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The first juvenile specimen of *Eolacerta* (Squamata: Eolacertidae) from the early–middle Eocene of the Messel Pit (Germany)

Le premier spécimen de juvénile d'Eolacerta (Squamata: Eolacertidae) de l'Éocène inférieur–moyen de Messel Pit (Allemagne)

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ABSTRACT

We describe the first juvenile specimen of an eolacertid lizard. The material comes from one of the most important Eocene localities, the Messel Pit in Germany. The new specimen provides unique information on the early ontogeny of *Eolacerta*, the largest known lizard from Messel, with a maximum snout-vent length greater than 30 cm and a mass approaching 1 kg. The specimen described here, with a SVL of 11.3 cm and an estimated mass of 21 g, can be allocated more precisely to *Eolacerta robusta* based on the co-occurrence and the combination of following features: (1) the nasal process of premaxilla is long; (2) position of lacrimal (being more anteriorly located in *Stefanikia siderea*); (3) the postorbital process of jugal is broad; (4) the ratio of the anterior and posterior region of the frontal between the sulcus interfacialis; (5) a mid-parietal constriction of the parietal table is present; (6) the interparietal shield broadens anteriorly; (7) the transverse sulcus is straight anteriorly. The incipient character of the parietal constriction and the slightly lower number of maxillary teeth (28 vs. 30–32 in adults) are consistent with a juvenile animal. Very important is evidence for the presence of pterygoid dentition (pointed teeth arranged in a single line) and the absence of palatine dentition. Ceratobranchial I is observed for the first time for this species, and its shape and length are very similar to those of Lacertidae. There are 27 presacral vertebrae in the juvenile, as in adults. In the juvenile specimen, ventral keel on the centrum is present in all vertebrae. The ventromedial portion of the ischium is well preserved here and gives information on the exact shape of this portion, at least in juvenile form. The scalation, as far as it is preserved, is similar to that of *Stefanikia*, except that the rectangular subdigital scales are longer in comparison with their width, and therefore have a broader appearance.

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RÉSUMÉ

Cet article décrit le premier spécimen de juvénile d'un lézard éolacertidé. Le matériel provient de l'une des plus importantes localités éocènes, Messel Pit en Allemagne. Le nouveau spécimen fournit une information unique sur l'ontogénie précoce d'*Eolacerta*, le plus grand lézard connu de Messel, avec une longueur maximum museau–orifice anal supérieure à 30 cm et une masse approchant le kilogramme. Le spécimen décrit ici, avec une SLV de 11,3 cm et une masse estimée à 21 g, peut être assigné plus précisément à *Eolacerta robusta* sur la base de la combinaison et de la cooccurrence des caractéristiques suivantes : (1) le long processus nasal de maxillaire ; (2) la position du lacrimal (situé plus en avant chez *Stefanika siderea*) ; (3) le large processus post-orbital du jugal ; (4) le ratio de la région antérieure/postérieure du frontal entre le sulcus interfacialis ; (5) une constriction pariétale centrale de la plaque pariétale ; (6) le bouclier interpariétal élargi antérieurement ; (7) le sulcus transversal droit antérieurement. Le caractère naissant de la constriction pariétale et le nombre légèrement inférieur de dents du maxillaire (28 au lieu de 30–32 chez les adultes) correspondent à un animal juvénile. Il y a une preuve très nette de présence d'une dentition de ptérygoïde (dents en pointe disposées sur une seule ligne) et d'absence de dents palatines. Le cératobranchial I est observé pour la première fois dans cette espèce, et sa forme et sa longueur sont similaires à celles des Lacertidae. Il y a 27 vertèbres présacrales chez le juvénile, comme chez les adultes. Chez le spécimen juvénile, il y a une quille ventrale au centre de toutes les vertèbres. La portion ventro-médiale de l'ischium est ici bien préservée et fournit une information sur la forme exacte de cette portion, au moins dans la forme juvénile. Les écailles, dans la mesure où elles sont préservées, sont semblables à celles de *Stefanikia*, excepté le fait que les écailles subdigitales rectangulaires sont plus longues que larges et de ce fait paraissent plus grandes.

1. Introduction

The Messel Pit in Germany is renowned due to the exceptional preservation of its fossils, both animals and plants, which have made it into one of the most important Eocene localities in the world (see, e.g., Schaal and Ziegler, 1988; Smith et al., 2018a). The fossils are preserved in a dark brown to black algal pelite ("oil shale") showing varve-like lamination, the Middle Messel Formation, which represents an ancient maar lake deposit. The basin in which this lake deposit accumulated was created during a phreatomagmatic eruption around 48.2 Ma (Lenz et al., 2015). The most recent age estimates suggest that the fossiliferous horizons of the Middle Messel Formation span the Ypresian–Lutetian (early–middle Eocene) boundary (Lenz et al., 2015).

Among the nearly three dozen reptile species reported from Messel thus far (Smith et al., 2018b) is the large lizard *Eolacerta robusta*. This taxon was first described from the lignite mines of Geiseltal in eastern Germany (Nöth, 1940), and later recognized at Messel on the basis of nearly complete skeletons (Müller, 2001; Rieppel, 1980). Its spatial distribution during the Eocene includes not only Germany, but also France (locality of Prémontré). There, isolated bones were described by Müller (2002). However, this taxon was for a long time an enigmatic one. Nöth (1940) originally assigned this species to Lacertidae. Studies since 1980 have emphasized the primitive features of *Eolacerta* in comparison with Lacertidae and so cast doubt on the relationships of the fossil taxon (e.g., Conrad, 2008; Müller, 2001; Rieppel, 1980). The most recent work, however, concludes that *Eolacerta* is indeed closely related to Lacertidae, the dominant group of reptiles in Europe today, but lies outside of the crown (Čerňanský and Smith, 2018). Together with the recently described taxon *Stefanikia siderea*, it forms the clade Eolacertidae (see Čerňanský and Smith, 2018). Moreover, it is possible that other taxa will be included here in the future. The presence of this clade in the early–middle Eocene is consistent with the previous ideas that the origin of Lacertidae is in Europe (Arnold et al., 2007), where the fossils considered closest to the lacertid crown are also found (Borsuk-Białynicka et al., 1999; Čerňanský and Augé, 2013) and descendants of the basalmost divergence in Lacertidae, between Gallotiinae and Lacertinae, are documented (Čerňanský et al., 2016).

