitt, F. P. Werneck, H. C. Wiederhecker & G. R. Colli (2012): Reproduction, body size, and diet of *Polychrus acutirostris* (Squamata: Polychrotidae) in two contrasting environments in Brazil. – Journal of Herpetology, **46**: 2–8.

Gorjanović-Kramberger, C. (1892): Aigialosaurus, eine neue Eidechse aus den Kreideschiefern der Insel Lesina, mit Rücksicht auf die bereits beschriebenen Lacertiden von Comen und Lesina. – Glasnik hrvatskoga naravoslovnoga drustva (Societas historico-naturalis croatica) u Zagrebu, **7**: 74–106.

Hallinan, T. (1920): Notes on lizards of the canal zone, Isthmus of Panama. – Copeia, **83**: 45–49.

Ifrim, C., M.-C. Buchy, K. T. Smith & S. Giersch (2008): Paleoenvironment and preliminary description of early Turonian (Late Cretaceous) aquatic squamates from Vallecillo, north-eastern Mexico. – pp. 47–62 in: M. J. Everhart (ed.): Proceedings of the Second Mosasaur Meeting (Fort Hays Studies, Special Issue 3). – Sternberg Museum of Natural History, Hays, Kansas.

Klaver, C. & W. Böhme (1986): Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. – Bonner Zoologische Monographien, **22**: 1–64.

Klein, M.-C. G. & S. N. Gorb (2012): Epidermis architecture and material properties of the skin of four snake species. – Journal of the Royal Society Interface, **9**: 3140–3155.

Köhler, G. (2008): Reptiles of Central America (2nd ed.). – Herpeton Verlag, Offenbach am Main.

Kornhuber, A. (1893): Carsosaurus Marchesettii, ein neuer fossiler Lacertilier aus den Kreideschichten des Karstes bei Komen. – Abhandlungen der k.k. (kaiserlich-königlichen) geologischen Reichsanstalt, Wien, **17**: 1–15.

Laerm, J. (1973): Aquatic bipedalism in the basilisk lizard: The analysis of an adaptive strategy. – American Midland Naturalist, **89**: 314–333.

Lang, M. (1989a): The morphology of the Oberhäutchen with the description and distribution of scale organs in basiliscine iguanians. – Amphibia-Reptilia, **10**: 423–434.

Lang, M. (1989b): Phylogenetic and biogeographic patterns of basiliscine iguanians (Reptilia: Squamata: "Iguanidae"). – Bonner Zoologische Monographien, **28**: 1–172.

Lenz, O. K., V. Wilde, D. F. Mertz & W. Riegel (2015): New palynology-based astronomical and revised $^{40}Ar/^{39}Ar$ ages for the Eocene maar lake of Messel (Germany). – International Journal of Earth Sciences, **104**: 873–889.

Lindgren, J., M. J. Everhart & M. W. Caldwell (2011): Three-dimensionally preserved integument reveals hydrodynamic adaptations in the extinct marine lizard *Ectenosaurus* (Reptilia, Mosasauridae). – PLoS One, **6**: e27343, 5 pp.

Luke, C. (1986): Convergent evolution of lizard toe fringes. – Biological Journal of the Linnean Society, **27**: 1–16.

McNamara, M. E., D. E. G. Briggs, P. J. Orr, S. Wedmann, H. Noh & H. Cao (2011): Fossilized biophotonic nanostructures reveal the original colors of 47-million-year-old moths. – PLoS Biology, **9**: e1001200.

Müller, J. (2001): Osteology and relationships of *Eolacerta robusta*, a lizard from the middle Eocene of Germany (Reptilia, Squamata). – Journal of Vertebrate Paleontology, **21**: 261–278.

Nicholson, K. E., B. I. Crother, C. Guyer & J. M. Savage (2012): It is time for a new classification of anoles (Squamata: Dactyloidae). – Zootaxa, **3477**: 1–108.

Peterson, J. A. (1983): The evolution of the subdigital pad in *Anolis*. I. Comparisons among the anoline genera. – pp. 245–283 in: A. G. J. Rhodin & K. Miyata (eds): Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams – Harvard University Press, Cambridge, Massachusetts.

Peterson, J. A. (1984): The microstructure of the scale surface in iguanid lizards. – Journal of Herpetology, **18**: 437–467.

Poe, S. (2004): Phylogeny of anoles. – Herpetological Monographs, **18**: 37–89.

Polcyn, M. J., J. V. Rogers, Y. Kobayashi & L. L. Jacobs (2002): Computed tomography of an *Anolis* lizard in Dominican amber: systematic, taphonomic, biogeographic, and evolutionary implications. – Palaeontologia Electronica, **5**: 1–13.

