

Fossil snake preserving three trophic levels and evidence for an ontogenetic dietary shift

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Abstract We report a fossil snake from the middle Eocene (48 Ma) Messel Pit, in whose stomach is a lizard, in whose stomach is an insect. This is the second known vertebrate fossil containing direct evidence of three trophic levels. The snake is identified as a juvenile of *Palaeopython fischeri* on the basis of new characters of the skull; the lizard is identified as *Geiseltaliellus maarius*, a stem-basilisk; and the insect, despite preserved structural colouration, could not be identified more precisely. *G. maarius* is thought to have been an arboreal species, but like its extant relatives may have foraged occasionally on the ground. Another, larger specimen of *G. maarius* preserves plant remains in the digestive tract, suggesting that omnivory in this species may have been common in larger individuals, as in extant *Basiliscus* and *Polychrus*. A general picture of the trophic ecology of *P. fischeri* is not yet possible, although the presence of a lizard in the stomach of a juvenile individual suggests that this snake could have undergone a dietary shift, as in many extant boines.

Keywords Messel · Middle Eocene · *Palaeopython fischeri* · *Geiseltaliellus maarius* · Gut contents · Food chain

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Introduction

Trophic relations in fossil organisms are notoriously difficult to study, and the evidence generally indirect or inferential in nature, based on adaptational considerations (ecomorphology) or traces (bite marks, microwear), which in turn are based on long-timescale (Ma), species-level properties or short-timescale (month), individual-level properties (Ungar 2010; Gailer et al. 2016). Only in *Konservat-Lagerstätten* are body fossils typically complete enough that contents of the digestive tract can be studied directly. The Messel Pit Fossil Site ('Messel'), a UNESCO World Heritage site near Darmstadt, Germany, is one such locality.

Messel is renowned for the fidelity of preservation. Contents of the digestive tract have already illuminated numerous aspects of the trophic ecology of the extinct species preserved there. The remains of grapes are found together with leaves in the stomachs of fossil horses (von Koenigswald and Schaarschmidt 1983; Franzen 2007). The remains of arthropods, including moth scales, are preserved in the digestive tract of fossil bats (Habersetzer et al. 1994). Abundant pollen grains in the stomach contents of the bird *Pumiliornis tessellatus* show that it visited flowers (Mayr and Wilde 2014). A large arboreal lizard, *Ornatocephalus metzleri*, contains both plant matter and insect cuticula in its stomach (Weber 2004). A crocodile was reported inside a boid (Greene 1983). Fish coprolites contain the remains of various kinds of arthropods (Richter and Baszio 2001; Richter and Wedmann 2005), and the coprolite of a mammalian carnivore yielded a primate jaw fragment (Franzen 1997).

Still, little is known of the trophic ecology of the squamates from Messel. We report here on a spectacular fossil specimen, a snake containing a lizard that in turn contains an insect. This specimen is the first described specimen from Messel, and the second ever, preserving a three-level trophic chain.

Materials and methods

The study is based primarily on SMF ME 11332 (Fig. 1), collected in a layer between 350 and 450 cm above marker bed ‘alpha’. This layer is correlated with the lower-most Lutetian (middle Eocene) in current age models (Lenz et al. 2015). The most obvious fossil in SMF ME 11332 is a coiled, complete snake. Most of it is preserved on the part (SMF ME 11332a), but a section of anterior vertebral column is found on the counterpart (SMF ME 11332b). Inside the snake is a lizard, and inside the lizard is an insect. The specimen was collected from the Middle Messel Formation, whence all fossil vertebrates from the Messel lake derive. As is typical for vertebrate body fossils from Messel, the specimen was exposed by splitting the laminated algal pellicle (‘oil-shale’; Goth 1990), cleaned in a moist state to avoid desiccation, embedded in epoxy resin, and prepared from the other side. The fossil is thus nearly completely freed from matrix and isolated on the epoxy plate.

