



Eolacertidae: a new extinct clade of lizards from the Palaeogene; with comments on the origin of the dominant European reptile group – Lacertidae

Andrej Čerňanský^{a,b} and Krister T. Smith^b

^aFaculty of Natural Sciences, Department of Ecology, Comenius University in Bratislava, Bratislava, Slovakia; ^bSenckenberg Research Institute and Natural History Museum Frankfurt, Palaeoanthropology and Messel Research, Frankfurt am Main, Germany

ABSTRACT

We describe a new lizard taxon, *Stefanikia siderea* gen. et sp. nov., from the early-middle Eocene locality of Messel in Germany based on a nearly complete skeleton, which we studied using μ CT methods. It shares many characters with the Eocene taxon *Eolacerta*, which is broadly distributed in the Eocene of central and Western Europe, but is much smaller and shows several important anatomical differences. The new discovery sheds light on the paleodiversity of these lizards in the Eocene of Europe, and the new family name Eolacertidae is proposed to encompass *Eolacerta* and *Stefanikia*. The relationships of *Eolacerta* have been intractable. Our phylogenetic analyses confirm that Eolacertidae is a member of the clade Lacertiformes and provide strong support for a sister-group relationship to Lacertidae. In some places, skin impressions are preserved, displaying the body scalation. As such, the exquisitely preserved specimens of Eolacertidae from Messel provide new insight into the morphology and ecology of lizards on the stem of Lacertidae, Europe's dominant group of living reptiles.

<http://zoobank.org/urn:lsid:zoobank.org:pub:DFD01563-A913-4286-B64B-E0912474FD08>

ARTICLE HISTORY

Received 20 March 2017
Accepted 3 May 2017

KEYWORDS

Squamata; Eocene; Messel; Germany

Introduction

In terms of species diversity, Lacertidae is Europe's dominant group of reptiles (Arnold et al. 2007). Only the snake clade Colubridae (sensu Szyndlar 2012) comes close. Whereas Colubridae is widely considered to have originated in Asia (Head et al. 2005; Rage et al. 2008; Chen et al. 2013) and successive waves of colubrids or colubrid relatives dispersed to Europe starting in the late Eocene (Ivanov 2001), the origin of Lacertidae is thought to be Europe (Arnold et al. 2007), where the fossils considered closest to the lacertid crown are also found (Borsuk-Białynicka et al. 1999; Čerňanský & Augé 2013). However, unambiguous fossils on the lacertid stem have not yet been recognized, or are fragmentary and have not been incorporated into phylogenetic analyses. Thus, evolution and ecology of the lacertid stem remain largely unknown.

The most complete possible relative of Lacertidae is a large lizard, *Eolacerta robusta*, originally described by Nöth (1940) from the middle Eocene of Geiseltal in eastern Germany. That author assigned this species to the family Lacertidae, emphasizing its close similarity to extant lacertids. Rieppel (1980a) first raised doubts about its relationship to Lacertidae. He investigated an incomplete skeleton (lacking most of the cranium) from the Messel Pit (Messel) and argued that *Eolacerta* is not related to Lacertidae and could be considered at most a primitive 'scincomorphan'. (Morphological support for the monophyly of

Scincomorpha continues to be strong [e.g. Gauthier et al. 2012], but paraphyly of this group is indicated by all genetic-based phylogenetic analyses [e.g. Townsend et al. 2004; Vidal & Hedges 2009; Pyron et al. 2013]). Later, Müller (2001) redescribed the osteology of *Eolacerta robusta* based on new complete skeletal material from Messel. He corrected the osteology in several respects and provided a detailed description of the entire skeleton. He concluded that *Eolacerta* is so primitive that it could not be assigned to any modern lizard 'family' and could at best be classified as *Scleroglossa incertae sedis*. One year later, Müller (2002) described disarticulated material from the early Eocene locality of Prémontré (France) as *Eolacerta* sp. More recently, Conrad (2008) suggested that *E. robusta* is the most basal known relative of the clade Anguimorpha. In Müller et al. (2011), *Eolacerta* was inferred to be a sister taxon to Mesozoic *Meyasaurus* within Scincoidea.

A new lizard fossil from the early-middle Eocene of Messel – a nearly complete skeleton lacking only the distal portion of the tail – sheds light on the problematic relationships of *Eolacerta*. The specimen derives from the Middle Messel Formation of the Messel Pit, an early-middle Eocene (Lenz et al. 2015) lake deposit near Frankfurt am Main, which is famous for the extraordinary preservation of its fossils (Schaal & Ziegler 1992; Smith et al. Forthcoming). Apart from its relatively small size, the new specimen is substantially similar to *Eolacerta robusta*. The new

taxon from the Messel locality, belonging to the same clade, sheds new light on this problematic taxon and demonstrates the paleodiversity of this archaic lizard clade in the middle Eocene of Europe.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, USA; BSPG, Bayerische Staatssammlung für Paläontologie, Munich, Germany; CM, Carnegie Museum of Natural History, Pittsburg, USA; DE, Department of Ecology, Comenius University in Bratislava, Slovakia; Pb, National Museum, Prague, Czech Republic; SMF, Senckenberg Research Institute and Natural History Museum in Frankfurt am Main, Germany; UF, University of Florida Museum of Natural History, Gainesville, USA; ZMB, Zoology collection of the Museum für Naturkunde, Berlin, Germany.

Material and methods

Material and computed tomography

The study is based on SMF ME 11241, a nearly complete skeleton from the Middle Messel Formation of the Messel Pit. Like other specimens from Messel, it was completely freed from the rock matrix and embedded in epoxy slabs. These slabs provide for excellent density contrast with the bone (e.g. Franzen et al. 2009; Müller et al. 2011). SMF ME 11241 was scanned on a TomoScape HV 500 (Werth Messtechnik GmbH) in an industrial μ CT facility funded by the Wolfgang Pfeiffer Stiftung at the Technical University in Deggendorf, Germany (200 mA, 165 kV, 1600 steps, voxel resolution 25.175 μ m). The volume file was analyzed using VG Studio Max v2.2 on a high-end computer workstation at Senckenberg.

Phylogenetic analysis

Our analysis of the phylogenetic relationships of SMF ME 11241 is based on the character-taxon matrix of Gauthier et al. (2012), which includes 610 characters. Although Simões et al. (2016) have concerns about some characters, their reanalysis did not affect the relationships of Lacertiformes, in which our initial analyses (not based on the Gauthier et al. matrix) placed the fossil. SMF ME 11241 and *Eolacerta robusta* were both scored. We excluded snakes, mosasaurs, and polyglyphanodontians, whose relationships are controversial. *Eolacerta* has never been thought close to those groups, and Gauthier et al. (2012) showed that the relationships of limbed taxa and of living taxa are robust to their exclusion. Due to this taxon deletion, 112 characters of the matrix became invariant.

We added nine characters of relevance for Lacertiformes, three of which are new:

611. Nasal length relative to frontal length: (0) nasals very short – 0.33 or less of the frontal length, (1) nasals short, from one-third to one-half (0.50) of frontal length, (2) more than one-half. (ordered) Note that this character is a refinement of the primitive state of Gauthier et al. (2012, character 28).

612. Medial ridge of jugal (Černanský et al. 2014): (0) Type 1, (1) Type 2, (2) Type 3, (3) Type 4. Note that this character deals with the relative position of the medial ridge, not its degree of expression (cf. Gauthier et al. 2012, character 157).

613. Osteoderm fused to angle of jugal: (0) absent, (1) present.

614. Interparietal shield (Estes et al. 1988): (0) overlaps frontal, (1) restricted to parietal.

615. Parietal cranial crests (cristae cranii) posteriorly (Peters 1962): (1) converge strongly in adults, forming a strong median crest with longitudinal sulcus ventral to parietal fossa (recessus processus ascendens), (0) do not converge.

616. Mandibular fossa (Estes et al. 1988): (0) restricted, (1) broadly open (at least 50% of width of mandible at mid-length of fossa).

617. Bodenaponeurosis (new): (0) Posterior crest of coronoid largely hidden in medial view by medial crest that descends posteromedial process, (1) posterior crest of coronoid visible in medial view for most of height of coronoid process (i.e. posteriorly extensive).

618. Discrete maxillary facet on frontal, bordered laterally by frontal (Arnold 1989): (0) absent, (1) present.

619. Lateral arms of interclavicle (Arnold 1989): (0) directed laterally or obliquely forwards, (1) directed obliquely backwards.

Following convention, between-state scaling (Wiens 2001) was employed. Following Gauthier et al. (2012), additive multistate characters were ordered. The matrix was analyzed by maximum parsimony (MP) and Bayesian inference (BI). MP was implemented in PAUP v. 4a150 (Swofford 2002), with the following parameters: heuristic search, TBR branch-swapping, 1000 repetitions. Bootstrap support was evaluated with 100 individual heuristic searches with identical parameters but only 100 repetitions each. In order to study the possible influence of differing sequence- and morphology-based trees, we also implemented a heuristic search with a ‘backbone’ topology in which *Amphisbaenia* is forced to be the sister-group to Lacertidae. BI was implemented in MrBayes v. 3.2.6 (Ronquist et al. 2012) with default parameters and additive characters ordered as above. The analysis was allowed to run for 10 Mg (million generations), and 25% of the trees were discarded as burn-in. Convergence was checked with ‘sump’.

Comparative specimens used

The following specimens of extant lizard species plus the *Sphenodon* outgroup, were used for comparison: Sphenodontidae: *Sphenodon punctatus* (SMF 7426); Lacertidae: *Lacerta viridis* (DE 51, SMF 84623 and 33207), *L. agilis* (DE 78–79, SMF 49552, 49555, 49554 and 49557), *Timon pater* (SMF 33208), *Zootoca vivipara* (SMF 49560 and 49561), *Podarcis muralis* (SMF 12477, 50060, 44976, 49566, 49570, 50059 and 49584), *Psammotromus algirus* (SMF 45478, 49551), *Gallotia galloti* (SMF 13452 + 3 specimens, pers. coll. of A.Č.); Teiidae: *Tupinambis teguixin* (SMF 69852, 33242, ZMB 13570, 19073, 19075, 19077, 25471, 25472), *Teius teyou* ZMB 13845, 14542, 16139); Gymnophthalmidae: *Neusticurus bicarinatus* (UF 54554); Xantusiidae: *Xantusia riversiana* (CM 56451 and 56457); Scincidae: *Plestiodon fasciatus* (CM 38472), *Eumeces algeriensis* (CM 144945); Iguanidae: *Basiliscus plumifrons* (UF 61951); Gerrhosauridae: *Gerrhosaurus flavigularis* (UF 51543; UF 62345), *Broadleysaurus major* (pers. coll. of A.Č.); Cordylidae: *Smaug giganteus* (SMF 69852 and 69842); Chamaeleonidae: *Chamaeleo calyptratus* (DE 65, 74–77), *Furcifer oustaleti* (SMF 59447 and 73685), *Trioceros jacksonii* (SMF 90037); Shinisauridae: *Shinisaurus crocodilurus* (UF 71623); Anguillidae: *Ophisaurus ventralis* (AMNH 73057; UF 52539; CM 1411; CM 144985), *Pseudopus apodus* (DE 1, 3–13, 22, 23, 29, 52, 54, 58, 59; BSPG 1982 X 2383). Additionally,

a specimen of *Gallotia atlantica* was CT-scanned at the Museum für Naturkunde in Berlin.

Geological setting

The Middle Messel Formation represents the stable phase of a former maar lake. The basin in which the lake deposit accumulated formed by phreatomagmatic explosions around 48.2 Ma (for details on age, see Lenz et al. 2015). The formation is dominated by a laminated algal pellicle, the dark-brown to black Messel 'oil-shale'. The most recent age estimates based on astronomical tuning suggest that the fossiliferous horizons of the Middle Messel Formation span the Ypresian-Lutetian (early-middle Eocene) boundary (Lenz et al. 2015).

The taphonomic history of the Messel vertebrates is debated (Richter & Storch 1980; Franzen & Köster 1994; Koenigswald et al. 2004; Joyce et al. 2012; Smith & Wuttke 2012). However they arrived at the lake bottom, they were preserved with extraordinary fidelity. Complete skeletons, outlines of soft body parts, integumentary remains such as hair, feathers, and skin, and contents of the digestive tract are commonly preserved. These offer a unique opportunity to study the adaptive strategies of locomotion, feeding, defence, orientation, and even reproduction. The diverse Messel fauna is composed of sponges, arthropods, fishes, amphibians, reptiles, birds, and mammals (Schaal & Ziegler 1992; Smith et al. *Forthcoming*). The Messel locality is inferred to represent a paratropical forest.

Systematic palaeontology

We first provide a definition of the new taxon name *Eolacertidae* that is consistent with the PhyloCode (Cantino & de Queiroz 2010). Subsequently we provide a definition for a corresponding family in the Linnean rank-based system. It should be noted that the clade name follows the taxon name *Eolacerta* and has nothing to do with 'Eolacertilia' erected by Robinson (1967; see also Estes 1983).

Eolacertidae New Clade Name

Definition – The most inclusive clade containing *Eolacerta robusta* Nöth, 1940 but not *Lacerta viridis* Linnaeus, 1758 or any other extant squamate

Hypothesized composition – *Eolacerta robusta* Nöth, 1940; *Stefanikia sidera* Čerňanský and Smith (this paper)

Diagnostic apomorphies – (1) osteoderm fused to angle of jugal; (2) frontals (partially) fused in adult individuals; (3) origin of adductor musculature dorsal on supratemporal process; (4) partial overlap of parietal by postfrontal; (5) Meckelian groove restricted; (6) angular reaches level of mandibular condyle.

Squamata Opper, 1811

Lacertiformes Estes, Queiroz and Gauthier, 1988

Eolacertidae fam. nov.

Type genus – *Eolacerta* Nöth, 1940

Included genera – *Eolacerta* Nöth, 1940; *Stefanikia* Čerňanský and Smith (this paper)

Known distribution – Paleocene to late Eocene of Belgium, France and Germany

Diagnosis – Shares with Lacertidae the following plesiomorphies: (1) osteoderms absent from body, (2) parietal foramen present, (3) sulcus dentalis present.

Shares with Lacertidae the following derived features: (1) two co-dominant supraoculars; (2) osteodermal shields fused to the dermal roofing skull bones; (3) occipital shield clearly defined; (4) osteoderms present along periphery of the skull table; (5) nasals ventral contact beneath premaxillary internasal process is absent, except near apex; (6) the maxilla-frontal contact present, the maxilla leaving a discrete facet on the frontal; (7) ectopterygoid posterior process prominent; (8) presence of incipient zygosphenes-zygantrum; (9) a posterior interruption of the ventromedial loop of the clavicle (assuming Gallotiinae is basal in Lacertidae); (10) preacetabular spine on ilium present.