Until now, there is an absence of information about ontogeny of *Eolacerta*, and many other anatomical characters about the palatal bones, hyoid and braincase are unknown as well. We report here the first juvenile specimen of an eolacertid lizard, a specimen that we refer to *E. robusta*. In this paper, we aim to fill that gap by describing this specimen with the help of micro-CT techniques.

2. Material and methods

A new specimen from the Middle Messel Formation – a nearly complete skeleton lacking only the tail – was studied. The specimen is housed in the Messel vertebrate collection (SMF–ME) of the Senckenberg Research Institute and Natural History Museum in Frankfurt am Main (Germany) as SMF-ME 3314. The skeleton was completely freed from the rock matrix and embedded in epoxy resin. The specimen consists of part and counterpart, SMF-ME 3314a and 3314b, respectively; the former contains most of the specimen, while the latter contains portions of the posteriormost presacral vertebrae, the pelvis and the right hindlimb. SMF-ME 3314 was scanned using micro-CT on the TomoScope HV 500 (Werth) at the Technische Hochschule, Deggendorf (Germany). The images were recorded over 360°. The settings were as follows: Voxel size = 0.025175; current = 150; voltage = 165; integration time = 2000; average = 1; steps = 1600; steps 360 = 1600. The CT datasets were analyzed using VG Studio Max v. 2.2. The image processing program ImageJ (Schneider et al., 2012) was used for measurements.

3. Systematic paleontology

Squamata Oppel, 1811
Lacertoidea Estes, Queiroz and Gauthier, 1988
Eolacertidae Čerňanský and Smith, 2018
Eolacerta Nöth, 1940

Eolacerta robusta Nöth, 1940
(Figs. 1–5)

Newly referred material. SMF-ME 3314

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

Description

Detailed descriptions of eolacertids have already been published (Čerňanský and Smith, 2018; Müller, 2001; Rieppel, 1980). For this reason, we focus here mainly on characters that were not previously observable or only poorly preserved for *E. robusta* from Messel or that are of ontogenetic relevance.

The SVL of the specimen is 11.3 cm [using the middle of the second sacral vertebra as the position of the vent; see Blob (1998)]. The body mass of the specimen is estimated to be 21 g, as calculated using SVL – weight allometries for lacertid lizards from Meiri (2010). Epiphyses are present on all, but fused on none, of the large bones of the limbs (stylopod and zeugopod). The skull is mostly dorsoventrally compressed diagenetically (Figs. 1 and 2). The skull as a whole is typically box-shaped (for a reconstruction, see Fig. 3A) with well-developed canthal and temporal crests, as suggested by strong edges on both the maxilla and postorbitofrontal.

Premaxilla. The premaxilla (Fig. 3D) is a T-shaped, unpaired element. The nasal process is long, narrow, and tapering, extending beyond the anteroposterior midpoint of the nasals. The maxillary process is well-developed. Only three teeth are preserved, but estimated tooth number (assuming mirror symmetry) is about seven. The teeth are conical and pointed, but distinctly smaller than those of the maxilla.

Frontal. The frontal is broad in dorsal view. Its anterior region in front of the sulcus interfacialis forms approximately 2/3 (7.0/11.5 = 0.61) of the entire frontal length. The ventral morphology of frontal (Fig. 3E, F) is made visible for the first time. Its morphology is very similar to that of *Stefanikia siderea* (see Čerňanský and Smith, 2018). The frontal is constricted at the orbits, but not strongly so. The cristae cranii frontalis are not deep (i.e. well-developed subolfactory processes are absent. Similar condition is also present in *Takydromus*, pers. obs. A.Č.).

Parietal. The morphology of this bone (Figs. 2A, 3G, H) is practically identical to that in a large specimen (see Čerňanský and Smith, 2018: fig. 12). The basic difference is that a constriction of the parietal at mid-length is less pronounced. The short, transverse sulcus between the interparietal and occipital shields is straight. The supratemporal fossa located laterally on the supratemporal process reaches anteriorly the level of the mid-length of the occipital shield (as in the adult). In ventral aspect, the parietal fossa (recessus processi ascendentis) is tongue-shaped and well defined. The medial branches of the cristae cranii parietalis do not converge posteriorly to form a strong median crest (unlike in many extant lacertids), but cranial crests run parallel to the lateral margin of the parietal table. The internal morphology resembles the specimen described by Müller (2002: p. 494, fig. 2B; see also Čerňanský and Smith, 2018: fig. 15A) from France.

Vomer. The two elements in the anterior region are interpreted as vomers (Fig. 2B). They are anteroposteriorly elongated, shallowly trough-like in cross section, and ventral longitudinal ridges are present. Pterygoid-vomer contact, as rarely seen, for instance, in some Mesozoic scincomorph lizards (see Estes, 1983; Borioteiioidea sensu Nydam et al., 2007; Polyglyphanodontidae sensu Conrad, 2008; Polyglyphanodontia sensu Gauthier et al., 2012), is absent here.

Palatine. Palatines are well recognizable, the determination is based on the shape and location (Fig. 2B). The body is robust, anteroposteriorly elongated, becoming broader posteriorly. Dentition is absent. The anterior region is triangular, and maxillary and vomerine processes are present.

Ectopterygoid. A structure that seems to form an articulation with the transverse process of the pterygoid is interpreted here as the pterygoid process of the ectopterygoid. The exposed portion of the bone is blunt (Fig. 2B).

Pterygoid. The pterygoid is a triradiate element (Fig. 2B). The palatine process is broad, bearing pointed teeth arranged in a line. The transverse process, which forms a contact with the ectopterygoid, is short. The suborbital fenestra between them is broad, forming an elongate oval. Posteromedially, a short and blunt flange emerges from the main body of the pterygoid. This flange forms a basipterygoid articulation. The long quadrate process is thinner than the palatine process.