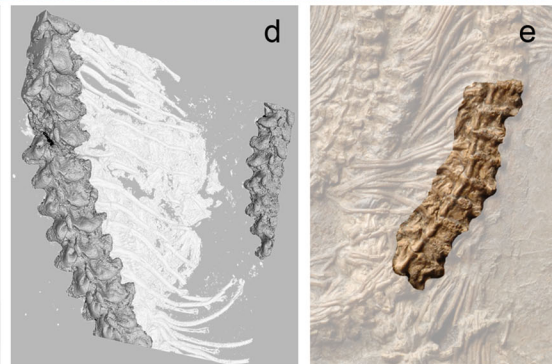
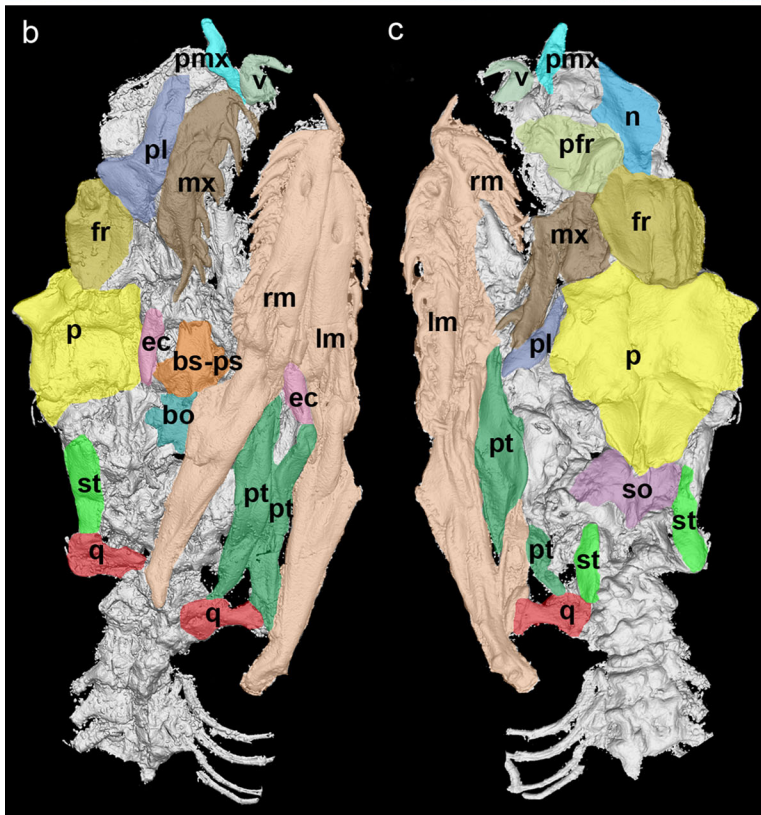
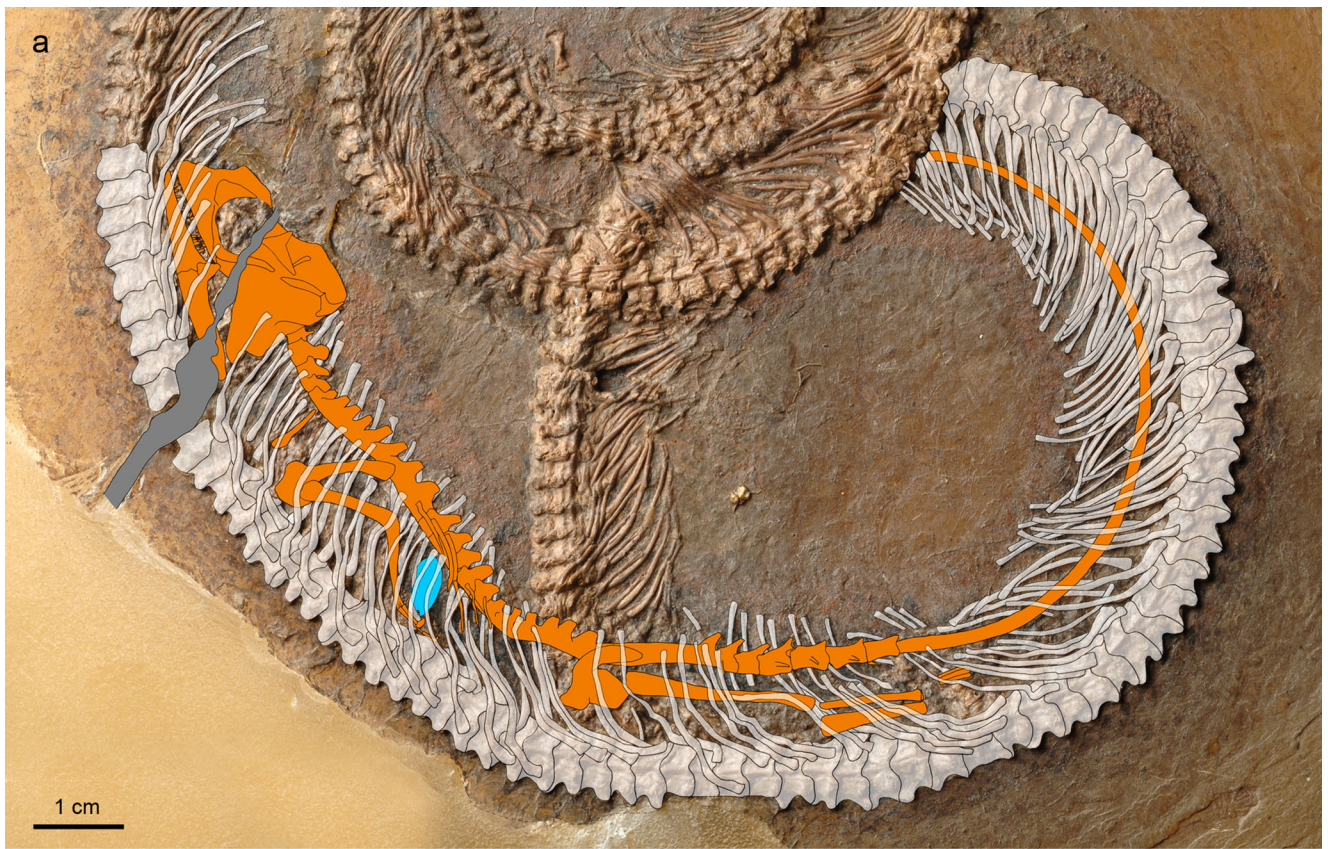
Three parts of SMF ME 11332 were CT-scanned on a Tomoscope HV 500 (Werth Messtechnik GmbH) with a 2K detector and a 225-kV μ -focus X-ray source in the industrial μ CT facility funded by the Wolfgang Pfeiffer Stiftung at the Technical University in Deggendorf, Germany: the snake skull