Possesses the following plesiomorphies with respect to Lacertidae: (1) interparietal shield of the parietal overlaps the posteromedial region of the frontal; (2) parietal foramen located more anteriorly, in the anterior quarter of the parietal; (3) parietal cranial crests (cristae cranii parietalis) run parallel rather than converging to form a median ridge with sulcus; (4) supratemporal fenestra only partially closed; (5) ornamentation of cranial osteoderms dominated by small grooves (not pits); (6) ventral margin of dentary nearly straight rather than convex; (7) anterolateral process of coronoid does not overlap dentary; (8) ilium is broad, relatively posterodorsally short.

Synapomorphies: (1) osteoderm attached to angle of jugal; (2) frontals (partially) fused; (3) origin of adductor musculature dorsal on supratemporal process; (4) partial overlap of parietal by postfrontal; (5) Meckelian groove restricted; (6) angular reaches level of mandibular condyle.

Stefanikia gen. nov.

Type species – *Stefanikia siderea* sp. nov.

Generic diagnosis – As for type and only known species.

Etymology of generic name – To recognize the contribution made by Dr. Milan Rastislav Štefánik (21 July 1880–4 May 1919), a Slovak scientist – astronomer, traveler, aviator, general and politician – one of the founders of the former Czecho-Slovakia. He tragically died in a plane crash at young age.

***Stefanikia siderea* sp. nov.**

Figures 1–11

Holotype – SMF ME 11241, a nearly complete skeleton, lacking only the distal portion of the tail.

Locality and horizon – Messel Pit, Germany, Middle Messel Formation; early–middle Eocene.

Etymology of specific name – Latin *siderea* – stellar (M. R. Štefánik was an astronomer)

Diagnosis – An eolacertid, differing from *Eolacerta robusta* by the following combination of features: (1) distinctly smaller body size: SVL (snout-vent length) around 15 cm (using the middle of the second sacral vertebra as the position of the vent; after Blob [1998]), whereas in *Eolacerta* it is 27 cm; (2) nasal process of premaxilla shorter, not reaching so far posteriorly; (3) postorbital ramus of jugal narrow rather than broad; (4) posteroventral process of the jugal long, pointed; (5) suborbital ramus of jugal long, such that the lacrimal is more anterodorsally situated and the prefrontal less ventrally extensive; (6) transverse sulcus of

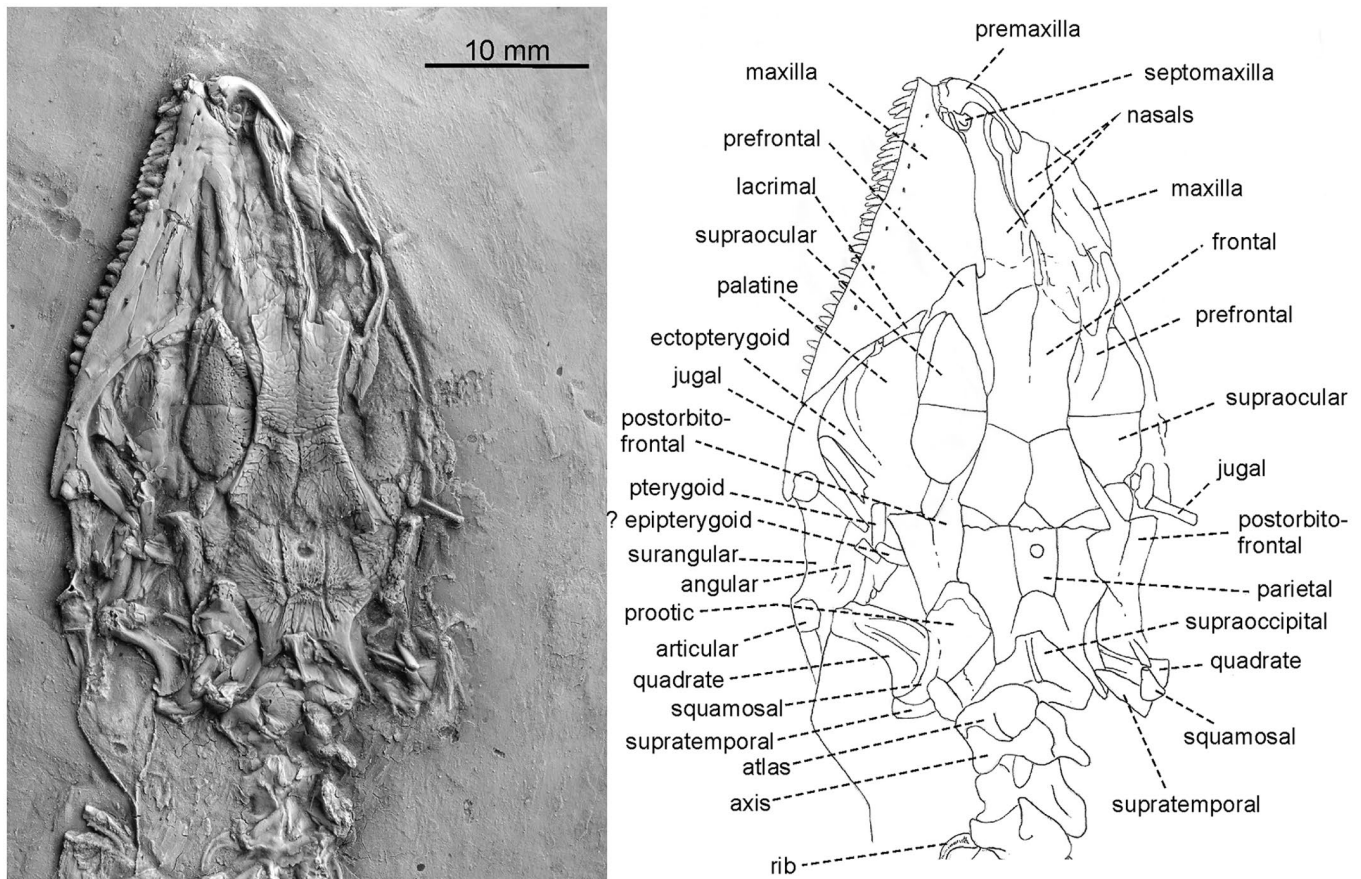


Figure 1. Skull of *Stefanikia siderea* gen. et sp. nov. in dorsal view, holotype SMF ME 11241.

the parietal distinctly convex anteriorly, rather than straight; (7) interparietal shield rectangular rather than laterally expanded anteriorly; (8) parietal table relatively broad in comparison to its length; (9) parietal constricted only posteriorly, lacking additional constriction in mid-region; (10) groove separating frontal and frontoparietal shields (sulcus interfacialis) V-shaped rather than straight; (11) frontal shields relatively longer: the posterior portion of the frontal, beyond sulcus interfacialis forms 30% of the whole frontal length, whereas in *E. robusta* it is around 40%; (12) lower maxillary tooth count (25 instead of 30–32 in *Eolacerta*); (13) shorter maxillary tooth row length, not extending posterior to midorbit (possibly correlated with tooth count); (14) maxillary–jugal suture smooth rather than stepped; (15) posterior end of ilium is squared-off rather than tapering.

Description

Skull. The skull is obliquely compressed diagenetically (Figures 1 and 2). On the whole the skull is box-shaped (for a reconstruction, see Figure 3) with well-developed canthal and temporal crests, as suggested by strong edges on both the maxilla and postorbitofrontal. The snout was probably low, as suggested by the strongly posteriorly curved nasal process of premaxilla.

Dermal skull roof

Premaxilla. The premaxillae are fused, forming a single T shaped element (Figure 4). Only one tooth is preserved; the others are

missing. The estimated tooth count is 6–7 (based on the mirror symmetry). The nasal process of the premaxilla is slender, forming a long, posterodorsally elongated process, tucked deeply between the nasals. Near its terminus it is slightly expanded laterally. The dorsal surface of the nasal process is smooth. The posterior premaxillary foramen for the ethmoidal nerve is located close to the base of the nasal process. The tooth-bearing base of the premaxilla has a well-developed posterior supradental shelf. The median incisive process forms a weakly bilobed structure that underlies the supradental shelf.

Septomaxilla. The septomaxilla is a paired, flat element forming the dorsal and posterior borders of the chamber for Jacobson's organ. Only a part of the left septomaxilla is visible at the posteroventral side of the left external naris. The visible portion is small, simple, and bowl-shaped (or D-shaped – medially concave with a central depression). Its dorsal margin was most likely in contact with the nasal bone.

Maxilla. The maxilla is a long, large element. It has a prominent facial process, nearly triangular in shape. Its dorsal portion contains a small, hook-shaped region that inserts in a discrete facet on the frontal, as seen in Lacertidae and occasionally in scinoid lizards. The external surface is pierced by 15 labial foramina arranged into two rows above the jaw parapet. Shallow grooves are associated with some of them. The rest of the surface of the facial process has a weak ornamentation, formed by several irregular grooves. Ventrally, the supradental table (sensu Rage & Augé 2010) bears about 25 tooth positions. The maxilla is excluded from the orbit by the long suborbital process of jugal

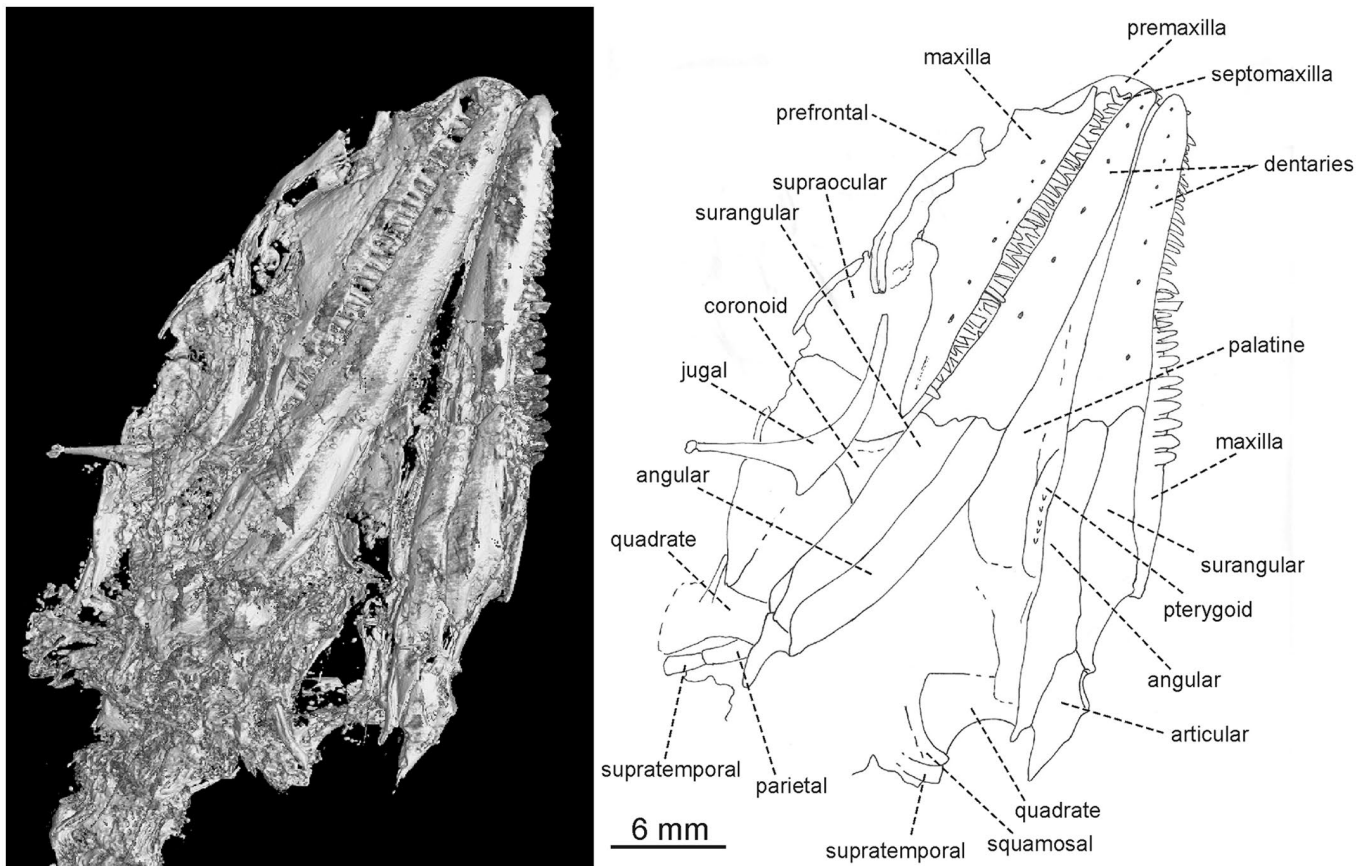


Figure 2. Skull of *Stefanikia siderea* gen. et sp. nov. in ventral view using computer tomography.

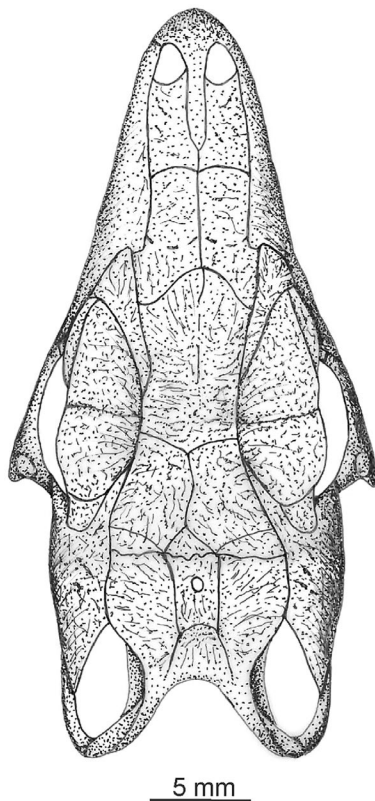


Figure 3. *Stefanikia siderea* gen. et sp. nov. Skull reconstruction in dorsal view.

and by the lacrimal. The contact with jugal is straight, without a step (sensu Arnold 1989; see also Čerňanský 2012; Gauthier et al. 2012). The suborbital margin slopes smoothly to the tip. A nasolacrimal ridge (sensu Smith & Gauthier 2013) is present, as in most scinoid, lacertiform and anguimorph lizards (Smith 2006; Čerňanský & Bauer 2010).