Hyoid. The paired first ceratobranchial elements are visible. They diverge posterolaterally, curving laterally and dorsally (Fig. 2). The curvature is more distinct in the posterior portion of the element. The ceratobranchial elements are long, reaching posteriorly approximately the level of the axis. They become thinner anteriorly, but swell slightly at the terminus. Cartilaginous elements such as basihyal and hypohyal are not recognizable.

Mandible (Figs. 2, 3B, C). The dentary is slender and slightly longer than the postdentary portion of the mandible, as in adult *E. robusta* (see Müller, 2001). The dentary possesses 27 tooth positions. The dentition is pleurodont. The teeth are large and unicuspid. Their apices are slightly recurved posterolingually, bearing a culmen lateralis anterior and posterior (terms after Richter, 1994). Meckel's groove is narrow, but this section of the dentary is badly preserved. The external surface of the bone is pierced

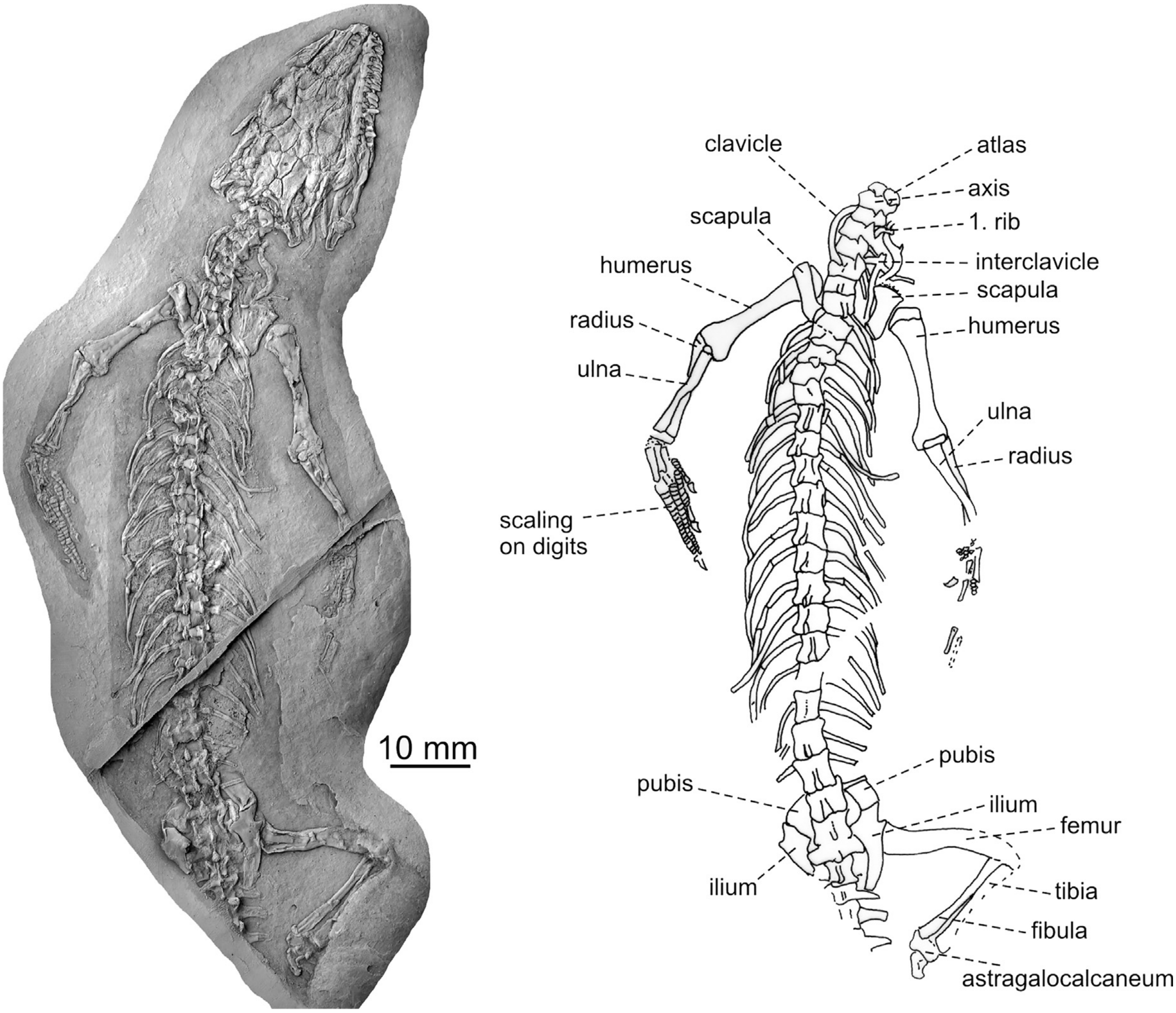

Fig. 1. *Eolacerta robusta*. The entire skeleton SMF-ME 3314a in dorsal aspect.

Fig. 1. *Eolacerta robusta*. Squelette entier de SMF-ME 3314a en vue dorsale.

by seven mental foramina arranged in a single line [six to seven foramina are present in the large specimens studied by Müller (2001)]. Only the anteromedial process of the coronoids is preserved. It reaches anteriorly the level of the posteriormost teeth in the tooth row. Dorsally to it, the coronoid is overlapped by coronoid process of dentary (see Fig. 3C). The angular is an anteroposteriorly elongated element that covers the mandible ventrally. In lateral view, it is more slender than the surangular. The surangular, which maintains a sutural contact with the prearticular, is a large, elongated bone. It narrows slightly posteriorly. The anterior end of the bone is slightly elevated dorsally. The mandibular fossa is widely open and lenticular in medial view. The prearticular and articular appear to be fused, forming the posterior and posteroventral margins of the mandible. The articular surface (*trochlea articularis*, glenoid) has a roughly square appearance. Posteriorly behind the articulation area, the prearticular forms a retroarticular process. It tapers distally with the blunt ending. Its dorsal surface is gently concave in transverse section, forming a shallow, wide anteroposteriorly oriented groove.