Fig. 2 **a** Interpretive drawing of SMF ME 11332a overlaid on a photograph. The lizard, *Geiseltaliellus maarius* (orange), is preserved in the stomach of the snake (white). The lizard was swallowed headfirst, and the tail does not appear to have been shed during the encounter with the snake. The position of the insect in the abdominal cavity of the lizard is indicated in outline (blue). All Rights Reserved. **b, c** CT reconstruction of the snake skull in right ventrolateral and left dorsolateral views, respectively. **d** CT reconstruction of mid-trunk vertebrae of the snake in dorsal view. **e** Photograph of mid-trunk vertebrae of the snake in ventral view. **f** Part of the string of vertebrae, to the same scale, comprising the holotype of *Palaeopython fischeri* (SMF ME 929), four trunk vertebrae in dorsal (left) and ventral (right) views (after Schaal 2004), showing the significant size difference between the holotype and the new specimen. Abbreviations: *bo* basioccipital, *bs-ps* basiparasphenoid, *ec* ectopterygoid, *fr* frontal, *lm* left mandible, *mx* maxilla, *n* nasal, *p* parietal, *ppf* prefrontal, *pl* palatine, *pmx* premaxilla, *pt* pterygoid, *q* quadrate, *rm* right mandible, *so* supraoccipital, *st* supratemporal. Published with kind permission of ©Krister T. Smith 2016

(CT mode 2, 150 μ A, 190 kV, 1200 steps, voxel resolution 20.2 μ m), the lizard skull together with the middle trunk vertebrae of the snake (CT mode 2, 110 μ A, 190 kV, 1200 steps, voxel resolution 20.2 μ m), and the whole lizard body (CT mode 2, 300 μ A, 190 kV, 1600 steps, voxel resolution 60.8 μ m). SMF ME 11398 was CT-scanned on a Phoenix v|tome|x s (GE) at the University of Tübingen Computed Tomography Laboratory



Fig. 1 SMF ME 11332a, comprising a juvenile specimen of the snake *Palaeopython fischeri* and its prey. Arrow points to the tip of the snout of the lizard inside the snake



funded by the German Research Foundation and the University of Tübingen (1K detector with detector shift = 2K, multiscan comprising 4 individual scans, section scan mode with 277.7° angular excursion, 130 μ A, 230 kV, 2500 steps, voxel resolution 30.0 μ m). The volume files were analysed using VG Studio MAX v2.2 on a high-end workstation at Senckenberg.

Abbreviation: SMF ME, Messel Collection, Senckenberg Research Institute, Frankfurt am Main, Germany.

Results

The snake

Description

SMF ME 11332 contains the nearly complete skeleton of a small snake (Fig. 1). This individual exhibits the skull in dorsolateral view, whereas the vertebral column is mostly seen in ventral or ventrolateral view. The snake has a total length (TL) of about 103 cm, of which around 89 cm is snout-vent length (SVL) and 14 cm is tail. The mandible length is around 26 mm, and head length from snout-tip to end of mandible around 29 mm. There are around 306 precloacal vertebrae and 72 cloacal and caudal vertebrae, for a total vertebral count of around 378.

The distorted skull is seen in left dorsolateral view (Fig. 2c), but CT reconstructions allow the observation of most of the ventral side of preserved bones (Fig. 2b). The edentulous premaxilla exhibits long transverse processes as in most boines. The frontals bear a conspicuous thin supraorbital shelf, which confers a quadrangular shape in dorsal view. This configuration can be observed in *Palaeopython fischeri*, as well as in juvenile and adult boines. The frontals show rounded posterior margins to fit in the U-shaped frontoparietal suture. However, a supraorbital bone is not in evidence. The parietal has moderate postorbital processes and a small, anteromedian projection. A parietal crest is present, extending approximately 60 % of the midline length of the bone. The posterior region of the parietal, which contains the supratemporal processes and the tip of sagittal crest, is poorly developed and does not cover the supraoccipital. The maxilla shows a moderately developed facial process (for a snake). The ectopterygoid is a short bone that exhibits a typical boine shape, with a forked anterior end and a posterior medial (convex) surface that articulates with a well-delimited lateral concave surface on the pterygoid. The right palatine is preserved but slightly compressed posteriorly. As in Boidae (sensu Reynolds et al. 2014), most of the palatine is composed of a prominent and toothed anterior (dentigerous) process, which preserves one anterior tooth. Both choanal and maxillary processes are located at the posterior end of the palatine, to either side of the palatine-ptyerygoid joint. The choanal process comprises a small triangle of bone, but the exact length of this process cannot be determined. A short stout projection is

interpreted as the maxillary process. As in boids, a palatine foramen is absent. Both quadrates are visible; they have a broad cephalic condyle that lacks a suprastapedial process, and the shaft is relatively long. The stylohyal lies at the middle of the quadrate shaft as in boines and other macrostomatans. In the mandible, the surangular crest is straight and rises anteriorly to form a process that projects well above the tooth row. The prearticular crest is rounded and lower, its apex well below the apex of the surangular crest as in most boids. Both dentaries show a single mental foramen, and the tooth counts are approximately 14–15, although a rigorous tooth count is not possible. The anterior teeth in the upper and lower jaws are much taller than the posterior teeth and strongly recurved.

Scale impressions are preserved in places. Assuming the body was merely compressed in one dimension and not expanded perpendicular to it, the body diameter at the level of vertebra ~113 was about 27 mm.