Nasals. The nasals are poorly preserved. They are paired and have a median contact posterior to the nasal process of the premaxilla. They are long and relatively slender but grow slightly in width anteriorly. They are slightly sculptured dorsally by several shallow grooves. Besides these, a deeper, more prominent, diagonally directed groove is located in their posterior half, marking the border between the prefrontal and frontonasal shields.

Prefrontal. The prefrontal is triangular in shape and contributes to the anterodorsal border of the orbit. It is mediolaterally narrow in dorsal aspect, with a long posterior frontal process along the orbital margin. Anteriorly, it is ventrolaterally extensive. Its dorsal surface is ornamented, particularly on the frontal process.

Lacrimal. The lacrimal is completely preserved on the left side along the posterodorsal margin of the facial process of the maxilla. It is a small, elongate bone. Its thickness increases anterodorsally, which lends it a club-shaped appearance in lateral view. Its external surface is almost smooth; only the anterodorsal region indicates a presence of a slight ornamentation. It has a dorsal contact with prefrontal.

Jugal. The jugal is L-shaped (Figure 5). It has two long, narrow processes or rami, postorbital and suborbital, that form

the ventral and posterior margin of the orbit. At the angle of the bone posteroventrally is a short but distinct posteroventral process. The orbital lamina is sharp and smoothly curved. The suborbital process is very long and contributes in part to the anteroventral margin of the orbit. There appears to be a small attached osteodermal mass on the angle of the jugal just above the posteroventral process. The external surface of the jugal is smooth, but it is pierced by several foramina, some with short associated grooves. On the medial surface, the medial ridge is revealed by the CT reconstruction. On the postorbital process, the medial ridge is located close to the anterior margin of the bone, creating a broad posterior region behind the ridge. On the suborbital process, the medial ridge runs ventral to mid-height, forming a broad orbital surface.

Frontals. The frontals (Figure 6(A)–(D)) are partially fused. The CT reconstruction clearly shows a synostosis in the middle part, but anteriorly the left and right elements were partly separated during diagenesis. The lateral margins of the frontals are slightly concave, and the bone is narrowest at mid-orbit. The frontals are elongate and relatively broad, widening posteriorly to form the wedge-shaped posterolateral corners. The dorsal sculpture is strongly developed, consisting of densely arranged ridges and grooves, with larger and deeper grooves marking the boundaries between epidermal shields (*sensu* Meszoely 1970). Beneath

the frontal shield, they are oriented transversely. The anterior region is long, and the bone grows slightly broader anteriorly. It possesses a V-shaped groove, pointed anteriorly, that marks the boundary between the nasofrontal and frontal shields. The terminus of the prefrontal articulation forms a small step on the lateral margin of the frontal. The postorbitofrontal articulations are located posteriorly. The prefrontals and postorbitofrontals are not in contact, so the frontal is exposed on the orbital margin. In ventral aspect, the frontal cranial crests (*cristae cranii frontalis*) are slightly arched medially, but well-developed subolfactory processes are not developed (Figure 6(C) and (D)). Their height increases very slightly anteriorly, reaching a maximum extent at approximately the level of the middle of the prefrontal facet.

Parietal. The parietal is a large azygous element consisting of the parietal table with an ornamented surface and two posterolaterally diverging supratemporal processes (Figure 6(E) and (F)). The posterior half of the parietal table is distinctly laterally constricted; its margins are rounded, concave. For this reason, the lateral margin can be divided into two regions. The anterior one bears a facet for the postorbitofrontal, while the posterior rounded one forms the medial margin of the supratemporal fenestra. The supratemporal fenestra is thus partially open posteriorly, unlike in extant lacertids. The table is divided by grooves arranged in the shape of the letter H, which mark the boundaries between shields. The interparietal shield covered the parietal foramen. The portion of it located on the parietal is rectangular in shape with a concave posterior margin. Its triangular anterior region overlaps the posterior region of the frontal on the midline. The parietal foramen is situated in the middle of the shield, near the frontoparietal suture. The occipital shield, immediately behind the interparietal shield, extends to the posterior end of the bone. The transverse sulcus is convex anteriorly. The parietal shields are butterfly-wing shaped, distinctly wider anteriorly than posteriorly. Their anterior portions overlap the frontal too. The parietal table is ornamented beneath all scutes. The ornamentation consists of distinct grooves, ridges, pits and foramina with a vaguely radial orientation. The supratemporal processes are relatively long and curved posteroventrolaterally. Their lateral surfaces form the medial margins of the supratemporal fossae, where the adductor musculature originated (Haas 1960). The supratemporal sits on the lateral surface of the supratemporal process. The nuchal fossae are narrow and laterally developed. On the ventral surface of the parietal, a pair of low ridges – the

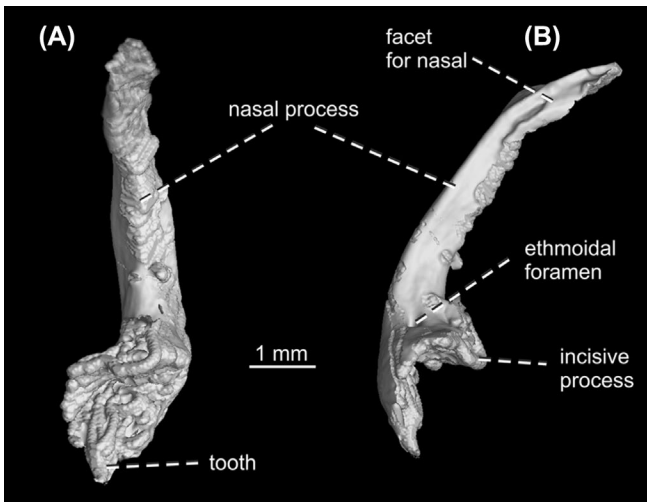


Figure 4. *Stefanikia siderea* gen. et sp. nov., premaxilla in posterior (A), and lateral (B) views.

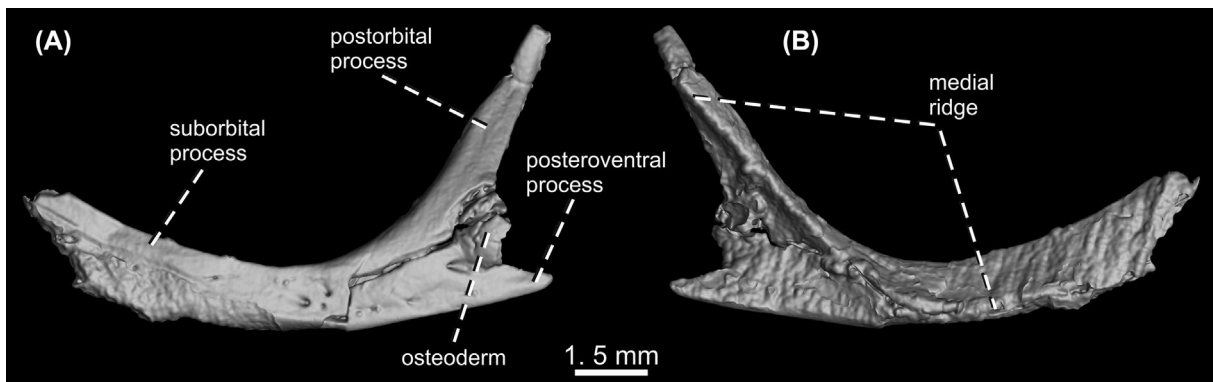


Figure 5. *Stefanikia siderea* gen. et sp. nov., jugal in lateral (A), and medial (B) views.

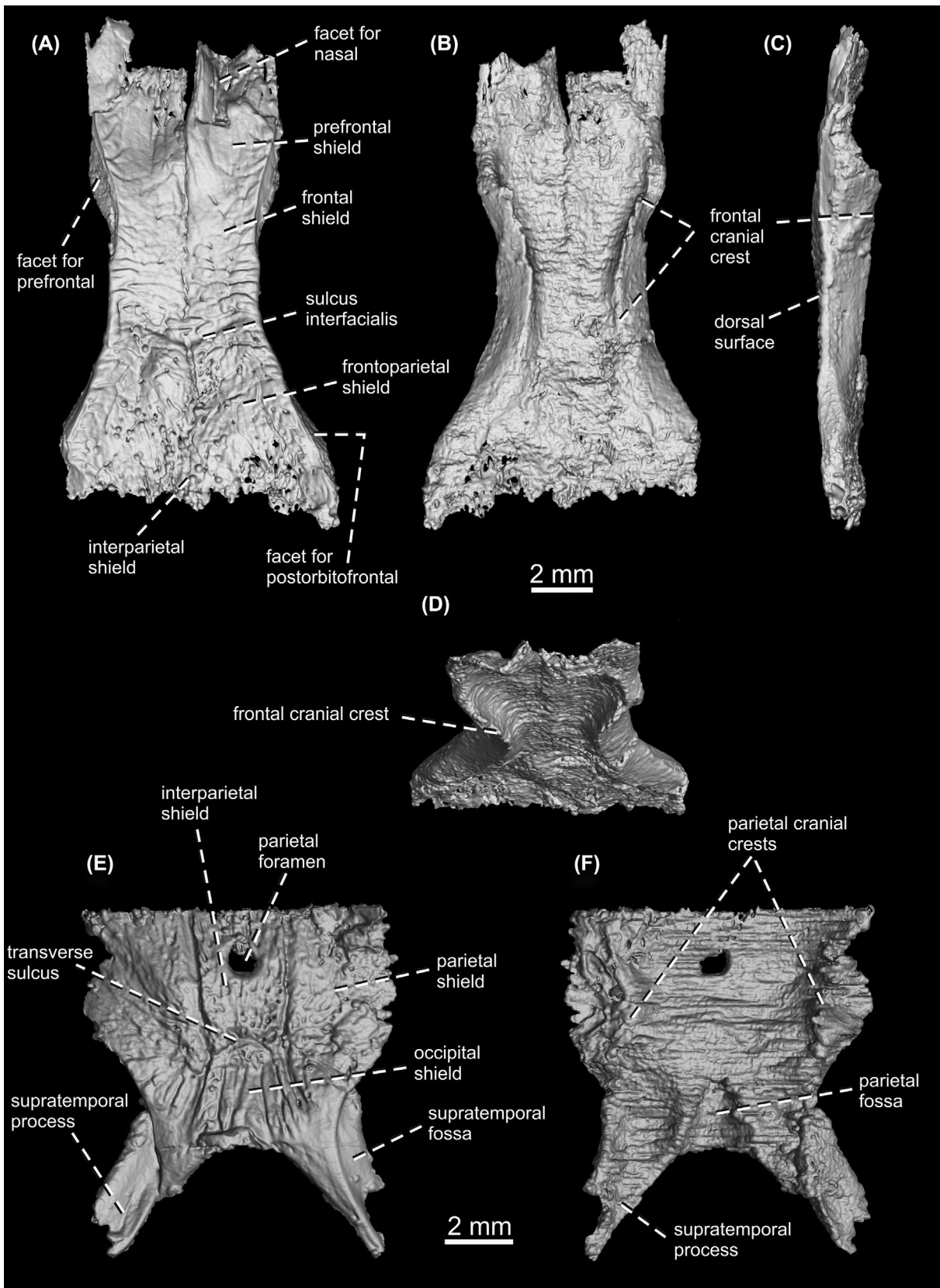


Figure 6. *Stefanikia siderea* gen. et sp. nov., frontal in dorsal (A), ventral (B), lateral (C) and anteroventral (D) views. Parietal in dorsal (E) and ventral (F) views.

parietal cranial crests (cristae cranii parietalis) – runs parallel to the lateral margin of the parietal plate (Figure 6(F)). Near mid-length, the cristae cranii branch, forming a medial pair that converge toward the midline and a lateral pair that form the

ventral edge of the supratemporal processes. The parietal fossa (recessus processu ascendenti) is tongue-shaped and its anterior margin is much more sharply demarcated. The medial branch of the cristae cranii do not converge to form a strong median crest

in front of, or posterior to the fossa, as in many extant lacertids. The juxtafoveal crest is a high, forming a sharp wall. Its posterior margin gradually diminishes and merges into the medial margin of the supratemporal process.

Postorbitofrontal. As indicated by the CT reconstructions, the postorbital is fused with the postfrontal on both sides to form a subrectangular element. The element is posteriorly expanded, tapering slightly posteriorly. The element is forked medially, with a long and narrow anterior process sutured to the posterolateral margin of the frontal. It also has a short anterolateral process that is weakly (Gauthier et al. 2012) sutured to the very short postorbital process of the jugal. The lateral portion is characterized by a strong temporal crest that points to a box-shaped skull. Dermal sculpturing is present along its dorsal and lateral surfaces, consisting of irregular grooves. A longitudinal groove medial to the temporal crest marks the boundary between the parietal shields medially and a labial shield laterally.

Squamosal. The squamosal is preserved on both sides. It is a slender, mediolaterally compressed bone, having a hockey-stick shape. It forms the posterolateral margin of the supratemporal fenestra. There is a short process descending to the quadrate. Some dermal rugosities are visible in the anterior region. Anteriorly, this bone tapers and attaches to the postorbitofrontal. There was likely no direct contact between the squamosal and parietal.

Supratemporal. The supratemporal is at least partially visible on both sides, and the mediolaterally broadened posterior region is especially visible on the left side. This narrow triangular bone attaches laterally to the supratemporal process of the parietal, forming a wedge between the parietal and squamosal. It seems that its rounded end attached the quadrate too. Its posterior portion is slightly curved ventrolaterally.

Palpebral. A palpebral could not unequivocally be identified.

Osteoderms. At least three and possibly four supraocular osteoderms are present in SMF ME 11391. The presence of the first (anterior-most) supraocular is difficult to ascertain due to crushing. Assuming it was present, the next two supraoculars are large and co-dominant. The fourth is much smaller. Lateral to the first large supraocular and nearly as long is a very narrow osteoderm corresponding to a supraciliary scale (sensu Gauthier et al. 2008), as is commonly found in lacertids. Small osteodermal masses appear to be present in the temporal region of the skull, but otherwise osteoderms are lacking in the skeleton.

Quadrate. The left quadrate is visible in lateral view. It is a massive, dorsoventrally elongate bone. The thick, rounded posterior crest arches posterodorsally and expands to form a condyle (*condylus cephalicus*), so that the bone has an oblique orientation. The lateral conch broadens dorsally; its edge is nearly straight and vertical. The ventral end forms a poorly preserved, saddle-shaped articular condyle (*condylus mandibularis*).