Braincase. Bones of the endocranium are apparently nearly complete, but partly damaged (Fig. 2). The unpaired basioccipital and otooccipitals (the unit formed by the co-ossified opisthotics and exoccipitals) are well preserved. Paraoccipital processes are robust. The basioccipital is broad, forming the central region of the occipital condyle. In general, the basioccipital is rhomboidal in shape, slightly concave dorsally. The basioccipital and basisphenoid maintain sutural contact only. The sphenooccipital tubercles are located at the level of the basisphenoid–basioccipital suture, and the basisphenoid participates in the tubercle by contributing to the ventral processes. The basipterygoid process is preserved only on the left side. It is broad and robustly built. The prootic could not clearly be identified. The supraoccipital is preserved, but mostly covered by the parietal.

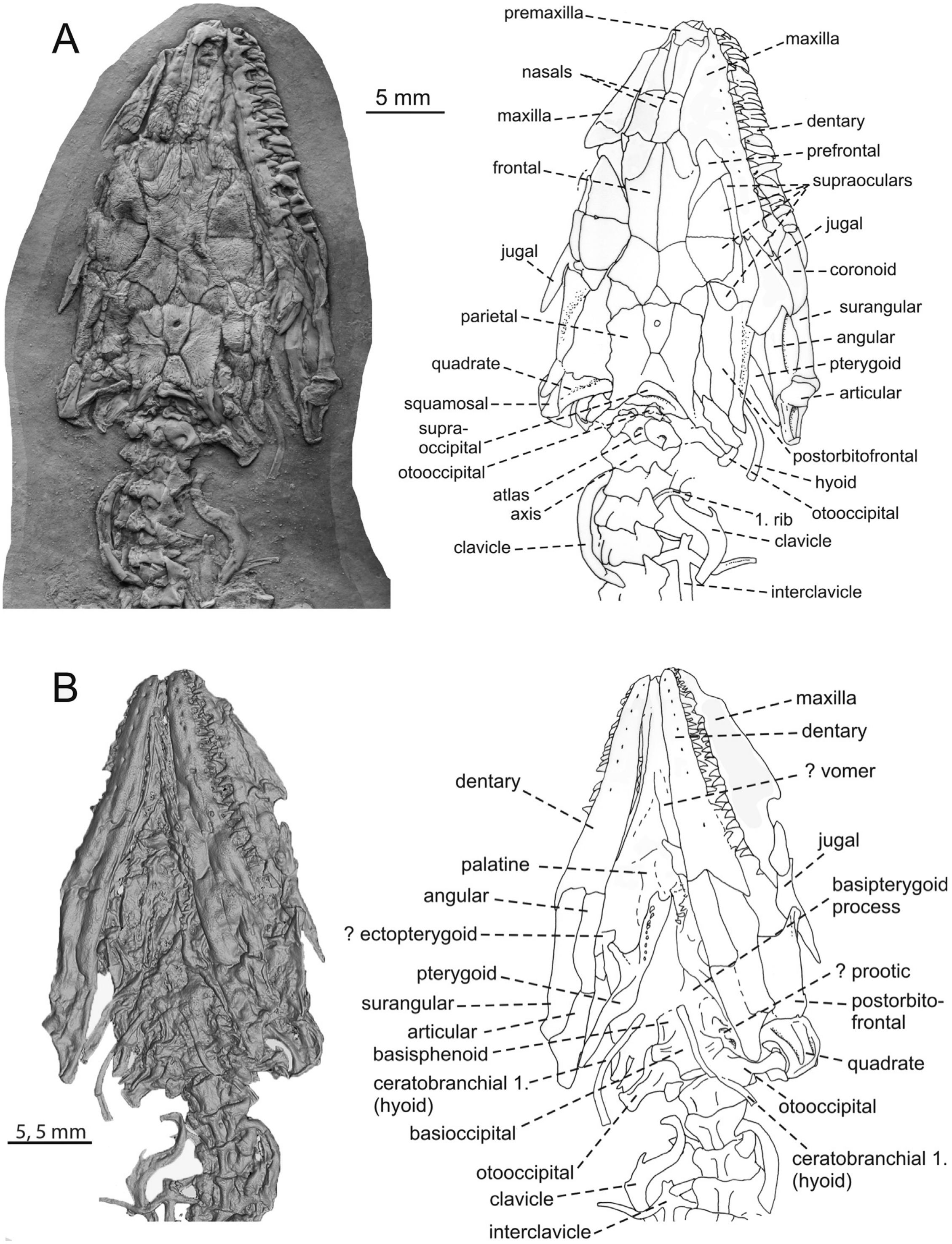

Fig. 2. *Eolacerta robusta*. The skull of the juvenile specimen SMF-ME 3314a in (A) dorsal, (B) ventral (using micro-CT visualization) aspects.

Fig. 2. *Eolacerta robusta*. Crâne du spécimen juvénile SMF-ME 3314a en vues dorsale (A) et ventrale (B) (visualisation par micro-CT).

Vertebrae. There are 27 presacral vertebrae, including eight cervicals, and two sacral vertebrae, but only the base of the tail is preserved, so it is impossible to determine the number of caudal vertebrae. The centrum of all vertebrae has a ventral mid-sagittal ridge (keel). The atlas was not clearly visible in specimens studied by Müller (2001). Here, the atlas is well preserved with very similar morphology to that in *Stefanikia siderea*. The neural arch is markedly