Taxonomic identification

The absence of a supraorbital ossification excludes the snake in SMF ME 11332 from the group comprising Pythonidae and *Loxocemus*. In contrast, the following combination of characters indicates that it belongs to Boidae (boines, erycines, and small forms): toothless premaxilla, short ectopterygoid with a convex rounded articular surface for pterygoid, palatine bone with both choanal and maxillary processes located at the posterior end, no palatine foramen, and a supraorbital shelf in the frontal bone (Scanferla et al. 2016). In comparison with the other Messel boids, the skull characters of the snake in SMF ME 11332 provide furthermore guidance. The short, anteriorly widening frontals with straight margins are seen, among known Messel snakes, only in *P. fischeri*, whereas in *Messelophis variatus* and *Rieppelophis ermannorum* these elements are much longer than wide (Scanferla et al. 2016). Although anterior teeth in *M. variatus* and *R. ermannorum* are longer than posterior teeth (Scanferla et al. 2016), the difference is much more dramatic in *P. fischeri*, as in the snake in SMF ME 11332. The relative development of the prearticular and surangular crests in the snake in SMF ME 11332 is similar to *P. fischeri*, whereas both crests are more subdued in *M. variatus* and *R. ermannorum* (see Scanferla et al. 2016).

The length of the snake is similar in size to *M. variatus*, which has a maximum total length of about 95 cm (Baszio 2004). *R. ermannorum* is much smaller, with a total length of about 40 cm (Schaal and Baszio 2004), and the medium-sized boid *P. fischeri* much larger, with a maximum total length (based on SMF ME 2504) of about 219 cm (Schaal 2004).

The vertebral morphology (Fig. 2d, e) provides additional data on the identification of the snake. The shortness of the trunk vertebrae and well-developed neural spines are generally consistent with 'booids'. CT reconstructions of the mid-dorsal vertebrae (around number 170) show a dorsal view of

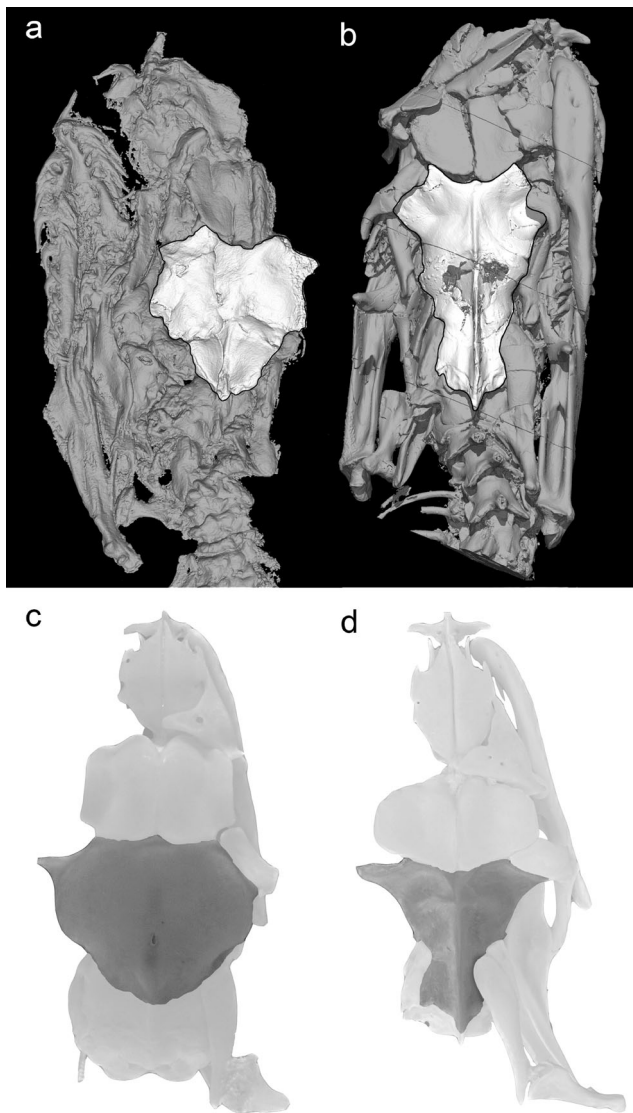


Fig. 3 Ontogenetic development of the parietal in boid snakes. **a** Juvenile specimen (SMF ME 11332) and **b** adult specimen (SMF ME 11398) of *Palaeopython fischeri* from Messel as seen in CT reconstructions. The parietal is highlighted. **c, d** Juvenile and adult specimens of *Boa constrictor*. The parietal is more darkly coloured

mid-trunk vertebrae. They have the typical ‘booid’ shape, that is a tall vertebra with a centrum wider than long, a well-developed neural spine restricted to the posterior region of the neural arch, and a defined haemal keel. The absence of interzygapophyseal ridge and club-like postcloacal vertebrae distinguishes the snake in SMF ME 11332 from pythonines and erylinae, respectively. The trunk vertebrae of described Messel minute boids *M. variatus* and *R. ermannorum* present a contrasting morphology with the snake in SMF ME 11332. Vertebral morphology and count is also consistent with *P. fischeri*. The most complete referred specimen, SMF ME 2504, has 296 precloacal vertebrae and 72 cloacal and caudal vertebrae, for a total vertebral count of 368 (Schaal, 2004).

Thus, the snake in SMF ME 11332 shows similarity in detail to *P. fischeri* and differs in all these respects from the other described Messel boids, *M. variatus* and *R. ermannorum*. The snake in SMF ME 11332 does not differ in any distinct way from *P. fischeri* that cannot be attributed to small size (see below on ontogenetic stage). We identify the snake in SMF ME 11332, therefore, as *P. fischeri*.