Ectopterygoid. The ectopterygoid is clearly visible inside of the left orbit, on the ventrolateral side. Its broad lateral portion is strongly oblique, extending anterolaterally to contact the maxilla and jugal. A well-developed posterolateral process is present. More medially, the ectopterygoid is anteroposteriorly short. The medial portion, which contacts the pterygoid, is relatively slender, so the suborbital fenestra is widely open.

Pterygoid. The pterygoid is poorly preserved. Remains of the bone are visible in the left orbit. The quadrate process is long and

narrow, and its posterior end is flattened. The CT reconstruction shows very fragmented remains of the left pterygoid and reveals a linear arrangement of small, conical teeth (Figure 7).

Mandible

Dentary. The dentary is a slender, anteroposteriorly elongated bone (Figure 8). The external surface is pierced by a series of 7–8 labial foramina, located in the dorsal third of the bone. Otherwise, the lateral surface is smooth. The dentary tapers anteriorly. A subdental groove (*sulcus dentalis*) is present and Meckel's groove is fully open. The ventral margin of the dentary is almost straight.

Coronoid. The coronoid is preserved, visible on the right side in the CT reconstruction. The bone is triangular in shape with a strong dorsal (coronoid) process. On the lateral side, the anterior margin bears a ridge (or keel, sensu Müller 2001), where the ventral aponeurosis of *M. adductor mandibulae externus pars superficialis* inserts (see Haas 1973).

Angular. The angular is an anteroposteriorly elongated element that forms the posteroventral region of the mandible. In lateral view, it is slightly more slender than the surangular.

Surangular. The surangular is a huge, elongated bone, forming the dorsal margin of the posterior region of the mandible. It narrows posteriorly, where it contacts the articular. The anterior end of the bone is slightly elevated dorsally. The anterior portion is partially visible in the left orbit of the specimen, underlying the ectopterygoid.

Prearticular + articular. The prearticular and articular are fused, forming the posterior and posteroventral margins of the mandible. The articular surface (*trochlea articularis*, glenoid) is rounded, slightly compressed laterally. It forms an extended dorsal process located behind the surangular. The whole articulation surface is slightly inclined posteroventrally, so its anterior margin is higher than the posterior one. Posteriorly behind the articulation area, the bone bears a retroarticular process. It appears to taper posteriorly. Its smooth dorsal surface is gently concave in transverse section, forming a shallow, wide anteroposteriorly oriented groove flanked by sharp ridges.

Dentition. The dentition is pleurodont. The teeth are conical and unicuspid in *Stefankia siderea*, like in *Eolacerta robusta* (see also Nöth 1940; Müller 2001). Müller (2001) mentioned that only in very few cases could an indistinct second cusp be observed.

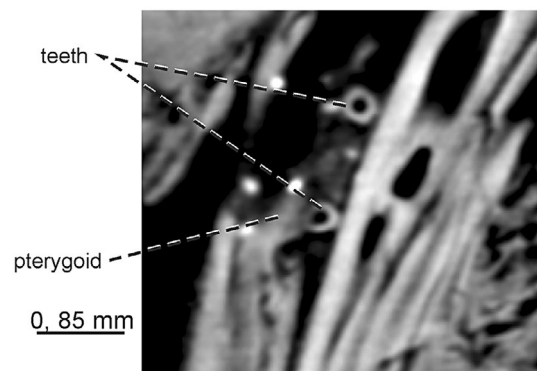


Figure 7. *Stefankia siderea* gen. et sp. nov., μ CT slice of pterygoid showing the presence of dentition.

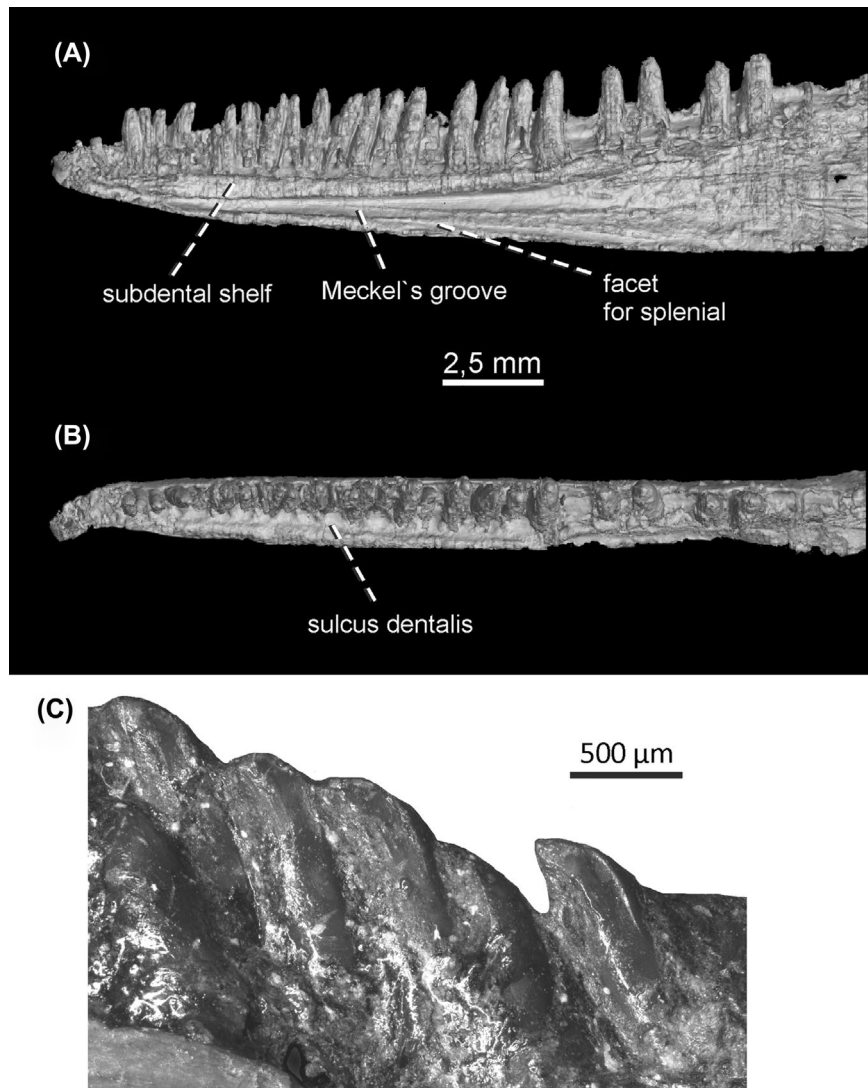


Figure 8. *Stefanikia siderea* gen. et sp. nov., dentary in medial (A), dorsal (B) views and (C) detail of teeth.

Some heterodonty is developed – teeth in the posterior region are larger and less curved than teeth in the anterior region. Teeth in the dentary are somewhat smaller than teeth in the maxilla. There is a high number (around 28) of pointed, recurved teeth in the dentary, each of which bears a culmen lateralis anterior and posterior (terms after Richter 1994). The teeth lack lingual cusps where they are visible in lingual view (right maxilla anteriorly) and are not clearly visible in the CT scan. Between the culmina, a pattern of striations can be observed on the lingual surface of the tooth crown. This condition is observed in Scincoidea (see e.g. Kosma 2004), which comprises extant Cordyliformes plus Scincidae and their fossil relatives Paramacellodidae, among others (Evans & Chure 1998; Gauthier et al. 2012). The presence of lingual striations and absence of lingual cusps make a tooth crown similar to that in Paramacellodidae.

Braincase

Supraoccipital. The supraoccipital is largely visible posteriorly behind the parietal. It is displaced so that its anterior region slightly overlaps the parietal around the midline. It is roughly

trapezoidal in shape and forms the dorsal surface of the braincase, the dorsal part of the inner ear capsule, and the dorsal margin of the foramen magnum. It is markedly expanded posterolaterally and the most prominent structure of its dorsal surface is the straight, median dorsal ridge that was continuous with the processus ascendans of the synotic tectum. The ridge does not reach the foramen magnum.

Prootic. The prootic is a triradiate bone that ossifies in the anterior half of the otic capsule and forms the dorsolateral extent of the braincase. The left prootic, only partially preserved, is visible in the region of the left supratemporal fenestra. The anterior region, which presumably formed an alar process, is unfortunately damaged (the elongate, anterodorsally oriented alar process of prootic was considered a synapomorphy of *Scleroglossa* by Estes et al. 1988). The anterior semicircular canal is discernible as a bulge on the surface of the prootic. However here, a part of it is exposed as distinct groove-like structure, because the bone roof that covered it collapsed during fossilization. Posteriorly, the bone forms a depression, which is distinct but likely exaggerated during fossilization – it seems to be more collapsed into the space of the acoustic recess. The posterior process, which overlaps the

paroccipital process of the otooccipital (=exoccipital + opisthotic; Evans 2008) anteriorly, is broken and slightly rotated from its normal posterodorsal direction. Its terminus appears forked.

Postcranial skeleton

The vertebrae are poorly preserved in general (Figure 9). Twenty-six presacral and two sacral vertebrae are present. The first eight represent cervical vertebrae. The lack of the greater part of tail distally makes impossible to know the original number of caudal vertebrae. All vertebrae are procoelous, as far as they can be observed.

Atlas. The atlas articulates with the occipital condyle, thus connecting the skull with the rest of the vertebral column. Each neural arch half consists of a pedicle and lamina. In lateral view, the pedicles appear thicker anteriorly, and the laminae are broad and rounded, giving the bone as a whole the shape of a ping-pong paddle. The neural arch is anteroposteriorly widest at the level of the short triangular posterodorsal process. The neural arch is nearly vertical and is markedly lower than the neural spine of the axis. Ventrolaterally there is a pointed transverse process. It is short and posterolaterally oriented. The posterodorsal process, positioned higher, is short and narrow and forms the connection with the prezygapophysis of the axis – still articulated in the specimen. The contact area is located on the ventromedial side of the posterodorsal process, which does not project posteriorly beyond this area.

Axis. The axis is markedly shorter than it is tall. The dorsally elevated neural spine is broad and fan-shaped. Its irregular dorsal margin is slightly concave. It is inclined anteriorly. The rounded prezygapophyses are preserved under the posterodorsal processes of the atlas. They are slightly medially inclined. The postzygapophyses are robust, tapered laterally. The centrum is short.

Cervical vertebrae. The cervical vertebrae have tall neural spines. Unfortunately, they are poorly preserved.

Dorsal vertebrae. The dorsal vertebrae are broad with a well-developed interzygapophyseal constriction. Laterally, the centrum bears a well-developed bulbous synapophysis, located anteriorly. The centrum is roughly triangular, and ventrally it possesses a blunt mid-sagittal ridge. Its lateral margins are concave. The neural spines are robust, elevated posterodorsally. Posteriorly they gradually become slightly shorter. The top of the median dorsal crest, the neural spine, is slightly convex. Many vertebrae are poorly preserved, but some anterior vertebrae show an incipient zygosphenes-zygantral articulation, which appears to become more strongly developed on posterior vertebrae

Sacral vertebrae. The sacral vertebrae, two in number, are fused. Their general shape is similar to that of the dorsal vertebrae, except for the extremely robust transverse processes that expand laterally to contact the ilium.

Caudal vertebrae. The caudal vertebrae are poorly preserved. The vertebrae are missing after about the middle of the 8th. The transverse processes of the first caudal vertebra are oriented slightly posterolaterally, but those of the second caudal are oriented laterally and those of more distal caudals slightly anterolaterally. They decrease in size posteriorly. The neural spine is preserved only on some vertebrae. It is long and thin, elevated posterodorsally. The prezygapophyses are well developed,

rounded, and medially inclined. The postzygapophyses are posterolaterally expanded. The hemal arches are prominently developed, having a small constriction in the middle region. The incipient zygosphenes-zygantral articulations seen in the dorsal series are present here as well.

An outline of the skin is preserved on the tail with scarcely visible imprints of rectangular dermal scales. It gives the impression that the tail in the living animal was massive in this region.

Ribs. The first rib is found on the 4th cervical vertebra and is different from other ribs. It is short and strongly curved. More posterior ribs are slightly wider proximally and flattened, being more stick-shaped distally. Posteriorly, the dorsal ribs are more or less stick shaped and possess knobs.

Elements of pectoral girdle are poorly preserved (Figure 10(A)).

Scapula. The scapula is partially preserved on both sides. It is paddle-shaped, growing gradually wider dorsally. Its dorsal end is slightly porous, suggesting that the cartilaginous suprascapula is preserved as well, as in *Geiseltaliellus maarius* (Smith 2009).

Coracoid. The CT reconstruction reveals the prominent coracoid foramen (for the *nervus supracoracoideus*). It is located close to the glenoid articulation. The anterior margin close to scapula is rounded, concave, and extends anteriorly as a process.

Clavicle. The clavicle is largely complete, a robust and strongly curved rod-shaped element. Ventromedially it is expanded for the pectoralis muscle. In *Eolacerta robusta*, a posterior interruption of the ventromedial loop of the clavicle is present. The preserved portion of clavicle in *Stefanikia* is nearly identical to *E. robusta*, and this interruption was very likely present here too.

Interclavicle. The interclavicle is poorly preserved. It is a cross shaped bone, with a long posterior and shorter anterior process. The lateral processes appear to be slightly posterolaterally directed.

Humerus. The humerus is a robust bone expanded at both ends. The proximal and distal epiphyses are fused, indicating that the holotype skeleton corresponds to an animal near adult size. The proximal and distal expansions of the bone are oriented in different planes. The proximal extremity, which forms the upper surface of the head of the bone, is broad. It is expanded slightly more medially than laterally. Here, a tubercle is developed. The deltoid crest is well developed. Directly below the epiphysis, several vascular foramina are developed. The bone becomes narrow distally, forming a robust diaphysis. The CT reconstruction shows a small rounded radial condyle and more medially located ulnar condyle, both located on the ventral side. The huge entepicondylar foramen, forming the orifice of the brachial nerve, is located above the condyle area at the apex of a triangular depression. The entepicondyle (attachment for flexor muscles) is robust and broad, slightly expanded medially. The ectepicondyle, forming the supinator process, is not so expanded. An ectepicondylar foramen is present. Its dorsal surface forms the attachment for the extensor muscles of forearm (see Romer 1956).

Ulna. The ulna is long and more robust than the radius. Its proximal end is slightly more expanded than the distal one. Proximally is the epiphysis that forms a short rounded olecranon process. Close to both epiphyses, some rugosities are located, forming muscular insertions. In the distal one-fourth, a small but well-defined bulge is developed.