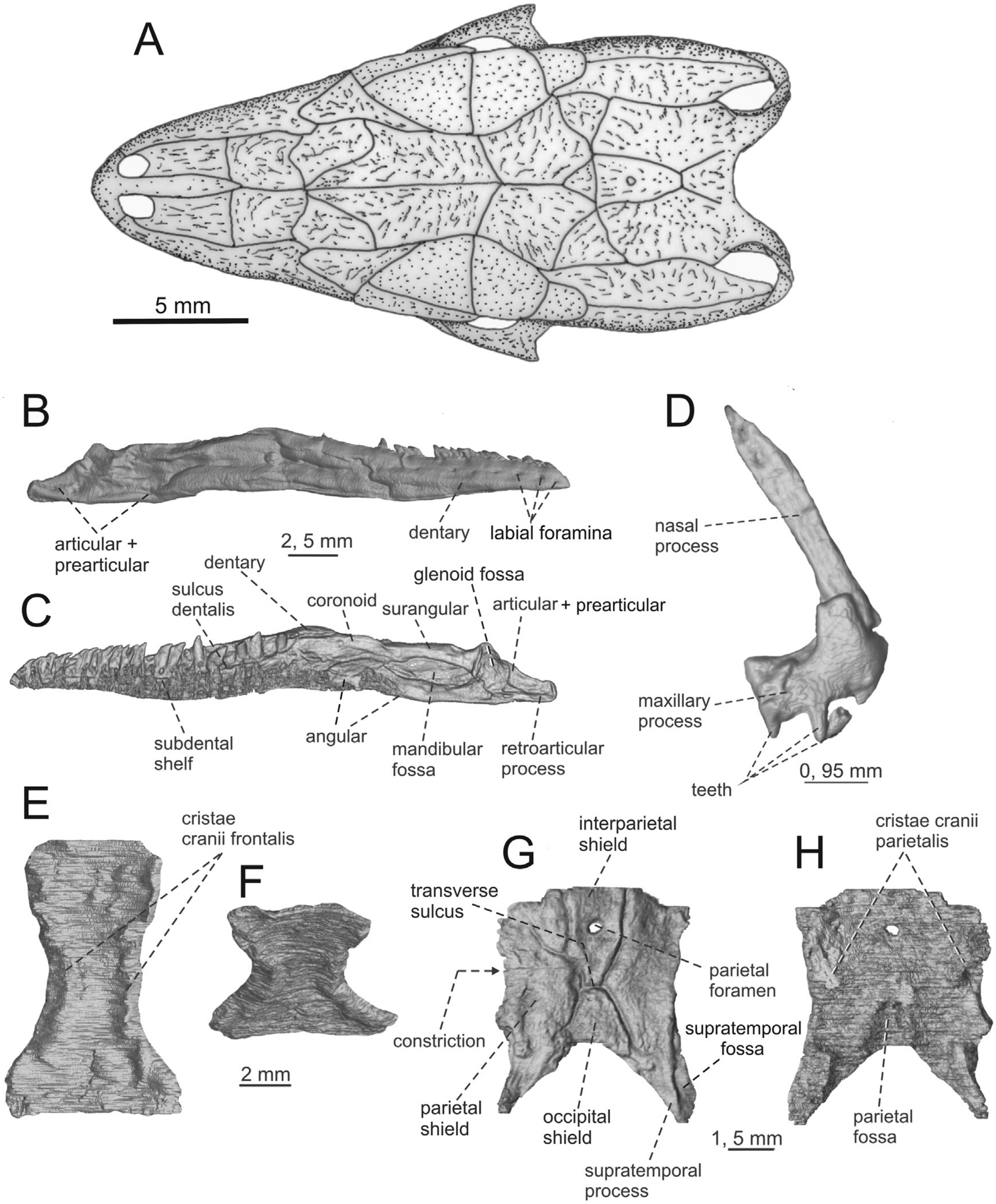

Fig. 3. *Eolacerta robusta*. (A) Reconstruction of skull in dorsal aspect. Right mandible in (B) external, (C) internal aspects. Premaxilla in (D) lateral aspect. Frontal in (E) ventral, (F) anteroventral aspects. Parietal in (G) dorsal, (H) ventral aspects.

Fig. 3. *Eolacerta robusta*. (A) Reconstitution en vue dorsale. Mandibule droite en vues externe (B) et interne (C). Prémaxillaire en vue latérale (D), frontal en vues ventrale (E), antéro-ventrale (F). Pariétal en vues dorsale (G) et ventrale (H).

broad, having a rounded dorsal margin. The posterodorsal process is well-developed and pointed. It is long, but does not distinctly reach further posteriorly than the posterior margin of the neural arch. Other aspects of the atlas are not sufficiently well preserved for description.

Clavicle. Both clavicles are preserved (Fig. 1), the morphology of the right element is especially clear (Fig. 4A, B). It is an S-shaped bone. It shows a typical interruption of the ventromedial loop, which is present in adult forms as well (see Müller, 2001).

Interclavicle. The interclavicle is well preserved. It is a cross-shaped bone, with a short anterior process and a long posterior one (Fig. 4A, B). The lateral processes appear to be very long and slightly posteriorly inclined (it should be