Ontogenetic stage of the snake

The snake in SMF ME 11332, with a SVL of about 89 cm, is only half the size of other specimens referred to *P. fischeri*. In paratype SMF ME 1002, SVL is 177 cm and in SMF ME 2504 it is 191 cm (Schaal 2004). SMF ME 1607 is missing the skull but the remainder of the body anterior to the cloaca is 186 cm. The holotype vertebrae, SMF ME 929 (Fig. 2f), are similar in size to those of the specimens mentioned above.

Based on personal observations, ontogenetic transformations in the parietal bone observed in boine snakes may be useful in determining the ontogenetic stage of the snake in SMF ME 11332. Like those of adult boine skulls examined (*Boa*, *Corallus*, *Epicrates*, *Chilabothrus*; Fig. 3d), the parietal of large specimens of *P. fischeri* (SMF ME 1002, 1607, 2504, and 11398; Fig. 3b) displays a distinctly projected posterior region, which includes supratemporal processes and a pointed sagittal crest that broadly overlap prootics and supraoccipital. Furthermore, the sagittal crest occupies most of the anterior region of the parietal. In contrast, juvenile specimens of extant boids (Fig. 3c), like SMF ME 11332 (Fig. 3a), exhibit a short parietal bone, which has a poorly developed posterior region and has a lateral contact with the rest of the neurocranial bones; the sagittal crest is restricted in the posterior region of the parietal only. We consider that these anatomical traits present in the parietal bone, together with the short SVL in comparison with large specimens, indicate a juvenile postnatal ontogenetic stage for the snake in SME ME 11332.

The lizard

Description

Overlapping relations of the snake ribs and lizard skeleton clearly show that the lizard was situated inside the snake body (Fig. 2a). The lizard was swallowed headfirst. The tip of the snout is at the level of snake vertebra c. 173, about 53 cm from the snout-tip or 60 % of SVL. The bone surfaces are well-preserved and show little evidence of corrosion, as by gastric fluids. A kink in the vertebral column centred on the fifth vertebra in front of the sacrum possibly represent an injury inflicted by the snake in the act of predation, but a postmortem cause cannot be ruled out.

The lizard has a SVL of about 7.9 cm. The tail was at least 11.8 cm in length; its distal portion is covered by the snake’s

vertebral column and cannot be identified (Fig. 2a). Assuming only compression perpendicular to the bedding plane, the lizard may have had a maximum torso diameter of around 17 mm. The skull is seen in left lateral view, except the skull roofing bones, whose ventral surface is turned toward the observer. The prefrontal evinces a groove beneath the boss. The jugal shows a restricted exposure below the orbit. The postorbital is large and contributed significantly to the posterior orbital margin. The squamosal has a strong dorsal process. The teeth are numerous, parallel-sided, and tricuspid; they were almost certainly pleurodont. Presacral vertebral count is roughly 23–25. Caudal vertebrae numbers c. 5–9 show transverse processes (fused caudal ribs) but lack evidence of an autotomy plane. More posterior vertebrae are difficult to individuate, but show in places that autotomy planes and transverse processes were absent. Thus, the lizard shows the *Basiliscus*-type caudal vertebral morphology (Etheridge 1967). Vertebral bone can be discerned even at the point where the tail disappears beneath the snake vertebral column, indicating that it had not been lost by that point. The hindlimb was elongate, much longer than the forelimb and roughly two-thirds of SVL. The scapula is elongate.

Taxonomic identification

The dorsal process of the squamosal is a characteristic found only among iguanian lizards among extant squamates, and the low vertebral count is consistent with this. (Whether these are plesiomorphies or apomorphies depends on the relative position of Iguania in Squamata; cf. Gauthier et al. 2012 and Reeder et al. 2015.) Tricuspid teeth with well-developed mesial and distal accessory cusps also belong in this category (Smith 2009), although they evolved independently in other squamate groups. Two apomorphies suggest a relation to extant basilisks (Corytophaninae, comprising the extant genera *Basiliscus*, *Corytophanes*, and *Laemanctus*) and their stem: a groove on the orbital rim beneath the prefrontal boss, and elongate hindlimbs (Smith 2009). The loss of transverse processes on most caudal vertebrae is also consistent with this identification, as is the restricted lateral exposure of the jugal beneath the orbit. The lack of autotomic planes on caudal vertebrae is furthermore an apomorphic, diagnostic features of the *Geiseltaliellus maarius* from Messel, a species on the stem of Corytophaninae (Smith 2009; Smith and Wuttke 2012). As no other iguanian is known from Messel, much less another one showing these diagnostic traits, we identify the lizard as *G. maarius*.

The insect

The insect is poorly seen in SMF ME 11332 as prepared, but it was clearly visible and documented on the originally exposed surface (Fig. 4a). It consists of parts of the cuticula, clearly