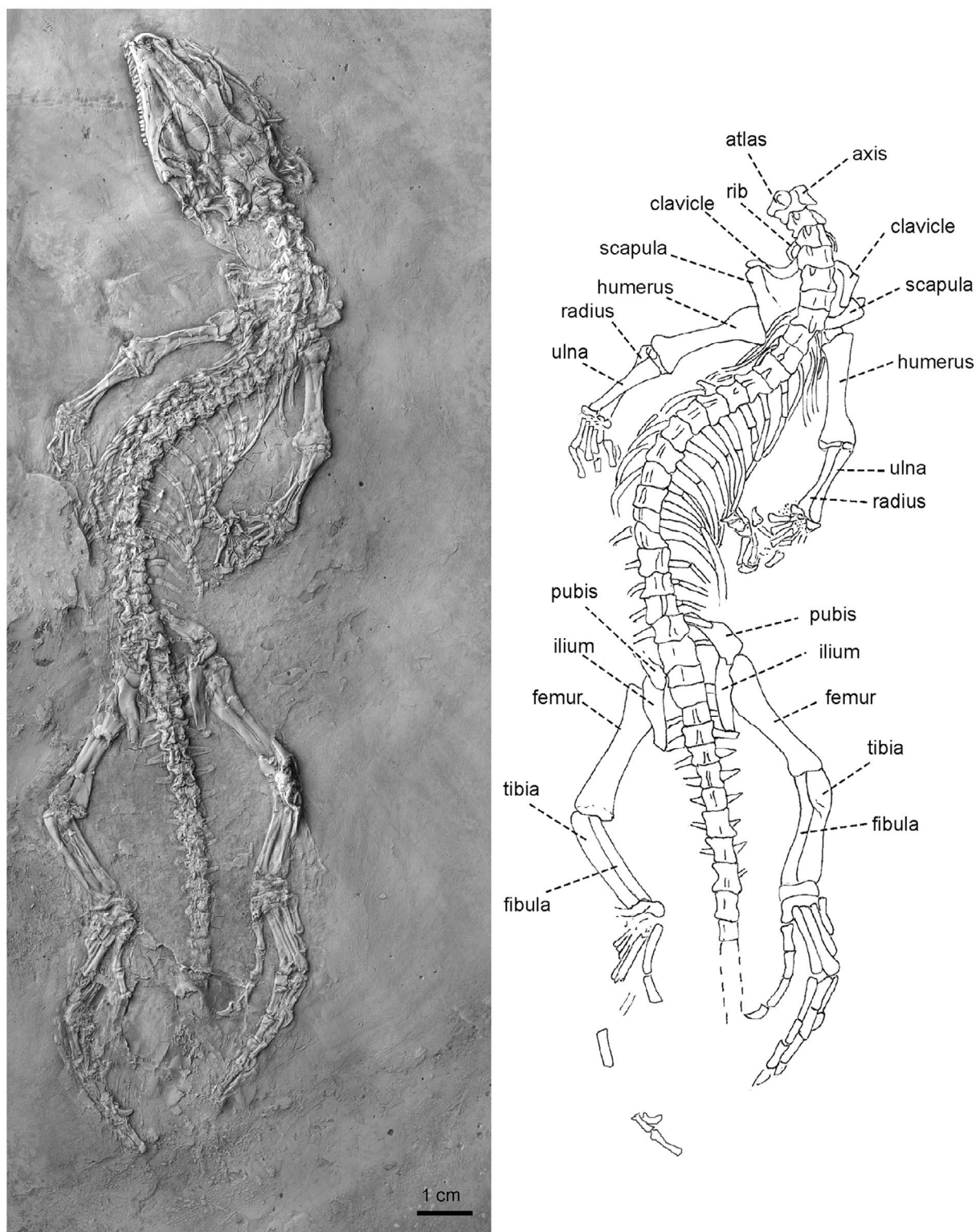


Figure 9. *Stefanikia siderea* gen. et sp. nov., the entire skeleton, holotype SMF ME 11241.

Radius. The proximal and distal expansions of the radius are not so pronounced. The bone is slightly more slender than the ulna. On the left side, the crossing of these two bones is visible.

Carpus, metacarpus and phalanges. The left and right carpus are slightly covered by preserved elliptical to polygonal epidermal scales. In the right carpus, radiale and ulnare are clearly visible. Only three rounded carpals are exposed. The ulnare is roughly

trapezoidal in shape, with rounded margins. It grows wider postaxially. The radiale is much more flattened, bean-shaped, and slightly smaller than ulnare. It increases slightly dorsally, forming a triangular flange. Except for metacarpal I, the metacarpals are long and slender. Metacarpal I is distinctly shorter and robust. The phalanges are long and thin, complete with large, pointed unguals.

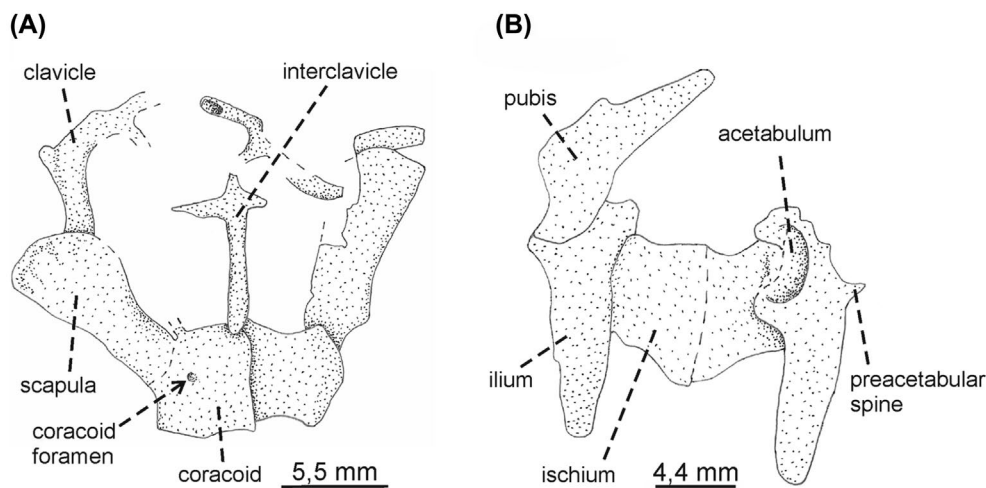


Figure 10. *Stefania siderea* gen. et sp. nov., pectoral region in ventral (A) view, pelvic region in ventral (B) view.

Pelvis. The ilium (Figure 10(B)) is well preserved on both sides. It is a mediolaterally compressed bone with a strong posterodorsal process. The anteroventral margin of the ilium borders the pubis, the posteroventral margin the ischium. Its posterodorsal margin forms a sharp crest, forming a flange encompassing two-thirds the length of the bone, while the anteroventral one is more rounded in cross section. The dorsal margin of this flange is serrated on the left ilium, which is exposed medially. This serration is not observed in the right ilium. Close to the terminus of the flange is a shallow groove. Proximally, the anterodorsally directed preacetabular spine is well developed. Posterodorsally, the ilium gradually tapers. However, the terminus is not pointed but rather squared in lateral view, perhaps representing an area for the origin of anterior caudal tendons. The pubis is visible on the right side. It is wide proximally, contributing to the anteroventral third of the acetabulum. Close to acetabulum is the obturator foramen. The pubis narrows distally, having a rounded dorsal margin. In the middle region of the dorsolateral margin, it forms a blunt process, the propubis. The pubis runs anteroventrally and terminates bluntly. The ischium is only partially preserved medial to the ilium. The exposed region is anteroposteriorly wide. In the CT reconstruction, it is possible to view the ischium ventrally. It is rectangular in shape, broad and flattened.

Femur. The hindlimbs are large, markedly longer than the forelimbs. The femur is a very robust, massively built bone. It is distinctly longer than a humerus. It is weakly S-shaped (especially observed in right femur) and moderately expanded proximally and distally. The articular head, fitting into the pelvic acetabulum, is oval (the left one is not preserved). More ventrolaterally, a tubercle for the attachment of the ischiotrochanteric muscle (Romer 1956) is present. Between it and the articular head, a triangular notch is present. The distal part is formed by tibial condyles, only weakly separated by a shallow trochlea and by distinctly smaller fibular articulation.

Tibia. The tibia is a robust and elongated bone, markedly more massive than the fibula. The proximal region forms a broad contact with femur. The distal part is flattened with a convex end. The tibia of *Stefania siderea* does not appear to taper as strongly in the distal part of the diaphysis as that of *Eolacerta robusta* (see Müller 2001).

Fibula. The fibula is a thin, elongated bone, columnar in shape, only slightly expanded proximally and distally. Its proximal region is oval, forming an articulation area with the fibular articulation of femur. The distal region is flattened, with a rounded articular end.

Metatarsus, tarsus and phalanges. The astragalus and calcaneus are fused to one element, forming an astragalocalcaneum. These two bones most likely fuse early in ontogeny, as is the case with most non-iguanian lizards (Romer 1949; Rieppel 1980b). This element is slightly irregular, expanded medially to form a tongue-shape portion (better preserved on the left side). The broad 4th tarsal is well preserved on the right side. Laterally, some other tarsal elements are exposed; a small 1st or 2nd tarsal is visible on the left side. Metatarsal bones are very elongated, relatively massively built, the longest being the 3rd. They are broader distally. The phalanges are robust, complete with massive pointed unguis.

Soft tissue

Skin impressions are preserved in some places (Figure 11). They are clearly recognizable especially on carpus of the right hand, where rounded, elliptical or even nearly hexagonal scaling is present. The right foot shows that scaling on internal side of digits was formed by rectangular subdigital lamellae, proximodistally short and preaxially-postaxially expanded. The scaling on tail was formed by rectangular, slightly anteroposteriorly elongated scales.

Phylogenetic analysis

Our initial analysis (using 135 characters) confirmed a close relationship with Lacertiformes, which led us to conduct an analysis using the larger Gauthier et al. (2012) matrix supplemented by new characters relevant to lacertiforms (see Supplemental data). Phylogenetic analysis using this matrix provides strong support for a sister-group relationship between *Eolacerta robusta* (for Keller/Pohl specimen, see Figure 12) and *Stefania siderea*, i.e. Eolacertidae as presently known (Figures 13 and 14). Bootstrap support in MP is 94%, and the posterior probability in BI is 1.0.

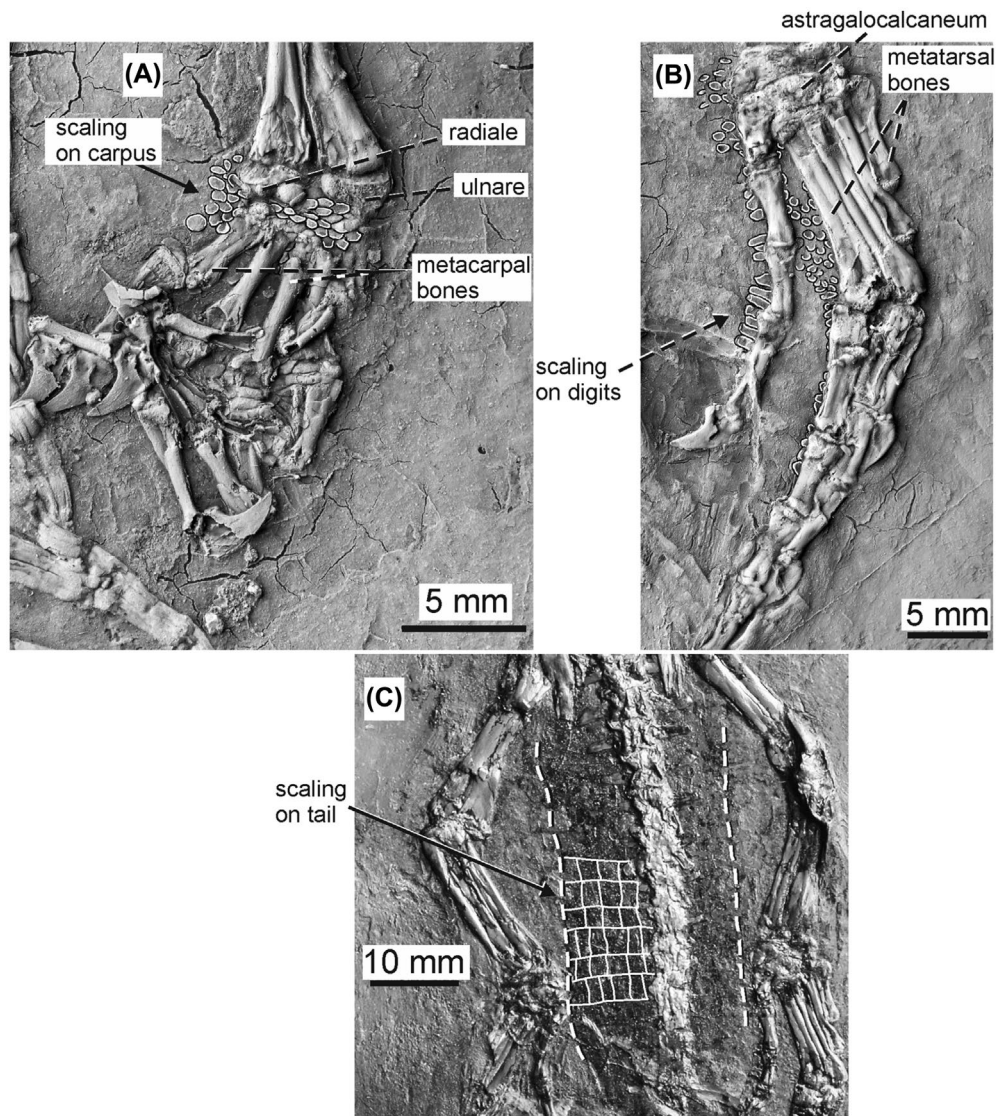


Figure 11. *Stefania siderea* gen. et sp. nov., scaling on hand (A), foot (B) and tail (C).

Seven unambiguous synapomorphies support this relationship (Table 1): fused frontals (character 36: 0→1), partial overlap of parietal table by postfrontal (character 65: 0→1), origin of adductor musculature becomes dorsal on supratemporal process (character 90: 2→1), restriction of Meckelian groove (character 372: 0→1), angular reaches level of mandibular condyle (character 381: 1→0), interruption in clavicle present (character 500: 2→1), and osteoderm fused to jugal (character 613: 0→1). The clavicular notch (character 500) is conceivably a synapomorphy of a larger clade, as it is found in some extant lacertids and various Mesozoic groups (see below). Remarkably, the fused osteoderm to the jugal appears to have evolved convergently within Lacertidae.

