

RESEARCH ARTICLE

The first Miocene fossils of *Lacerta cf. trilineata* (Squamata, Lacertidae) with a comparative study of the main cranial osteological differences in green lizards and their relatives

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Abstract

We here describe the first fossil remains of a green lizard of the *Lacerta* group from the late Miocene (MN 13) of the Solnechnodolsk locality in southern European Russia. This region of Europe is crucial for our understanding of the paleobiogeography and evolution of these middle-sized lizards. Although this clade has a broad geographical distribution across the continent today, its presence in the fossil record has only rarely been reported. In contrast to that, the material described here is abundant, consists of a premaxilla, maxillae, frontals, parietals, jugals, quadrate, pterygoids, dentaries and vertebrae. The comparison of these elements to all extant green lizard species shows that these fossils are indistinguishable from *Lacerta trilineata*. Thus, they form the first potential evidence of the occurrence of this species in the Miocene. This may be also used as a potential calibration point for further studies. Together with other lizard fossils, Solnechnodolsk shows an interesting combination of survivors and the dawn of modern species. This locality provides important evidence for the transition of an archaic Miocene world to the modern diversity of lizards in Europe. In addition, this article represents a contribution to the knowledge of the comparative osteological anatomy of the selected cranial elements in lacertids. This study gives special emphasis to the green lizards, but new data are also presented for related taxa, e.g., *Timon lepidus*, *Podarcis muralis* or *Zootoca vivipara*. Although the green lizards include several cryptic species for which determination based on isolated osteological material would be expected to be difficult, our comparisons show several important morphological differences, although a high degree of variability is present.

Introduction

Although the fossil record of squamates is well documented in western and central Europe, many aspects of eastern Europe remain unknown. However, this area can be crucial for our

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understanding of the biogeography and evolution of this currently dominant group of non-avian reptiles [1–3]. We here describe a significant find of fossil remains that can be allocated to the lizard family Lacertidae from upper Miocene beds near the town of Solnechnodolsk (Fig 1; the Ponto-Caspian steppe region) in southern European Russia—MN 13 of the European Neogene Mammal biochronological system [4]. The lizard clade Lacertidae includes over 300 small- to medium-sized living species [5], which are broadly distributed in Eurasia and Africa. Lacertids form the dominant reptile group in Europe, where this group is also suggested to have originated [6]. This is supported by the fossil record [7–9]. The Lacertidae forms a monophyletic group [10] consisting of two lineages: Lacertinae and Gallotiinae [6]. Descendants of the basalmost divergence in Lacertidae, between Gallotiinae and Lacertinae, are also documented from Europe [11–12]. The members of the clade Lacertidae exhibit an extensive range of body sizes. The medium-sized lacertids, belonging to Lacertinae, are represented by the green lizards of the genus *Lacerta*. Molecular and morphological phylogenetic analyses show that *Lacerta* is the sister taxon to *Timon* [13–17, 6].

The oldest finds of green lizards are documented from the lower Miocene (MN 4) locality Dolnice near Cheb in the Czech Republic [18]. The oldest known remains potentially allocated to *Lacerta cf. viridis* have been described on the basis of several isolated jaw elements from the late Miocene (MN 11) localities of Kohfidisch in Austria [19], and Polgárdi in Hungary [20]. Nowadays, green lizards inhabit a large area extending from the Iberian Atlantic coast to Central Asia [21]. However, this group includes several morphologically cryptic species [22] for which determination based on isolated osteological material has been extremely difficult [18]. Even though there is useful published data concerning the osteology of these animals, it is not sufficiently detailed to allow reliable interpretation of fossil remains to species level. Peters [23] already recognized five species: *L. agilis*, *L. schreiberi* (Schreiber's green lizard or the Iberian Emerald lizard), *L. strigata* (the Caucasus green lizard), *L. trilineata* (Balkan green lizard or three-lined green lizard) and *L. viridis*. Based on morphological studies [24], *L. trilineata* was recently split into three species, *L. trilineata*, *L. media* (Levant green lizard) and *L. pamphylica* (Turkish pamphylic green lizard). Within *Lacerta viridis* clade, two main lineages were recognized—Western European lineage of *L. bilineata* and Eastern European *L. viridis* [25]. The taxonomy, evolution and biogeography of these taxa has been highly discussed [21, 16, 25–27]. However, the fossil record of green lizards from the crucial time period—Miocene, when the speciation within the group very likely occurred [16], is almost absent. This leads to a gap in our knowledge of the evolution of this group and to the absence of calibration points, resulting in wide confidence intervals for divergence time estimates [16, 27–28]. An essential requirement for enabling progress in interpreting the fossil record of *Lacerta* is a comparative study of extant taxa for the purpose of discovering characters useful in species level identification.