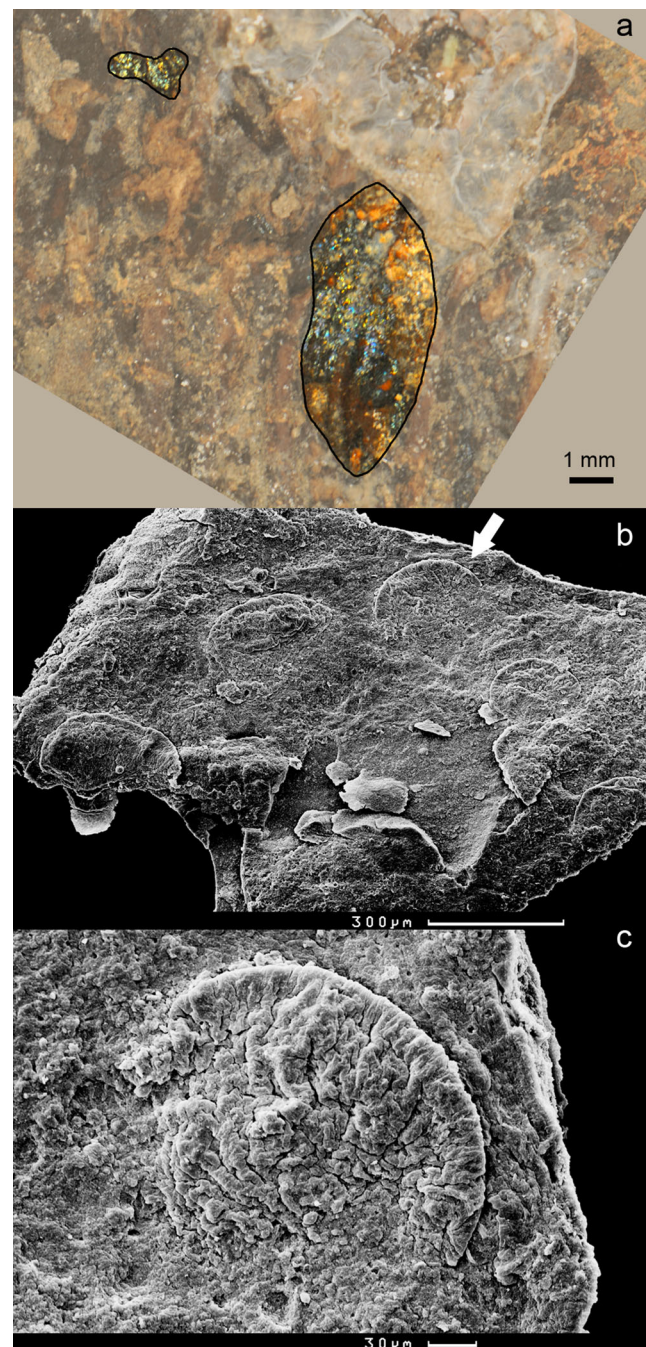


Fig. 4 **a** Photograph of the insect in the abdominal cavity of the lizard on the excavated side (now embedded in epoxy resin) of SMF ME 11332. Insect cuticle shimmers blue-green, indicating that structural colour is preserved. Cuticle was accentuated by drawing of contour and fading of surroundings. The insect is scarcely visible in the prepared specimen. **b** Scanning electron micrographs of gut tract contents of *Geiseltaliellus maarius* SMF ME 11380. Arrow points to the globule shown at higher magnification in **c**

distinguished by the preserved structural colouration so well known in Messel insects (Parker and McKenzie 2003; McNamara et al. 2011). However, structural colouration and visible morphological features do not allow a more precise

identification of the insect (S. Wedmann, pers. comm., 2016). It is located at a transverse level about midway between the pectoral and pelvic appendages of the lizard.

Diet in other specimens of *Geiseltaliellus maarius*

G. maarius SMF ME 11380 has a SVL of 9.1 cm (Smith and Wuttke 2012). Identifiable gut contents did not contain insect cuticula but rather plant remains. These consisted of a cluster of five small (200–300 µm in maximum length), apparently organic globular structures (Fig. 4b). These globular structures are slightly flattened on the well-defined end, which we interpret to be apical. The structures become indistinct basally. All of them show a similar apicobasal orientation. They are highly compressed in the bedding plane (parallel to observer's viewpoint and perpendicular to the apicobasal axis). The surface of these structures is highly crenellated (Fig. 4c). The size, shape, clustering, and surface texture do not correspond to known animal parts, as far as we know. Thus, this individual may have consumed plant matter (V. Wilde, pers. comm. 2016).

Discussion

To our knowledge, SMF ME 11332 represents only the second reported three-level trophic chain embodied in a single specimen. Previously, Kriwet et al. (2009) reported on a Devonian shark that had ingested two temnospondyls, one of which had ingested a small acanthodian. It is also one of the few direct records of squamate diet in the fossil record. Apart from the henophidian snake studied by Greene (1983), which is similar in size and habitus to *P. fischeri*, and *Ornatocephalus metzleri* (Weber 2004), the contents of the digestive tract have only been reported in aquatic mosasaurian squamates (e.g. Martin and Fox 2007; Lindgren et al. 2010; Buchy and Smith 2011).

Vertebrate meals are processed relatively fast in the stomach of macrostomatan snakes. Studies on gastric digestion rates in pythons, colubrids, and viperids show that non-elongate prey animals like rodents can be almost completely digested in 3–4 days. Moreover, in the second day post-feeding, snakes had reduced the mass of the ingested prey in the stomach by about 25 %, with clear signs of digestion in those body regions that first reach the stomach such as head and

Table 1 Position of the posterior end of the stomach in extant snakes (AS, pers. obs.)