Support is even stronger for a sister-group relationship between Eolacertidae and Lacertidae (bootstrap support in MP 96%; posterior probability in BI 1.0). Fifteen synapomorphies support this relationship (Table 1): nasal anterior width less than anterior frontal width (character 18: 1→2), nasal-prefrontal suture absent (character 19: 0→1), nasals not in contact below nasal process of premaxilla (character 24: 0→1),

frontal interorbital width 44–47% (character 48: 3→4 and character 49: 0→1), postfrontal fused to postorbital (character 62: 0→2), short postfrontal supratemporal shelf (character 67: 0→1), postfrontal broad and flat (character 70: 0→1), prominent ectopterygoid posterior process (character 283: 1→0), surangular adductor fossa shallow and not ventrally extensive (character 399: 1→0), iliac tubercle present (character 521: 1→0), osteoderms in supraorbital scales (character 575: 0→1), osteoderms in cheek scales (character 577: 0→1), posterior crest of coronoid extensively visible in medial view (character 617: 0→1), facet on frontal for discrete process of maxilla (character 618: 0→1). Notably, several of these characters were previously inferred – in the absence of identified stem taxa – to be synapomorphies of Lacertidae (Gauthier et al. 2012): 18(2), 49(1), 283(0), 521(0) (ambiguous), 575(1) and 577(1). It is expected that as the evolutionary history of an extant clade becomes better known, features that once diagnosed that clade are found to be synapomorphies of more inclusive clades. That is, the extinction of intermediate forms makes the surviving portions of clades more distinctive (e.g. Darwin 1859).



Figure 12. *Eolacerta robusta*, the skull of Keller/Pohl specimen.

Eolacertidae + Lacertidae forms the sister-group to Teioidea, and together they comprise Lacertiformes. However, as in other morphology-based phylogenetic analyses (e.g. Müller et al. 2011; Gauthier et al. 2012), in contrast to analyses incorporating sequence data (e.g. Müller et al. 2011; Pyron et al. 2013; Hipsley et al. 2014; Reeder et al. 2015), Amphisbaenia is not recovered as part of the lacertiform radiation but instead is pulled into a clade that includes other limbless taxa such as the anguid *Anniella* and the scincids *Feylinia* and *Acontias* ('Krypteia' of Gauthier et al. 2012). Other workers (Estes et al. 1988; Lee 1998; Gauthier et al. 2012; Reeder et al. 2015) have extensively discussed the problems of convergent evolution and limblessness in Squamata. For our purposes, it suffices to note that when we constrain Amphisbaenia and Lacertidae to form a clade to the exclusion of other extant squamates, the sister-group relationship between Eolacertidae and Lacertidae is unaffected in MP analyses. Further analysis with an increased sample of fossil lacertids and other Lacertiformes in future works should test the interpretations of eolacertid relationships provided in this work.

Discussion

Europe has been considered the likely origin of Lacertidae (Arnold et al. 2007), and a number of Palaeogene fossil species have been referred to that clade (e.g. Augé 2005). Particularly strong cases have been made for a close relationship between Lacertidae and the Eocene taxa *Succinilacerta succinea* and *Plesiolacerta lydekkeri* (Borsuk-Białynicka et al. 1999; Čerňanský & Augé 2013). However, these putative close relationships have not yet been corroborated by phylogenetic analyses. Moreover, the relationships of other species have been controversial. Long

after its first description, *Eolacerta* was considered close to extant lacertids, particularly *Lacerta* (Nöth 1940; Estes 1983). On the basis of numerous plesiomorphies, Rieppel (1980a) and Müller (2001) raised doubt about its allocation to Lacertidae, but no consensus has emerged on an alternative hypothesis. As those authors noted, *Eolacerta robusta* (Figure 12) cannot be assigned to any modern lizard family.

Stefanikia siderea is highly similar to *Eolacerta robusta*. The epiphyses of the long bones are not yet fully fused in the former, indicating a subadult stage (frontals are partially fused, postorbital and postfrontal are completely fused). However, the holotype of *S. siderea* has numerous morphological features that distinguished it from *E. robusta* and which cannot be ascribed to ontogeny (there is another specimen of early juvenile of *Eolacerta* which exhibits morphological characters present in adult forms and this will be published later). We propose a new clade name, Eolacertidae, to refer to these taxa. Eolacertidae shows many plesiomorphic characters and cannot be ascribed to crown Lacertidae (Rieppel 1980a; Müller 2001). For instance, the coronoid does not overlap dentary and the interparietal shield overlaps the mid-posterior region of frontal. It should be noted that previous allocation of disarticulated material from the Palaeogene of Europe, such as vertebrae, to *Eolacerta* needs to be met with caution, since Eolacertidae comprises at least two genera. Further revisions of such material might shed more light on this problem.

Additionally, it should be noted that recent phylogenetic studies of *Cryptolacerta hassiaca*, also from Messel and originally considered to be a stem amphisbaenian (Müller et al. 2011), have also placed that species on the stem of Lacertidae (Longrich et al. 2015). This is particularly noteworthy because *C. hassiaca* shows an expanded postorbitofrontal and the typical lacertid pattern of the parietal (Peters 1962), in which the posteromedial branch of the cristae cranii meet anterior to the parietal fossa (recessus processus ascendentes), forming a median crest with a small median groove (pers. obs.).

Comparison of cranial elements

In *Eolacerta robusta*, the suborbital process of jugal is short, and the lacrimal is situated more posteriorly on maxilla, so that its orientation is more horizontal. Because of the long suborbital process of jugal in *Stefanikia siderea*, the lacrimal is situated more anteriorly and more oblique to the horizontal plane. The osteoderm in jugal is much larger in *E. robusta*. Such a fused osteoderm occurs in some lacertids as well. The medial ridge of jugal is of Type 1, as described by Čerňanský et al. (2014), and is probably plesiomorphic.

The triangular anterior region of the interparietal shield of the parietal that overlaps the frontal is a feature present in anguid lizards, but in that clade, the parietal foramen is located more centrally. From this viewpoint, the position of the parietal foramen is more similar to that of the shinisaurid lizards (see Conrad 2004; Klembara 2008). Among 'scincomorphans', the interparietal shield is isolated on the parietal and separated from the frontal bone in Lacertidae (but reversed in some members of the African radiation, e.g. *Meroles* and *Pedioplanis*) and Cordylidae (independently), but it generally overlaps the frontal bone in Scincidae. An occipital shield on the parietal is

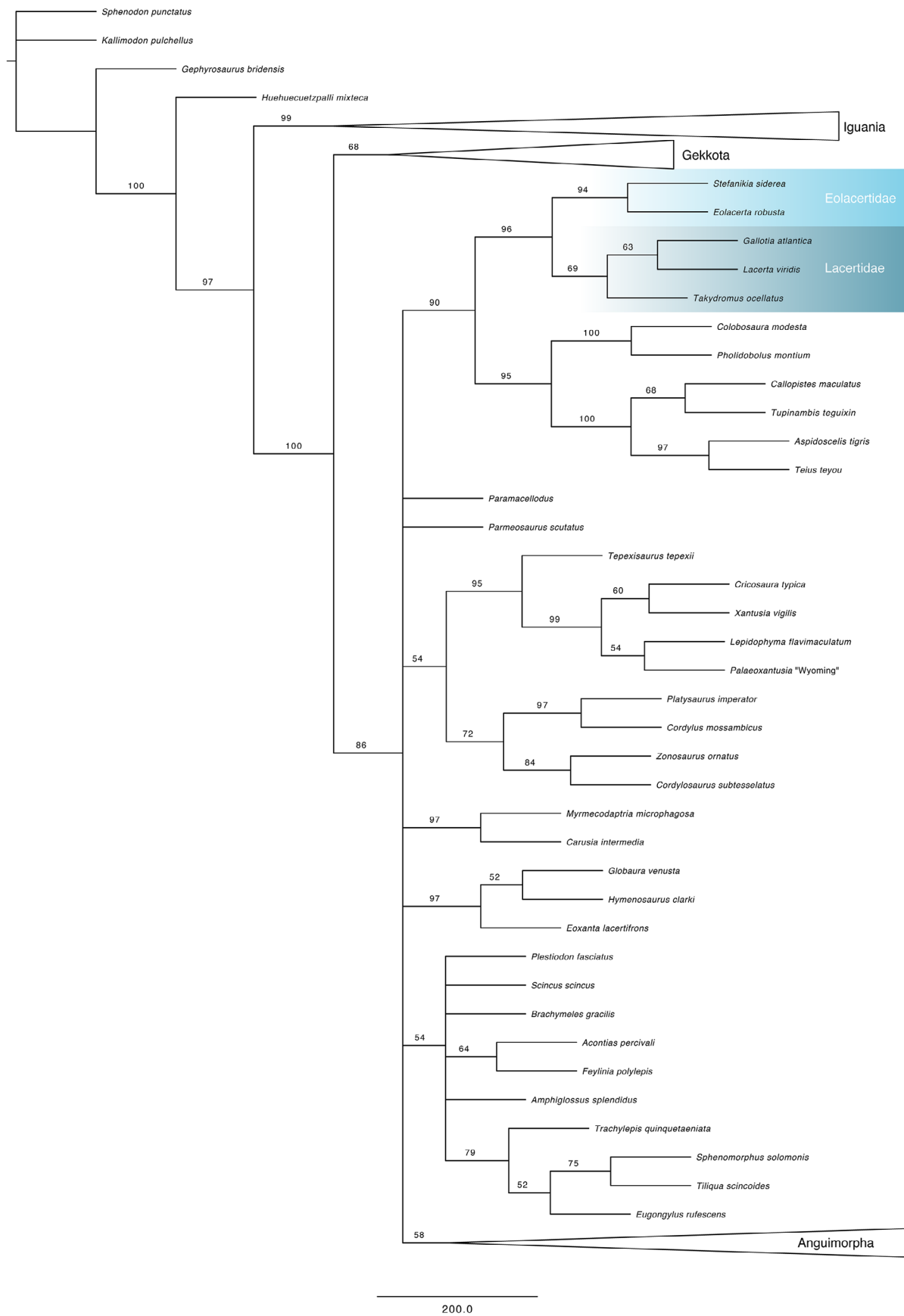


Figure 13. Strict consensus of four most-parsimonious trees recovered from unconstrained maximum parsimony analysis of data matrix based on Gauthier et al. (2012) in PAUP*. Numbers above branches indicate bootstrap support.

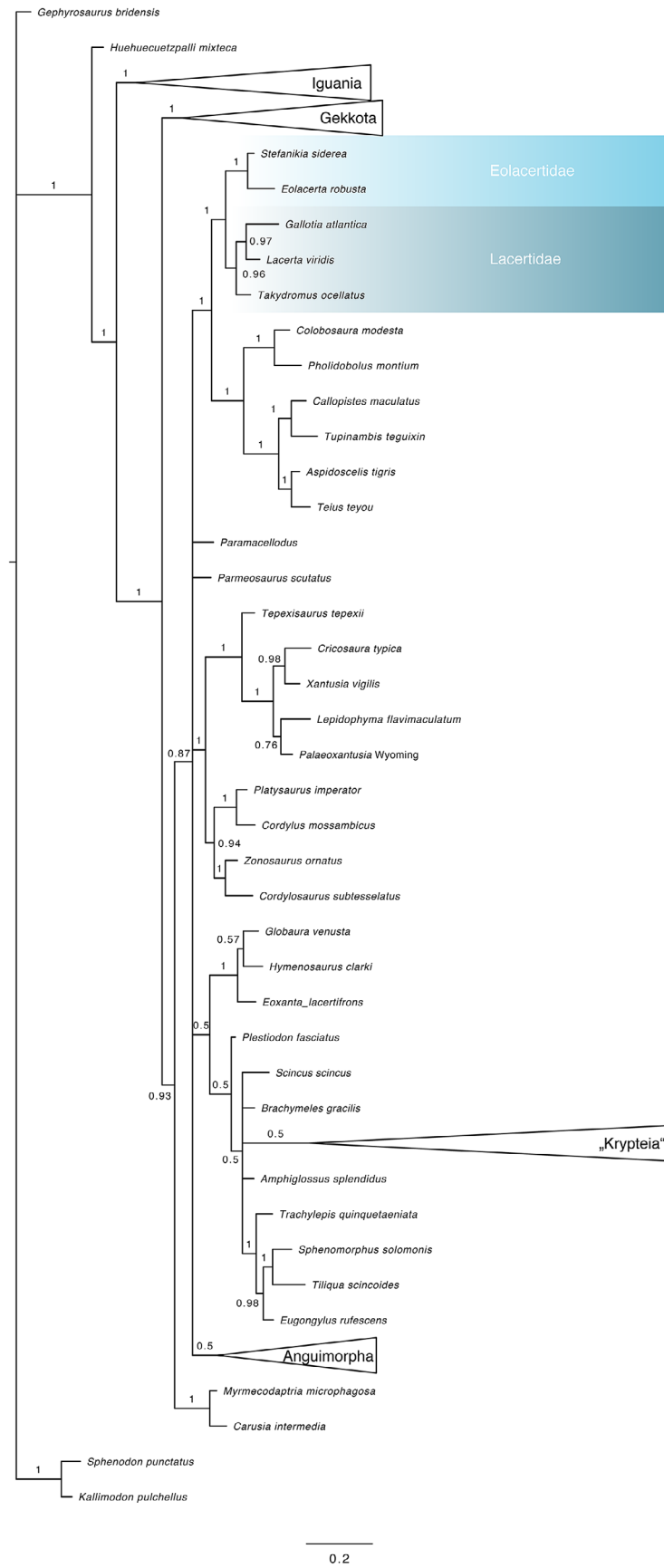


Figure 14. Tree resulting from Bayesian inference of data matrix based on Gauthier et al. (2012) in MrBayes. Numbers above branches indicate posterior probability when >50%.

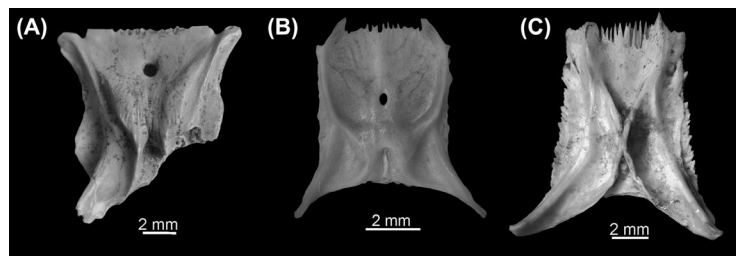


Figure 15. Comparison of parietals in ventral aspect: *Eolacerta* sp. from Prémontre (MP 10, France) (A); extant *Podarcis muralis* (B); and extant *Lacerta viridis* (C).