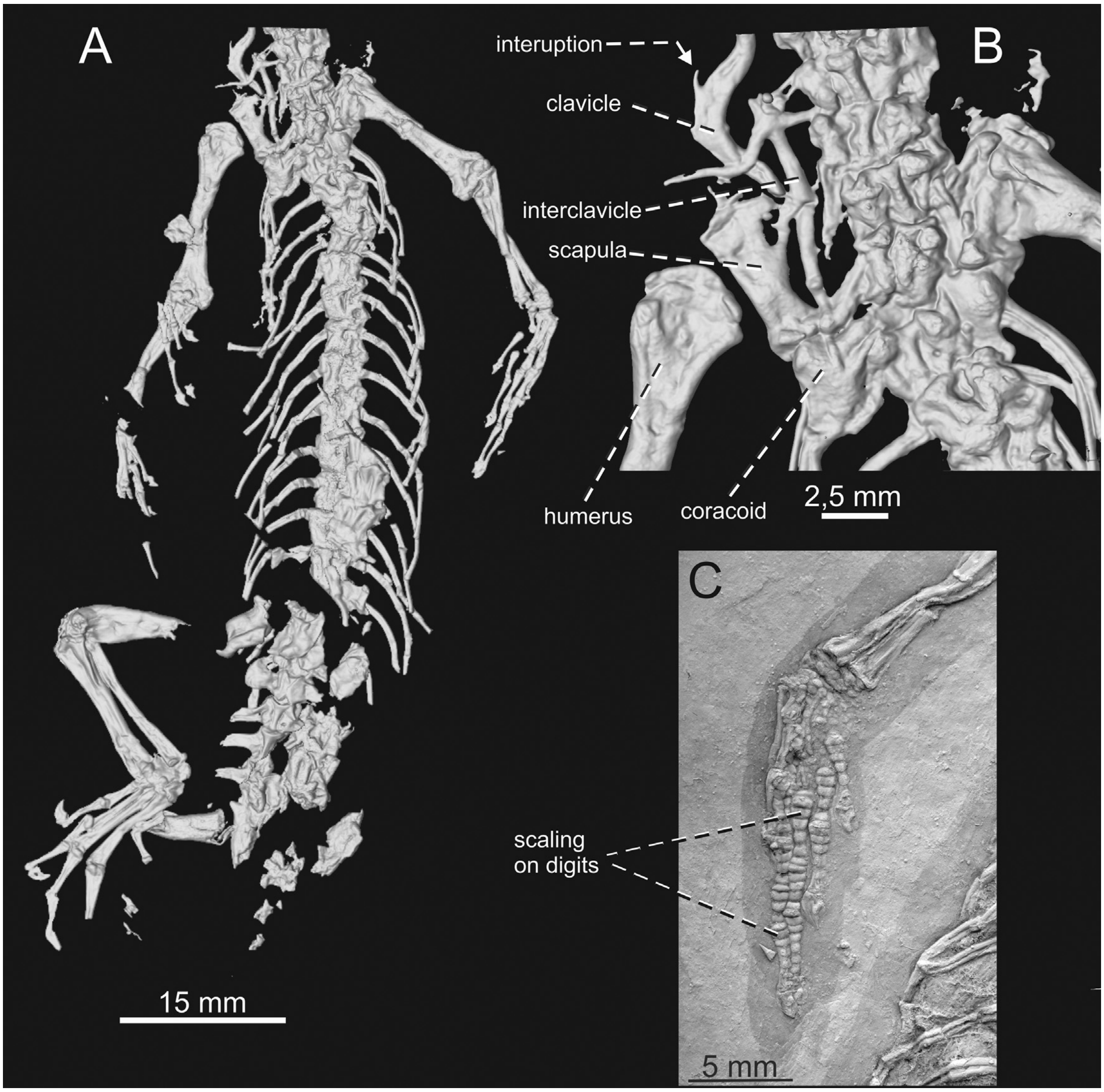

Fig. 4. *Eolacerta robusta*. A. The entire skeleton of SMF-ME 3314a in ventral aspect revealed from µCT. B. Detail of the pectoral region. C. Scaling on the left hand in dorsal aspect.

Fig. 4. *Eolacerta robusta*. A. Squelette entier de SMF-ME 3314a en vue ventrale révélée à partir de µCT. B. Détail de la région pectorale. C. Écailles sur la main gauche en vue dorsale.

noted that strong curvature of the right branch is a diagenetic artifact). The lateral processes are basically laterally directed in Müller's (2001: fig. 9) reconstruction of the pectoral girdle in the adult.

Ischium. The bone is broad but flattened (Fig. 5). Its ventral margin is rounded. The ventral portion appears to project slightly anteriorly into a triangular process. The anterior margin is therefore strongly concave here.

Soft tissue. Skin impressions are preserved in some places, particularly on digits and partly on the carpus and the metacarpus of the left hand (Fig. 4C). On the carpus and the metacarpus, elliptical or even nearly hexagonal scales of relatively small size are present. Larger, rectangular scales are present on the underside of the digits, which are transversely wide. They correlate in size with the width of the bone (i.e. in the middle of a phalanx they are less wide, at the joints they are wider). The shape here is square or elliptical rather than rectangular.

4. Discussion

4.1. Taxonomy and comparison of SMF-ME 3314

SMF-ME 3314 shares numerous characters (the same combination of plesiomorphic and derived features) with *Eolacerta* and *Stefanikia* (see Čerňanský and Smith, 2018), e.g.:

- interparietal shield of the parietal overlaps the posteromedial region of the frontal;

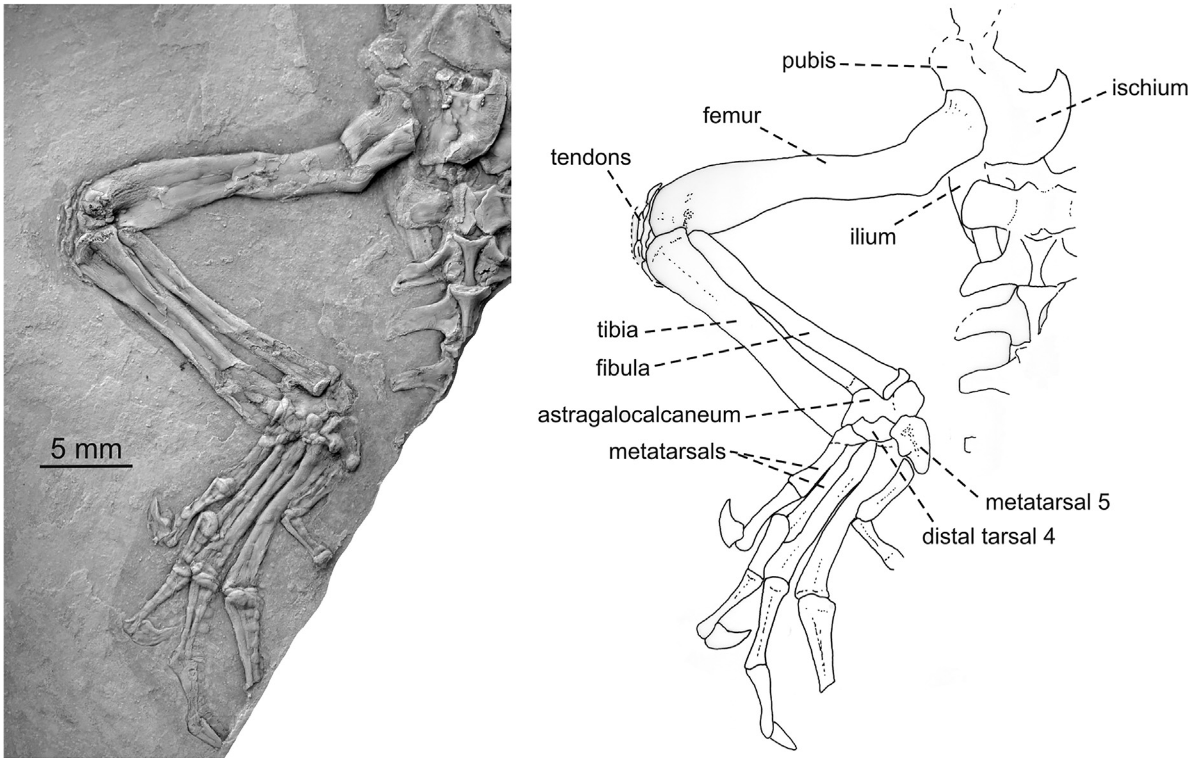

Fig. 5. *Eolacerta robusta*. The counterpart, SMF-ME 3314b.