Species	SVL (cm)	Snout- posterior tip length (cm)	% SVL
<i>Epictia australis</i>	15.8	10.5	66.4
<i>Epictia albipuncta</i>	23.3	15.0	64.4
<i>Amerotyphlops brongersmianus</i>	22.4	15.3	68.3
<i>Anilius scytale</i>	64.7	45.5	70.3
<i>Cylindrophis maculatus</i>	35.3	26.9	76.2
<i>Rhinophis sp.</i>	34.4	21.6	62.8
<i>Python regius</i>	64.4	36.6	56.8
<i>Epicrates cenchria</i>	67.2	38.6	57.4
<i>Boa constrictor</i>	162.3	70.8	43.6
<i>Corallus hortulanus</i>	84.7	49.8	58.8
<i>Ahaetula prasina</i>	64.2	46.8	72.9
<i>Bothrops diporus</i>	63.4	32.0	50.5
<i>Chironius bicarinatus</i>	101.3	58.0	57.2
<i>Leptodeira annulata</i>	45.8	27.5	60.0
<i>Leptophis ahaetula</i>	89.3	45.5	50.9
<i>Lygophis anomalus</i>	44.0	24.4	55.4
<i>Lystrophis dorbignyi</i>	43.7	22.7	51.9
<i>Micrurus pyrrochryptus</i>	94.2	71.3	75.7
<i>Mussurana bicolor</i>	42.0	26.5	63.1
<i>Oxyrhopus rhombifer</i>	74.5	43.9	58.9
<i>Philodryas baroni</i>	95.5	60.7	63.6
<i>Philodryas psammophidea</i>	58.4	30.4	52.1
<i>Sibynomorphus turgidus</i>	47.4	27.4	57.8
<i>Tomodon ocellatus</i>	43.9	23.4	53.3
† <i>Palaeopython fischeri</i> (SMF ME 11332)	89	53	59.6

limbs (Blain and Campbell 1942; Skoczylas 1970; Secor and Diamond 1995, 2000; Secor 2008). The completeness of the lizard specimen in SMF ME 11332, especially the skull and distal regions of the limbs, and the lack of obvious digestive corrosion on the bone surface, indicate that the snake died soon after its last meal, at most 1 or 2 days after.

Anatomical remarks

In general, the stomach of macrostomatan snakes is an elongated saccular organ (Retzius 1830 [1831]), which is joined with the tubular esophagus by a poorly defined gastroesophageal junction (Helmstetter et al. 2009; pers. obs.). The posterior tip, in contrast, is easier to recognise due to the presence of a thick muscular pyloric sphincter. In post-prandial snakes, the prey may completely fill the stomach, but part of it may also be accommodated in the esophagus. In consequence, only the posterior tip of the stomach can be marked with accuracy in post-prandial snakes through the position of the prey. Taking into account the absence of digestion in the lizard in SMF ME 11332 and its position within the snake ribcage, we suggest that the posterior tip of the stomach in *P. fischeri* was positioned approximately in the vertebrae 173, about 53 cm from the snout-tip or 60 % of SVL (Table 1). Although there exists a small ontogenetic shift in the position of the visceral organs in snakes (Anderson and Secor 2015), we consider this spatial inference applicable also for adult specimens of *P. fischeri*. This position is normal for snakes, which have the posterior tip of the stomach between 50–75 % of the SVL (Table 1).

Assuming the insect was present in its stomach (as opposed to the esophagus or intestine), the stomach of the lizard would be situated about midway between the pectoral and pelvic appendages. This position appears to be unremarkable for lizards, particularly iguanians (Reynolds 1939; Harris 1963; Zaher et al. 2012).

Prey-handling behaviour

Prey-handling behaviour in snakes may depend on prey taxonomic identity and prey size (Loop and Bailey 1972; Mori 1991). It is thought that prey with appendages, such as lizards or mice, are easier to swallow headfirst, such that the snake expends less energy doing so (de Queiroz and de Queiroz 1987), and it has been observed that relatively larger prey are more commonly swallowed headfirst (Mori 1991). The lizard in SMF ME 11332 was of low diameter by comparison with the snake (relative prey size around 0.63), which is associated in extant species with a lower probability of headfirst ingestion (Mori 1991). The crocodylian in the snake studied by Greene (1983), with a much higher ratio, was also swallowed headfirst.

Niche relations

G. maarius is the most common lizard species in Messel, represented by nearly a dozen specimens (Smith and Wuttke 2012). The elongated penultimate phalanges, long hindlimbs and tail (Smith 2009), and pseudoautotomy (intervertebral urotomy; see Slowinski and Savage 1995) seen in *G. maarius* are most consistent with arboreal habits (Smith 2009; Smith and Wuttke 2012). The SVL of the lizard in SMF ME 11332, c. 7.9 cm, is 81 % of highest-recorded SVL and 160 % of SVL of the smallest known specimens, SMF ME 901. [This measurement is from the tip of the snout to the sacro-caudal joint, the approximation for SVL used by Smith and Wuttke (2012). It must be noted, however, that they overlooked the careful X-radiographic study by Blob (1998), who found that the vent is typically located around the level of the boundary between the first and second caudal vertebrae. Thus, the measurement used here and by Smith and Wuttke probably underestimates true SVL.] One specimen of *G. maarius* that unfortunately lacks a skull may represent an animal distinctly larger than the largest measurable specimen (Smith 2009). Thus, the lizard in SMF ME 11332 was ontogenetically advanced but not fully grown.