Table 1. Character state changes (synapomorphies) supporting the relationships of Eolacertidae resulting from unconstrained maximum-parsimony analysis of the data matrix based on Gauthier et al. (2012).

Eolacertidae + Lacertidae		<i>Stefanikia</i> + <i>Eolacerta</i>	
Character	State change	Character	State change
18	1→2	36	0→1
19	0→1	65	0→1
24	0→1	90	2→1
48	3→4	372	0→1
49	0→1	381	1→0
62	0→2	500	2→1
67	0→1	613	0→1
70	0→1		
283	1→0		
399	1→0		
521	1→0		
575	0→1		
577	0→1		
617	0→1		
618	0→1		

generally absent in ‘scincomorphans’ apart from Lacertidae (see Borsuk-Białynicka et al. 1999). In contrast, the presence of an occipital shield, wedged between the parietal and the interparietal shields on the parietal bone, is the rule in lacertids, and it is considered synapomorphic for this clade. According to Borsuk-Białynicka et al. (1999), its absence (*Acanthodactylus*, *Eremias*, and occasionally in *Psammotromus*) is secondary. However, a distinct occipital shield is present in some Cordyliformes (see Lang 1991) and anguids too (see e.g. Klembara et al. 2010; Klembara & Green 2010; Klembara 2012; Smith & Gauthier 2013). The supratemporal fenestra was partially closed in *Eolacerta* (Müller 2001) and *Stefanikia* by a posterior expansion of the postorbitofrontal. This is a derived feature in squamates (Estes et al. 1988). Furthermore, the adductor musculature takes its origin dorsally on the parietal in the posterior part of the bone. In both respects, however, the two genera differ from most extant lacertids, where the supratemporal fenestra is completely closed by the postfrontal and the adductor musculature originates exclusively ventrally. In Teioidea, in contrast, the adductor musculature is almost fully dorsal, and there is no tendency to close the supratemporal fenestra (Estes et al. 1988). One of the most distinctive features of the parietal of many lacertids is the convergence of the posteromedial branch of the cristae cranii, which frequently approach one another so closely anterior to the level of the parietal fossa (recessus processus ascendentes) that they form a deep median crest with a small longitudinal groove (Figure 15(C); Peters 1962). This feature is clearly seen in basal (Arnold et al. 2007) Gallotiinae (*Gallotia* and *Psammotromus*) as well as many members of Lacertini. Among fossils it is also

found in *Cryptolacerta hassiaca* (Müller et al. 2011). Both *Eolacerta* (Müller 2002) and *Stefanikia* (this work) show medial convergence of the cristae cranii, but in the plesiomorphic manner of iguanians and extant lacertids like *Zootoca*, *Podarcis* (Figure 15(B)) and *Acanthodactylus*.

Interestingly, the isolated parietals of *Eolacerta* sp. from Prémontre (MP 10, France) described by Müller (2002) have interdigitated contact with the frontal in its middle region, like *Stefanikia siderea* and Lacertidae. However, the presence of parietal tabs is unknown. The presence of parietal tabs that underlain the frontal is a synapomorphy of lacertiform lizards (Estes et al. 1988), although less well-developed tabs can occur in other taxa as well (e.g. *Eumeces algeriensis* CM 144945).

According to Müller (2001), the postfrontal and postorbital are separate in the Keller (now Pohl) specimen of *Eolacerta robusta*, but fused in HLMD Be 146. He suggested that this was probably the result of synostosis, possibly related to sexual dimorphism, because in many extant lizards the skull of the males is more strongly ossified than that of the females. Müller (2002) later described disarticulated postorbitofrontals, one of which (from Prémontre) is distinctly smaller and may stem from a semiadult representative of *Eolacerta*, indicating that the fusion probably occurred early in ontogeny (Müller 2002). Although the preservation in specimens of *Eolacerta* from Messel is problematic, we believe that they are fused also in the Keller/Pohl specimen (pers. obs.). The postfrontal and postorbital are separate at hatching in the majority of species of Lacertini but fused in some members of *Gallotia*, in all *Psammotromus* species, in *Zootoca vivipara* and in *Lacerta schreiberi* (Arnold 1973).

Müller (2001) found that the supratemporal could not unequivocally be identified in *Eolacerta robusta* from Messel and suggested that this bone was very small, as in some ‘scincomorphans’ from the Upper Cretaceous of Mongolia described by Borsuk-Białynicka (1988). In *Stefanikia* the supratemporal is well developed.

In the studied specimen, there is no clear evidence for palpebral ossification, although due to crushing its presence cannot be excluded. It should be noted that the elements described as palpebrals in *E. robusta* by Müller (2001), are supraocular osteoderms, however. The occurrence of a palpebral in *Lanthanotus* shows that palpebrals are present in all extant anguimorphs except *Heloderma* (Maisano et al. 2002; Gauthier et al. 2012). Among fossil anguimorphs, palpebrals are known for *Carusia*, *Bainguis*, *Parophisaurus*, *Necrosaurus*, *Parviderma*, *Aiolosaurus*, *Saniwa*, and *Estesia* (Sullivan 1987; Norell et al. 1992; Gao & Norell 1998). There, the palpebral is long posteriorly. This character is present, for instance, in *Shininaurus* (see Conrad 2004) and *Varanus*. In

Lacertidae, a long posterior process of the palpebral is present only in *Takydromus* (Arnold et al. 2007).

Nöth (1940) described four supraocular osteoderms in the topotypic material of *Eolacerta robusta* from Geiseltal, with the anterior and posterior ones being distinctly smaller than the middle two. According to him, slender supraciliary osteoderms are also present, resembling many extant ‘scincomorphans’. According to Borsuk-Białynicka et al. (1999), the occurrence of four supraocular scales is highly consistent within Lacertidae but not in the other ‘scincomorphans’. Within the last named group, it is present in most cordyliforms, some scincids (e.g. *Chalcides ocellatus*, but not in *Eumeces*), some teioids (e.g. *Proctoporus striatus*, but not in *Callopietes*) and some xantusiids (*Cricosaura*; see Friederich 1978: fig. 7, Gauthier et al. 2008: fig. 1A) but absent in non-scincomorphans. There are five supraoculars in many anguids (Borsuk-Białynicka et al. 1999) and in *Shinisaurus* (Bever et al. 2005), but only three in *Heloderma* (Bhullar 2011); the ancestral number for Anguimorpha, between four and six, depends on ingroup topology (Bhullar 2011). Posterior to the fourth supraocular in teiids is a narrow space filled by a mosaic of small scales. The small scales continue along the external margin of the supraoculars and supratemporals. The first supraocular is, too, often represented by several units. A fragmentation of the large second and third supraoculars is rare, and homology of these large scales among ‘scincomorphs’ is most probable (Borsuk-Białynicka et al. 1999). Among ‘scincomorphs’ only lacertids, scincids and cordyliforms have osteoderms in the supraocular scales.

The quadrate of extant lacertids has a strongly convex edge of the lateral conch, giving the bone a strongly arched appearance. The quadrate of e.g. *Tupinambis* (see Digimorph.org 2002–2012) has not this anterior rounded margin – an angle is present and the whole quadrate is nearly triangular in shape – the broad dorsal region gradually tapers ventrally. In *Stefanikia*, it is more similar to this type, which is probably primitive.

The pterygoids are poorly known in *Eolacerta robusta* from Messel, where only the quadrate processes are exposed (Müller 2001). For this reason, it is not clear whether pterygoid dentition is present in this taxon. It is very likely that a pterygoid dentition was present in *E. robusta* too, given its presence in teiids, many gymnophthalmids, and lacertids (although it should be noted that not all lacertids have pterygoid dentition, see e.g. Arnold 1973; Barahona 1996; Barahona & Barbadillo 1998).

A lateral process of the coronoid does not overlap the dentary. It is very similar situation as it is present in Scincoidea (Estes et al. 1988) and *Shinisaurus* (see Conrad 2004). In contrast, all extant Lacertiformes have a strong anterior process of the coronoid overlapping the dentary (Estes 1969, Estes et al. 1988). In *Eolacerta robusta* and *Cryptolacerta hassiaca*, as in Lacertidae and basal Xantusiidae but unlike Scincidae and Cordyliformes, the posterior crest of the bone is posteriorly extensive and strongly exposed in medial view behind the medial crest, which runs down the posteromedial process of the bone. Examined teioids were somewhat variable. In most of them, including Gymnophthalmidae, the posterior crest was not visible, but *Teius* and *Tupinambis* were like Lacertidae.

Comparison of postcranial elements

The conical centrum and blunt sagittal ridge on the ventral surface may have existed since the Late Jurassic. This character is very common in Iguanidae, Agamidae, Cordylidae, Gerrhosauridae, Lacertidae, and Teiidae (together with true procoely; see Hoffstetter & Gasc 1969). Müller (2001) reported a presence of zygosphenes-zygantral articulations in *Eolacerta robusta*. In the Keller/Pohl specimen, this character can be seen only in some of the posterior presacral vertebrae (see Müller 2001). They correspond to an incipient condition, where the zygosphenal articulation surfaces are directed laterally and a flange still connects the zygosphenes with the prezygapophysis (character 468, state 2 in Gauthier et al. 2012). In *Stefanikia siderea*, the evidence of an incipient condition is observed in anterior region of column. Better-developed zygantrum-zygosphenes articulations are observed especially in caudal vertebrae. In *Plesirolacerta*, the zygosphenes and zygantrum are strongly developed on the dorsal and caudal vertebrae but still incipient in the sense described above (see Čerňanský & Augé 2013).

In ribs, a well developed posterodorsal process is present in *Stefanikia*. Lack of any process for muscular insertion is characterized in scincoids (Hoffstetter & Gasc 1969).

A posterior interruption of the ventromedial loop of the clavicle, as seen in *Stefanikia siderea*, was considered by Arnold et al. (2007) to be a synapomorphy of Lacertini. But Arnold et al. (2007) also noted that this feature was present in *Atlantolacerta*, probably the basal-most lineage in Eremiadini, indicating that it might be a synapomorphy of greater generality, such as Lacertinae. Moreover, this character is present in many Mesozoic lizards (e.g. *Meyasaurus*, see Vidal 1915; Hoffstetter 1966; Evans & Barbadillo 1996) and possibly represents a plesiomorphy for Eolacertidae + Lacertidae.

The ilium and pubis in *Stefanikia siderea* and *Eolacerta robusta* (see Müller 2001) are relatively short in comparison with lacertids, where these bones are narrow and long (Rieppel 1980a). The general shape of the ilium is very similar to that of *Shinisaurus* (see Conrad 2006). However, there is an absence of the preacetabular spine in *Shinisaurus*.

Conclusions

Lacertidae is Europe’s dominant clade of reptiles, but its evolutionary history has long been problematic. Despite their copiousness, even genetic sequence data have not yet elucidated many relationships within the clade (Fu 2000; Arnold et al. 2007). One possibility suggested by genetic studies is that (crown) Lacertidae radiated rapidly in the Neogene (Fu 2000; Arnold et al. 2007), possibly in response to environmental forcing. With this in mind, it is not surprising that the fossil record has thus far played little role in clarifying the evolutionary history of Lacertidae, apart from the observation that its earliest close relatives are found in the Eocene of Europe (Borsuk-Białynicka et al. 1999; Čerňanský & Augé 2013), thus providing support for the notion that the clade originated in Europe. Members of the crown are known in the Oligocene, and maybe even earlier (see e.g. Čerňanský et al. 2016).

Our study of eolacertid lizard skeletons from the early-mid-Eocene of the Messel Pit, Germany, suggests a new model of the origin and early history of Lacertidae. The Palaeogene of Europe, rather than being dominated by archaic forms only distantly related to Lacertidae, in fact hosted a large radiation of the total clade of Lacertidae (Pan-Lacertidae, the stem-based clade). Their ecological breadth is amply demonstrated by the differences in size and body form (e.g. small semifossorial forms like *Cryptolacerta*, mid-sized and large terrestrial forms like *Stefanikia* and *Eolacerta*). Some of these (*Succinilacerta*, *Plesiolacerta*) were more closely related to crown Lacertidae than others, and even crown representatives may have been present (Čerňanský et al. 2016). Gradually or suddenly, most of these lineages were extinguished, until only members of the crown remained. Meanwhile one lineage (Lacertinae) radiated spectacularly in the Neogene, coming to dominate Lacertidae as we know it today. Further study of Palaeogene species using a variety of methods and preferably combining paleontological and neontological data (e.g. Hipsley et al. 2014) will be required to test this model against its alternatives.

Acknowledgement

The photographs using camera were taken by A. Vögel (Senckenberg Research Institute, Frankfurt am Main). Peter Hornberger (Deggendorf) conducted the μ CT scan. We thank J.-C. Rage (Muséum national d'Histoire naturelle Paris), A. Bolet (Institut Català de Paleontologia Miquel Crusafont) and two anonymous reviewers for their critical reading of earlier versions of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Alexander von Humboldt Foundation in Germany. This project was supported by the Senckenberg Gesellschaft für Naturforschung.