Fig. 5. *Eolacerta robusta.* Analogue SMF-ME 3314b.

- the parietal foramen located more anteriorly, in the anterior fourth of the parietal;
- an only partially closed supratemporal fenestra;
- the first anterior supraocular osteoderm forms a long tapered process directed posteriorly, bordering anterolaterally the second supraocular osteoderm;
- the ornamentation of the cranial osteoderms comprising hair-like grooves, reminiscent dried-up riverbeds;
- straight ventral margin of dentary rather than convex;
- high dentary tooth number;
- teeth are unicuspid, pointed, recurved, with the presence of culmen lateralis anterior and culmen lateralis posterior;
- postorbital and postfrontal are fused;
- a posterior interruption of the ventromedial loop of the clavicle;
- the first rib appears on the 4th cervical vertebra and is distinctly posteriorly recurved;
- the zygantrum–zygosphene articulation is present;
- 27 presacral vertebrae;
- absence of body osteoderms;
- astragalus and calcaneum are fused.

The specimen described here represents a juvenile stage of *Eolacerta* and can be allocated more precisely to *E. robusta* based on the combination of the following characters (see Čerňanský and Smith, 2018):

- the nasal process of the premaxilla is long, rather than short. It is long in adults of *E. robusta*, but short in *Stefanikia siderea*;
- the position of the lacrimal is identical to that in *E. robusta*, whereas in *S. siderea* it is more anteriorly located because of the long suborbital process of the jugal;
- the postorbital process of the jugal is broad, as in the adult *E. robusta*, whereas in *S. siderea* the postorbital process is thin;
- the ratio of the anterior and posterior region of the frontal between the sulcus interfacialis is around 0.61 as in *E. robusta*, whereas in *S. siderea* the anterior region is much longer;
- a mid-length constriction of the parietal table is present, even if less pronounced than in the adult, whereas in *S. siderea* it is absent;
- the interparietal shield becomes wider anteriorly, whereas in *S. siderea* the lateral margins of interparietal shield are more or less parallel;
- the transverse sulcus between interparietal and occipital shields is straight rather than anteriorly convex;
- the number of maxillary teeth is 28 compared to 30–32 in large *E. robusta*, whereas the tooth count in *S. siderea* is only about 23.

4.2. New characters observed in *E. robusta*

The tooth number in the premaxilla of *Eolacerta* is often discussed. According to Nöth (1940), five teeth can be recognized in the premaxilla of the Geiseltal holotype, and this author estimated seven tooth positions. In the Messel specimens studied by Müller (2001), all premaxillary teeth are damaged. If the allocation of the isolated incomplete premaxilla from Prémontré to *Eolacerta* is correct (see Müller, 2002: p. 492, fig. 1A, B), then seven tooth positions are present in this taxon. The same number can be estimated in the specimen studied here. Among the members of the clade Lacertidae, seven premaxillary teeth can be found in the tribe Eremiadini, e.g., in *Acanthodactylus* or *Mesalina*, and six or seven in *Eremias persica* (see Evans, 2008; Khosravani et al., 2011). However, such a tooth count can be observed in *Gallotia* as well, whereas in *Psammodromus* and Lacertini, the premaxillary tooth count is higher – nine or more (Čerňanský et al., 2016). Nine teeth can be also observed in the late Eocene taxon *Plesiolacerta lydekkeri* (see Čerňanský and Augé, 2013).

The presence of pterygoid dentition and the absence of palatine dentition are important new observations for *E. robusta*. On this basis, it is highly likely that teeth on the pterygoid were also present in the adult *E. robusta*. The pterygoid dentition among members of Eolacertidae was previously observed only in *Stefanikia siderea* (Čerňanský and Smith, 2018). SMF-ME 3314 is the first evidence of pterygoid dentition in *Eolacerta*, showing that the teeth were pointed and arranged in a single line.

A hyoid element is observed here for the first time. The shape and length of the preserved elements are very similar to those of Lacertidae (see, e.g., Herrel et al., 2005: p. 564, fig. 1) rather than to, e.g., anguimorphs (for *Pseudopus*, see Klembara et al., 2017: p. 36, fig. 29). In *Shinisaurus*, they are straight (see Conrad, 2004: p. 429, fig. 18). In teiids such as *Callopistes* and *Tupinambis* (see Digimorph.org, 2002–2012), there is only very little curvature of ceratobranchial I. *Teius* shows similar overall curvature as a Messel specimen described here, but it is more gradual. In gymnophtalmid *Colobosaura*, the curvature of these elements is markedly developed (both two limbs of the ceratobranchial form nearly a right angle). The ceratobrancial I in *Pholidobolus* has a sharp curvature rather than being gradual (see Digimorph.org, 2002–2012). Previously, only a small fragment in a big specimen of *E. robusta* was questionably marked as hyoid (see Müller, 2001; this element was described as a cervical rib by Nöth, 1940).

There are 27 presacral vertebrae in the juvenile as well as in adults. Müller (2001) described the presence of ventral keel on the centra, but mentioned that it might be only an artifact of preservation. In the juvenile specimen, a keel is clearly present in all vertebrae.