Table 2 Ontogenetic dietary shift in extant boids. Order of taxa in the diet of *Boa constrictor* reflects decreasing relative importance

Species	Juvenile diet	Adult diet	Macrohabitat	References
<i>Boa constrictor</i>	Lizards, birds, mammals	Mammals, birds, lizards	Terrestrial	Boback 2005; Pizzatto et al. 2009; Sironi et al. 2000
<i>Candoia aspera</i>	Lizards (skinks)	Mammals	Terrestrial	Harlow and Shine 1992
<i>Candoia bibroni</i>	Lizards (skinks)	Mammals	Arboreal	Harlow and Shine 1992
<i>Chilabothrus striatus</i>	Lizards (anoles)	Birds, mammals	Arboreal	Henderson et al. 1987
<i>Chilabothrus gracilis</i>	Lizards (anoles)	Lizards (anoles)	Arboreal	Henderson et al. 1987
<i>Corallus enydris</i>	Lizards (anoles)	Lizards, mammals, birds	Arboreal	Henderson 1993
<i>Corallus grenadensis</i>	Lizards (anoles)	Lizards, mammals, birds	Arboreal	Henderson and Pauers 2012
<i>Corallus hortulanus</i>	Frogs, lizards	Lizards, mammals, birds	Arboreal	Pizzatto et al. 2009; Henderson and Pauers 2012
<i>Epicrates crassus</i>	Mammals	Mammals, birds	Terrestrial	Pizzatto et al. 2009

The extant lineages of basilisks have relatively similar habits. *Basiliscus* has been most intensively studied. Small individuals (SVL <9 cm) feed exclusively on arthropods, but larger individuals have a greater dietary breadth, including shrimp, fish, frogs, snakes, birds, and mammals, in addition to arthropods, and commonly 20 % plant matter (sometimes much more): especially flowers, fruits, and seeds (Echelle et al. 1972; Hallinan 1920; Barden 1943; Fleet and Fitch 1974; Duellman 1990). *Basiliscus* is known to spend considerable time on the ground (Hirth 1963), and indeed its common name ('Jesus Christ lizards') refers to the propensity to run across water (e.g. Hallinan 1920). *Corytophanes* was regarded as an arboreal ambush predator (Andrews 1979). Although it feeds largely on arthropods (Andrews 1979; Sasa and Monrós 2000), it also includes annelids, coleopteran larvae, and snakes in its diet, suggesting that it occasionally ventures to the ground to forage (Sasa and Monrós 2000). *Laemanctus* has a diet that includes arthropods, snails, frogs, and lizards (McCoy 1968; Lee 2000). It is predominantly arboreal but is observed to run bipedally when encountered on the ground (McCoy 1968; Lee 1996).

The sister-clade to Corytophaninae is probably *Anolis* (Pyrón et al. 2013) or *Anolis* + *Polychrus* (cf. Smith 2009; Reeder et al. 2015). *Polychrus* is considered arboreal (Vitt and Lacher 1981; de Avila Pires 1995). *P. acutirostris* was only observed to descend to the ground for oviposition (Vitt and Lacher 1981). Its diet consisted of a large variety of arthropods as well as up to 22 % plant parts by volume (Vitt and Lacher 1981; Garda et al. 2012), one-quarter of which was seeds (Vitt and Lacher 1981). *P. guttuosus* also consumes plant material as an adult (Duellman 1990). Most members of the clade *Anolis* are arboreal, although some species spend varying amounts of time on the ground (Williams 1972; Köhler 2008; Losos 2011). Plant consumption by *Anolis* is apparently quite rare (Cooper and Vitt 2002).

In summary, extant basilisks and their probable sister group are predominantly arboreal. Extant basilisks may all forage on the ground to some extent, most notably *Basiliscus*. Plant consumption by larger individuals is well known in *Polychrus* and *Basiliscus* but unknown in *Corytophanes* and *Laemanctus*.

The question is now raised whether anything can be determined about the habitat of *P. fischeri* based on the occurrence of *Geiseltaliellus* in the stomach of a juvenile specimen. Boid snakes—including Ungaliophiinae as well as Boinae—and *Loxocemus* are the only booid taxa that are currently sympatric with corytophanine lizards. Adult individuals of the tree boa *C. ruschenbergerii* (SVL = 113–161 cm) are recorded as taking adult *B. basiliscus* (Henderson and Pauers 2012), but we know of no other record of boids preying on basilisks.

Most macrostomatan snakes experience an ontogenetic dietary shift, which implies the dietary change from small ectothermic prey as juveniles to bulky prey as adults (Cundall and Greene 2000). In the case of boines, lizards are the most

common prey of juvenile individuals (Table 2), especially those arboreal species, and moreover in some arboreal forms lizards constitute the most important prey type during the entire lifespan (Henderson et al. 1987; Harlow and Shine 1992; Henderson 1993; Boback 2005; Pizzatto et al. 2009; Henderson and Pauers 2012).

Conclusions

In conjunction with dietary data on extant basilisks (Corytophaninae) and phylogenetic position, the consumption of plant matter by larger individuals of *G. maarius*, an early stem relative of Corytophaninae (Smith 2009), suggests that this propensity might be primitive for Corytophaninae or Corytophaninae + (*Polychrus* + *Anolis*) as a whole. This interpretation would be strengthened if Conrad's (2015) view of the relationships of *Geiseltaliellus* is correct. Available data suggest dietary shift from insectory to omnivory in *G. maarius*.

Similarly, in conjunction with the presence of a crocodile in the large boid specimen from Messel studied by Greene (1983), the presence of an arboreal lizard in the alimentary canal of a juvenile individual of *P. fischeri* indicates that this dietary preference during juvenile stages and perhaps an ontogenetic dietary shift was present in boid snakes since the middle Eocene.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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