References

- Arnold EN. 1973. Relationship of the palaeartic lizards assigned to genera *Lacerta*, *Algyroides* and *Psammotromus* (Reptilia: Lacertidae). *Bull Br Mus Nat Hist Zool Ser.* 25:291–366.
- Arnold EN. 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an old-world family of lizards derived from morphology. *Bull Br Mus Nat Hist Zool Ser.* 55:209–257.
- Arnold EN, Arribas O, Carranza S. 2007. Systematics of the Palaeartic and Oriental lizard tribe Lacertini (Squamata: Lacertidae: Lacertinae), with descriptions of eight new genera. *Zootaxa.* 1430:1–86.
- Augé M. 2005. Évolution des lézards du Paléogène en Europe [Evolution of Palaeogene lizards in Europe]. *Mém Mus natl Hist nat.* 192:1–369.
- Bever GS, Bell CJ, Maisano JA. 2005. The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Palaeontol Electron.* 8:1–36.
- Barahona F. 1996. Osteología craneal de lacértidos de la Península Ibérica e Islas Canarias: análisis sistemático filogenético [PhD thesis]. Spain: Universidad Autónoma de Madrid; p. 514.
- Barahona F, Barbadillo LJ. 1998. Inter- and intraspecific variation in the post-natal skull of some lacertid lizards. *J Zool.* 245:393–405.
- Bhullar BAS. 2011. The power and utility of morphological characters in systematics: a fully resolved phylogeny of *Xenosaurus* and its fossil relatives (Squamata: Anguimorpha). *Bull Mus Comp Zool.* 160:65–181.
- Blob RW. 1998. Evaluation of vent position from lizard skeletons for estimation of snout: vent length and body mass. *Copeia.* 1998:792–801.
- Borsuk-Białynicka M. 1988. *Globaura venusta* gen. et sp. n. and *Eoxantala certifrons* gen. et sp. n.-non-teiid Lacertoids from the Late Cretaceous of Mongolia. *Acta Palaeontol Pol.* 33:211–248.
- Borsuk-Białynicka M, Lubka M, Böhme W. 1999. A lizard from baltic amber (Eocene) and the ancestry of the crown group lacertids. *Acta Palaeontol Pol.* 44:349–382.
- Cantino PD, de Queiroz K. 2010. International code of phylogenetic nomenclature, version 4c: International Society for Phylogenetic Nomenclature [Internet]; 102 pp. Available from: <http://www.ohio.edu/phylocode/PhyloCode4c.pdf>.
- Čerňanský A. 2012. The oldest known Miocene girdled lizard fauna (Squamata, Cordylidae) from central Europe, with comments on early Miocene immigration of African taxa. *Geodiversitas.* 34:837–848.
- Čerňanský A, Augé M. 2013. New species of the genus *Plesiolacerta* (Squamata: Lacertidae) from the upper Oligocene (MP 28) of southern Germany and a revision of the type species *Plesiolacerta lydekkeri*. *Palaeontology.* 56:79–94.
- Čerňanský A, Bauer AM. 2010. *Euleptes gallica* Müller (Squamata: Gekkota: Sphaerodactylidae) from the Lower Miocene of North-West Bohemia, Czech Republic. *Folia Zool.* 59:323–328.
- Čerňanský A, Klembara J, Smith KT. 2016. Fossil lizard from central Europe resolves the origin of large body size and herbivory in giant Canary Island lacertids. *Zool J Linn Soc.* 176:861–877.
- Čerňanský A, Smith KT, Klembara J. 2014. Variation in the position of the jugal medial ridge among lizards (Reptilia: Squamata): its functional and taxonomic significance. *Anat Rec.* 297:2262–2272.
- Chen X, Huang S, Guo P, Colli GR, Nieto Montes de Oca AN, Vitt LJ, Pyron RA, Burbrink FT. 2013. Understanding the formation of ancient intertropical disjunct distributions using Asian and Neotropical hinged-teeth snakes (*Sibynophis* and *Scaphiodontophis*: Serpentes: Colubridae). *Mol Phylogenet Evol.* 66:254–261.
- Conrad JL. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). *Zool J Linn Soc.* 141:399–434.
- Conrad JL. 2006. Postcranial skeleton of *Shinisaurus crocodilurus* (Squamata: Anguimorpha). *J Morphol.* 267:759–775.
- Conrad JL. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bull Am Mus Nat Hist.* 310:1–182.
- Darwin C. 1859. On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life. London: J. Murray.
- Digimorph.org. 2002–2012. Digital morphology: a national science foundation digital library at the University of Texas at Austin [Internet]. Austin: The High Resolution X-ray Computed Tomography Facility at the University of Texas at Austin. Available from: <http://www.digimorph.org/>.
- Estes R. 1983. Sauria terrestria, Amphisbaenia Encyclopedia of Paleoherpology, part 10 A. New York (NY): Gustav Fischer Verlag.
- Estes R, de Queiroz K, Gauthier J. 1988. Phylogenetic relationships within Squamata. In: Estes R, Pregill G, editors. Phylogenetic relationships of the lizard families. Stanford: Stanford University Press; p. 119–282.
- Evans SE. 2008. The skull of lizards and tuatara. In: Gans C, Gaunt AS, Adler K, editors. Biology of the reptilia, volume 20 (Morphology H, the skull of Lepidosauria). Ithaca (NY): Society for the Study of Reptiles and Amphibians; p. 1–348.
- Evans SE, Barbadillo LJ. 1996. The early Cretaceous lizards of Montsec (Catalonia, Spain). *Treballs Museu Geol Barcelona.* 5:5–13.
- Evans SE, Chure DC. 1998. Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *J Vertebr Paleontol.* 18:99–114.
- Franzen JL, Gingerich PD, Habersetzer J, Hurum JH, von Koenigswald W, Smith BH. 2009. Complete primate skeleton from the middle Eocene of Messel in Germany: morphology and paleobiology. *PLoS ONE.* 4:e5723.
- Franzen JL, Köster A. 1994. Die eozänen Tiere von Messel – ertrunken, erstickt oder vergiftet? *Nat Mus.* 124:91–97.

- Friederich U. 1978. Der Pileus der Squamata. Stuttg Beitr Naturkd A. 307:1–64.
- Fu J. 2000. Toward the phylogeny of the family Lacertidae – why 4708 base pairs of mtDNA sequences cannot draw the picture. Biol J Lin Soc. 71:203–217.
- Gao K, Norell MA. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of anguimorph lizards. Am Mus Novit. 3230:1–51.
- Gauthier JA, Kearney M, Bezy RL. 2008. Homology of cephalic scales in xantusiid lizards, with comments on night lizard phylogeny and morphological evolution. J Herpetol. 42:708–722.
- Gauthier JA, Kearney M, Maisano JA, Rieppel O, Behlke ADB. 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bull Peabody Mus Nat Hist. 53:3–308.
- Haas G. 1960. On the trigeminus muscles of the lizards *Xenosaurus grandis* and *Shinisaurus crocodilurus*. Am Mus Novit. 2017:1–54.
- Haas G. 1973. Muscles of the jaws and associated structures in the Rhyngocephalia and Squamata. In: Gans C, Parsons T, editors. Biology of the reptilia. London: Academic Press, vol. 4; p. 285–490.
- Head JJ, Holroyd PA, Hutchison JH, Ciochon RL. 2005. First report of snakes (Serpentes) from the late middle Eocene Pondaung Formation, Myanmar. J Vertebr Paleontol. 25:246–250.
- Hipsley CA, Miles DB, Müller J. 2014. Morphological disparity opposes latitudinal diversity gradient in lacertid lizards. Biol Lett. 10:20140101.
- Hoffstetter R. 1966. Les Sauria (=Lacertilia) du Jurassique supérieur du Montsech (Espagne). Bull Soc Geol Fr. 7:549–557.
- Hoffstetter R, Gasc JP. 1969. Vertebrae and ribs of modern reptiles. In: Gans C, Bellairs AdA, Parsons TS, editors. Biology of the reptilia 1. Morphology. London: Academic Press; p. 201–310.
- Ivanov M. 2001. Changes in the composition of the European snake fauna during the early Miocene and at the early/middle Miocene transition. Paläontol Zeitschrift. 74:563–573.
- Joyce WG, Micklich N, Schaal S, Scheyer TM. 2012. Caught in the act: the first record of copulating fossil vertebrates. Biol Lett. 8:846–848.
- Klembara J. 2008. A new anguimorph lizard from the lower Miocene of north-west Bohemia, Czech Republic. Palaeontology. 51:81–94.
- Klembara J. 2012. A new species of *Pseudopus* (Squamata, Anguidae) from the early Miocene of Northwest Bohemia (Czech Republic). J Vertebr Paleontol. 32:854–866.
- Klembara J, Böhme M, Rummel M. 2010. Revision of the anguine lizard *Pseudopus laurillardii* (Squamata, Anguidae) from the Miocene of Europe, with comments on paleoecology. J Paleontol. 84:159–196.
- Klembara J, Green B. 2010. Anguimorph lizards (Squamata, Anguimorpha) from the middle and late Eocene of the Hampshire Basin of Southern England. J Syst Paleontol. 8:97–129.
- Koenigswald Wv, Braun A, Pfeiffer T. 2004. Cyanobacteria and seasonal death: a new taphonomic model for the Eocene Messel lake. Paläontol Zeitschrift. 78:345–352.
- Kosma R. 2004. The dentitions of recent and fossil scincomorph lizards (Lacertilia, Squamata) – systematics, functional morphology, paleoecology [PhD dissertation]. [Hannover (Germany)]: University of Hannover.
- Lang M. 1991. Generic relationships within Cordyliformes (Reptilia: Squamata). Bull Inst Royal Sci Nat Belgique Biol. 61:121–188.
- Lee MSY. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. Biol J Lin Soc. 65:369–453.
- Lenz OK, Wilde V, Mertz DF, Riegel W. 2015. New palynology-based astronomical and revised ⁴⁰Ar/³⁹Ar ages for the Eocene maar lake of Messel (Germany). Int J Earth Sci. 104:873–889.
- Longrich NR, Vinther J, Pyron RA, Pisani D, Gauthier JA. 2015. Biogeography of worm lizards (Amphisbaenia) driven by end-Cretaceous mass extinction. Proc Royal Soc B Biol Sci. 282:20143034.
- Maisano JA, Bell CJ, Gauthier JA, Rowe T. 2002. The osteoderms and palpebral in *Lanthanotus borneensis* (Squamata: Anguimorpha). J Herpetol. 36:678–682.
- Meszoely CAM. 1970. North American fossil anguid lizards. Bull Mesum Comp Zool. 139:87–149.
- Müller J. 2001. Osteology and relationships of *Eolacerta robusta*, a lizard from the Middle Eocene of Germany (Reptilia, Squamata). J Vertebr Paleontol. 21:261–278.
- Müller J. 2002. *Eolacerta* from the Eocene of Prémontré, France (Reptilia, Squamata). Neues Jahrbuch Geol Paläontol Monatshefte. 2002:490–500.
- Müller J, Hipsley CA, Head JJ, Kardjilov N, Hilger A, Wuttke M, Reisz RR. 2011. Eocene lizard from Germany reveals amphisbaenian origins. Nature. 473:364–367.
- Norell MA, McKenna MC, Novacek MJ. 1992. *Estesia mongoliensis*, a new fossil varanoid from the Cretaceous Barun Goyot Formation of Mongolia. Am Mus Novit. 3045:1–24.
- Nöth L. 1940. *Eolacerta robusta*, n. g. n. sp., ein Lacertilier aus dem mittleren Eozän des Geiseltales. Nova Acta Leopold 8:439–460.
- Peters G. 1962. Die Zwerggeidechse (*Lacerta parva* Boulenger) und ihre Verwandtschaftsbeziehungen zu anderen Lacertiden, insbesondere zur Libanon-Eidechse (*L. fraasii* Lehrs). Zool Jahrbücher Syst. 89:407–478.
- Pyron RA, Burbrink FT, Wiens JJ. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. BMC Evol Biol. 13:93.
- Rage JC, Augé M. 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. Geobios. 43:253–268.
- Rage JC, Folie A, Rana RS, Singh H, Rose KD, Smith T. 2008. A diverse snake fauna from the early Eocene of Vastan Lignite Mine, Gujarat, India. Acta Palaeontol Pol. 53:391–403.
- Reeder TW, Townsend TM, Mulcahy DG, Noonan BP, Wood PL Jr, Sites JW Jr, Wiens JJ. 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. PLoS ONE. 10:e0118199. doi:10.1371/journal.pone.0118199.
- Richter A. 1994. Lacertilia aus der Unteren Kreide von Una und Galve (Spanien) und Anoual (Marokko). Berliner geowiss Abh. 14:1–147.
- Richter G, Storch G. 1980. Beiträge zur Ernährungsbiologie eozäner Fledermäuse aus der “Grube Messel”. Nat Mus. 110:353–367.
- Rieppel O. 1980a. Ein Lacertilier aus dem Eozän von Messel bei Darmstadt. Beitr naturk Forsch Südwdt. 39:57–69.
- Rieppel O. 1980b. The postcranial skeleton of *Lanthanotus borneensis* (Reptilia, Lacertilia). Amphib-Reptil. 1:95–112.
- Robinson P. 1967. Triassic vertebrates from lowland and upland. Sci Cult. 33:169–173.
- Romer AS. 1949. The vertebrate body. Philadelphia (PA): WB Saunders.
- Romer AS. 1956. Osteology of the reptiles. Chicago (IL): University of Chicago Press; p. 772.
- Ronquist FM, Teslenko M, van der Mark P, Ayres D, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol. 61:539–542.
- Simões TR, Caldwell MW, Palci A, Nydam RL. 2016. Giant taxon-character matrices: quality of character constructions remains critical regardless of size. Cladistics. 33:198–219. doi:10.1111/cla.12163.
- Schaal S, Ziegler W, editors. 1992. Messel – an insight into the history of life and of the Earth. Oxford: Clarendon Press.
- Smith KT. 2006. A diverse new assemblage of late Eocene squamates (Reptilia) from the Chadron Formation of North Dakota, U.S.A. Palaeontol Electron. 9:5A.
- Smith KT. 2009. Eocene lizards of the clade *Geiseltaliellus* from Messel and Geiseltal, Germany, and the early radiation of Iguanidae (Reptilia: Squamata). Bull Peabody Mus Nat Hist. 50:219–306.
- Smith KT, Gauthier JA. 2013. Early Eocene lizards of the Wasatch Formation near Bitter Creek, Wyoming: diversity and paleoenvironment during an interval of global warming. Bull Peabody Mus Nat Hist. 54:135–230.
- Smith KT, Schaal S, Habersetzer J, editors. Forthcoming. Messel: a ancient greenhouse ecosystem. Stuttgart: Schweizerbart.
- Smith KT, Wuttke M. 2012. From tree to shining sea: taphonomy of the arboreal lizard *Geiseltaliellus maarius* from Messel, Germany. Palaeobio Palaeoenv. 92:45–65.

- Sullivan RM. 1987. *Parophisaurus pawneensis* (Gilmore, 1928) new genus of anguid lizard from the middle Oligocene of North America. *J Herpetol.* 21:115–133.
- Swofford DL. 2002. PAUP* phylogenetic analysis using parsimony (*and other methods). Sunderland (MA): Sinauer Associates.
- Szyndlar Z. 2012. Early Oligocene to Pliocene Colubridae of Europe: a review. *Bull Soc Geol Fr.* 183:661–681.
- Townsend TM, Larson A, Louis E, Macey JR. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Syst Biol.* 53:735–757.
- Vidal LM. 1915. Nota geológica y paleontológica sobre el Jurásico superior de la provincia de Lérida. *Boletín Instit Geol Minero España.* 36:1–43.
- Vidal N, Hedges SB. 2009. The molecular evolutionary tree of lizards, snakes, and amphisbaenians. *CR Biol.* 332:129–139.
- Wiens JJ. 2001. Character analysis in morphological phylogenetics: problems and solutions. *Syst Biol.* 50:689–699.