The ischium was previously described (see Müller, 2001: fig. 10), but here its ventromedial portion is complete and well preserved, giving information on the exact shape of this part, at least in juvenile form. In the large specimen, Müller (2001) described a horizontal symphyseal edge as resembling a flat plate with a parallelogram-like shape.

As for soft tissue, similar scalation is present in *Stefanikia*, where, however, the rectangular subdigital scales appear to be more slender in comparison with those of SMF-ME 3314.

4.3. Ontogeny of *E. robusta*

Besides new morphological characters, the new specimen also sheds light on the ontogeny of *Eolacerta*. The juvenile stage of SMF-ME 3314 is supported by a variety of unfused elements: unfused epiphyses of the long bones and unfused basisphenoid and basioccipital. The other main differences between SMF-ME 3314 and adult specimens are:

- smaller size (SVL 11 cm vs. 30 cm);
- the juvenile skull is not so robust, its posterior half is not markedly expanded laterally;
- the upper supratemporal fenestra is less open than in the adult;
- the groove (or sulcus) that separates the frontal from the prefrontal shields has a medial contact with the suture with nasal bones, whereas in large specimens this groove is completely restricted on the frontal;
- incompletely fused frontals;
- an absence of a big osteoderm fused to the angle of the jugal.

An increase in the tooth count between the juvenile and adult stages is expected. For instance, in the Canary Island, the maxillary tooth count of the giant lacertid *Gallotia stehlini* is thought to increase from 15 to 25, and the dentary tooth count from 16 to 29 (summarized in Bannert, 1998). Similarly, we have documented an increase in the dentary tooth count in the teiid lizard *Ameiva* sp. from 24 to 31 in specimens ranging in skull length from 29.6 to 47.9 mm (KTS unpublished data from San Diego State University). Thus, the slightly lower tooth count observed in SMF-ME 3314 compared to that in large *E. robusta* is not inconsistent with conspecificity.

SMF-ME 3314 has an SVL that is roughly one third of the SVL of large *E. robusta*. By comparison, in the Canary Island, giant lacertids show that this difference is much less than the difference between hatchlings and adult animals. In *Gallotia stehlini*, hatchlings have a mean SVL of 44.5 mm, whereas in fully grown adults the SVL is 260–280 mm (summarized in Bannert, 1998). Adults, therefore, are about six times as large in linear dimensions as hatchlings. In *G. simonyi*, hatchlings have a mean SVL of 50–51 mm, whereas in fully grown adults SVL is roughly 250 mm (Naeslund and Bischoff, 1998). Adults, therefore, are about five times as large in linear dimensions as hatchlings. If *E. robusta* grew in a similar way, then it would be 50–100% larger than a hatchling. This comparison cannot, of course, be taken at face value, but it suggests that the overall state of ossification of SMF-ME 3314 is not inconsistent with its attribution to *E. robusta*.

We regard these small morphological differences between the juvenile described here and adults of the species as caused by ontogeny and/or individual variation. The ornamentation is well formed, showing that it was clearly developed already in juveniles. A large osteoderm on jugal, which is fused to the bone in adults, is absent here. It seems that this osteoderm developed only later in ontogeny (or at least its fusion to jugal appeared later in ontogeny). The specimen also shows that frontals fuse together later in ontogeny by synostosis and even in large specimens, the traces of fusion are still visible. This support a suggestion of Müller (2001) that fusion of frontals in this taxon appeared later in ontogeny. The less open upper supratemporal fenestra (relative to adult stage) is particularly interesting because of the close relationship of eolacertids to the clade Lacertidae (see Čerňanský and Smith, 2018). In many crown lacertids, this fenestra is closed (in contrast to members of Teioidea; see Estes et al., 1988). Thus, a closed fenestra in the lacertid skull could be interpreted as a paedomorphic feature within this modern clade. However, there are some objective conflicts to such statement. In lacertids, the opposite trend appears to be present–the supratemporal fenestra becomes smaller during ontogeny, which appears to be connected to the ossification of the postorbitofrontal (see ontogenetic series figured for *Gallotia* in Barahona, 1996; Barahona and Barbadillo, 1998). Moreover, a small opening in the posterior portion of the supratemporal fenestra exists even in adults of some lacertid species. The real extent of this opening is hard to interpret in fossils of *E. robusta* due to preservation, although, admittedly, it seems to be larger in the adult than in the specimen here (and seems to be larger also in *Stefanikia*). The condition in the juvenile specimen described here does not markedly differ, however, from the condition in the adult specimen of *Acanthodactylus erythrurus*, *Eremias persica*, or *Mesalina watsonana* (see Barahona, 1996; Khosravani et al., 2011). For all these reasons, it seems to be more plausible that the difference in the size of the supratemporal fenestra between the juvenile specimen described here and adults of *E. robusta* is simply intraspecific variation. New fossil specimens of different ontogenetic stages of *E. robusta* could shed more light on this character.

The slightly different location of the groove between frontal and prefrontal shields is most likely a result of intraspecific variation. The lateral processes of the interclavicle appear to be much longer in comparison with the adult of *E. robusta* (see Müller, 2001); however, this might be explained by the bad preservation of large, previously described specimens. In the hyoid, only ceratobranchial I can be recognized, whereas other elements such as basihyal and hypohyal are not preserved. Cartilaginous elements are sometimes preserved in Messel lizards (e.g., inscriptional ribs and suprascapula in a specimen of *Geiseltaliellus maarius*; Smith, 2009), but the cartilaginous elements of the hyoid apparatus have not yet been described. Usually the first ceratobranchials are the most robust hyoid elements in lizards. In *Anolis*, for example, the hyoid apparatus is entirely cartilaginous, except for the ceratobranchials I (see Bels, 1990). In lacertids, the first pair of ceratobranchials was calcified in all specimens examined by Herrel et al. (2005) and the primitive condition for the group as represented by *Gallotia galloti* is regarded that one, where only the first pair of ceratobranchials ossified (Herrel et al., 2005). Some spongy remains of the cartilaginous suprascapula appear to be preserved just above the right scapula, but the main portion is decayed. According to Müller (2001), sternum, epicoracoid, and suprascapula are chondrified in a large specimen too.

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