Pyron, R. A., F. T. Burbrink & J. J. Wiens (2013): A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. – BMC Evolutionary Biology, **13**: 93.

Reynoso, V. H. (1997): A "beaded" sphenodontian (Diapsida: Lepidosauria) from the Early Cretaceous of central Mexico. – Journal of Vertebrate Paleontology, **17**: 52–59.

Reynoso, V. H. (1998): *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, central México. – Philosophical Transactions of the Royal Society of London, Series B, **353**: 477–500.

Reynoso, V. H. (2000): An unusual aquatic sphenodontian (Reptilia: Diapsida) from the Tlayua Formation (Albian), central Mexico. – Journal of Paleontology, **74**: 133–148.

Reynoso, V. H. & G. Callison (2000): A new scincomorph lizard from the Early Cretaceous of Puebla, Mexico. – Zoological Journal of the Linnean Society, **130**: 183–212.

Rieppel, O. & L. Grande (2007): The anatomy of the fossil varanid lizard *Saniwa ensidens* Leidy, 1870, based on a newly discovered complete skeleton. – Journal of Paleontology, **81**: 643–665.

Rossmann, T. (2000): Osteologische Beschreibung von *Geiseltaliellus longicaudus* Kuhn, 1944 (Squamata: Iguanoidea) aus dem Mittleren Eozän der Fossillagerstätten Geiseltal und Grube Messel (Deutschland), mit einer Revision der Gattung *Geiseltaliellus*. – Palaeontographica A, **258**: 117–158.

Schaal, S. & W. Ziegler (1988) Messel: Ein Schaufenster in die Geschichte der Erde und des Lebens. – Waldemar Kramer, Frankfurt am Main, Germany.

Schleich, H. H., W. Kästle & K. Kabisch (1996): Amphibians and Reptiles of North Africa: Biology, Systematics, Field Guide. – Koeltz Scientific Publishers, Koenigstein, Germany.

Schweitzer, M. H., J. A. Watt, R. Avci, C. A. Forster, D. W. Krause, L. Knapp, R. R. Rogers, I. Beech & M. Marshall (1999): Keratin immunoreactivity in the Late Cretaceous bird *Rahonavis osteromi*. – Journal of Vertebrate Paleontology, **19**: 712–722.

Slowinski, J. B. & J. M. Savage (1995): Urotomy in *Scaphiodontophis*: evidence for the multiple tail break hypothesis in snakes. – Herpetologica, **51**: 338–341.

Smith, K. T. (2009): Eocene lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Squamata: Iguania). – Bulletin of the Peabody Museum of Natural History, **50**: 219-306.

Smith, K. T. & M.-C. Buchy (2008): A new aigialosaur (Squamata: Anguimorpha) with soft tissue remains from the Upper Cretaceous of Nuevo León, Mexico. – Journal of Vertebrate Paleontology, **28**: 85–94.

Smith, K. T. & M. Wuttke (2012): From tree to shining sea: Taphonomy of the arboreal lizard *Geiseltaliellus maarius* from Messel, Germany. – Palaeobiodiversity and Palaeoenvironments, **92**: 45–65.

Vinther, J., D. E. G. Briggs, R. O. Prum & V. Saranathan (2008): The colour of fossil feathers. – Biology Letters, **4**: 522–525.

Vinther, J., D. E. G. Briggs, J. Clarke, G. Mayr & R. O. Prum (2010): Structural coloration in a fossil feather. – Biology Letters, **6**: 128–131.

Vitek, N. S., J. Vinther, J. D. Schiffbauer, D. E. G. Briggs & R. O. Prum (2013): Exceptional three-dimensional preservation and coloration of an originally iridescent fossil feather from the middle Eocene Messel oil shale. – Paläontologische Zeitschrift, **87**: 493–503.

von Holstein, I. C. C., K. E. H. Penkman, E. E. Peacock & M. J. Collins (2014): Wet degradation of keratin proteins: linking amino acid, elemental and isotopic composition. – Rapid Communications in Mass Spectrometry, **28**: 2121–2133.

von Koenigswald, W., G. Richter & G. Storch (1981): Nachweis von Hornschuppen bei *Eomanis waldi* aus der "Grube Messel" bei Darmstadt (Mammalia, Pholidota). – Senckenbergiana Lethaea, **61**: 291–298.

Werner, F. (1896): Über die Schuppenbekleidung des regenerirten Schwanzes bei Eidechsen. – Sitzungsberichte der kaiserlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Classe, Abtheilung I, **105**: 123–146, pl. I–II.

Wilson, A. S., H. I. Dodson, R. C. Janaway, A. M. Pollard & D. J. Tobin (2007): Selective biodegradation in hair shafts derived from archaeological, forensic and experimental contexts. – British Journal of Dermatology, **157**: 450–457.