The Solnechnodolsk locality (45° 18'N, 41° 33'E) is situated in the Northern Caucasus, 40 km NW of the city of Stavropol. In paleogeographical terms, it is located at the southern shore of the Pontian marine basin. The vertebrate fossils occurred as disassociated bones coming from fluvial and lacustrine beds incised in middle Sarmatian (Bessarabian) limestones. Mostly preliminary accounts of the fauna have been so far published [29–31]. The data obtained from small mammals correlates the Solnechnodolsk fauna with the late Turolian. The locality yielded one of the most abundant and diverse vertebrate faunas of the late Miocene in Russia. Among them, only remains of *Pelobates*, amphisbaenians and anguimorphs have recently been described [3, 32]. In addition, the first Neogene mabuyid skinks are also documented from this site [33].

The aims of this paper are as follows: (1) to describe the fossil lacertid material from the late Miocene of Solnechnodolsk in detail; (2) to compare it with other lacertids, with the main



Fig 1. The location of the Solnechnodolsk locality.

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focus on extant green lizards; (3) to do a comparative anatomy of selected cranial elements useful for diagnostic purposes in extant lizards. This will serve as a reference for other comparative anatomical studies of any other lacertids extant, or extinct (such a study is crucial for the determination of the abundant record of the fossil lacertid cranial elements).

Material and methods

Specimens examined

The lizard specimens described here are housed in the Geological Institute of the Russian Academy of Sciences, Moscow, Russia, prefixed under individual GIN numbers. Since the site discovery in 2009, the material was sampled in 2009, 2010, 2014, and 2017 by expeditions from of the Russian Academy of Sciences. Fossils were extracted from sediments by screen washing with the mesh size 0.5, 0.7, and 1 mm. The excavated vertebrate material includes fishes, amphibians, reptiles, birds, small and large mammals.

Specimens used for comparisons

The following specimens of extant lizard species were used for comparison: *Lacerta viridis* (NHMV 40137, DE 51, 131, 132, UF 65017 male), *L. schreiberi* (NHMV 10809, 10808–1, 10808–4), *L. bilineata* (NHMV 18599–1, 35860–1, 35860–2), *L. pamphylica* (ZSM 1047/2005—male; ZSM 939/2005—female, NHMV 35861—juvenile), *L. strigata* (NHMV 39765, 10917–1, 10917–2), *L. trilineata* (NHMV 27665 male; 26524–1 male, 26524–2 female), *L. media* (NHMV 34808, 18956–1, 18956–4), *L. agilis* (NHMV 39028, 36392–1—male, 30885–1—female), *Timon lepidus* (NHMV 10921–1), *Podarcis muralis* (NHMV 39359–1; DE 133), *Zootoca vivipara* (NHMV 32438–1), *Takydromus sexlineatus* (DE 134), *Merolestes ctenodactylus* (NHMV 31376); *Psammotromus algirus* (NHMV36038-2) and *Gallotia stehlini* (NHMV 11031–1).

Institutional abbreviations: DE, Department of Ecology, Comenius University in Bratislava, Slovakia; GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; NHMV, Museum of Natural History, Vienna; UF, University of Florida, Florida Museum of Natural History (USA); UMJGP, Universalmuseum Joanneum, Graz, Austria; ZSM, The Bavarian State Collection of Zoology, Munich, Germany.

X-ray microtomography, three-dimensional visualization and photography

The specimens of extant lacertids (see [S1 Dataset](#)) were scanned by the micro-computed tomography (CT) facility at the Slovak Academy of Sciences in Banská Bystrica, using a Phoenix mikro-CTv|tome|x L240. The specimen UF 65017 was scanned at the University of Florida's Nanoscale Research Facility, using a Phoenix v|tome|x M dual tube micro-Computed Tomography (CT) system. The CT data sets were analyzed using VG Studio Max 3.2 and Avizo 8.1 on a high-end computer workstation at the Department of Ecology (Comenius University in Bratislava). The fossil specimens and the maxilla of *Lacerta viridis* (DE 51) were photographed under a Leica M125 binocular microscope with axially mounted DFC 500 camera LAS software (Leica Application Suite) version 4.1.0 (build 1264).

Anatomical terminology, character reconstruction and measurements

The standard anatomical orientation system is used throughout this paper. The image processing program ImageJ [34] was used for measurements. We used Mesquite (Version 2.75; [35]) to optimize characters using parsimony. The Mesquite metatree is based on Marzahn et al. [26], Kornilios et al. [27], Pyron et al. [15] and Čerňanský & Smith [9] for lacertids and out-group relationships.

Results

Systematic paleontology

Squamata Opper, 1811 [36]

Lacertoidea Estes, Queiroz and Gauthier, 1988 [37]

Lacertidae Opper, 1811 [36]

Lacerta Linnaeus, 1758 [38]

Lacerta cf. trilineata Bedriaga, 1886 [39]

Figs 2–7

Material—One premaxilla GIN 1145/270, six right maxillae 1145/271–276, five right frontals 1145/277–281, one left frontal 1145/282, four parietals 1145/283–285, 304, one left prefrontal 1145/286, two right jugals 1145/287–288, one left jugal 1145/289, two right postfrontals 1145/290–291, one right quadrate 1145/292, one right pterygoid 1145/293, two left dentaries 1145/294–295, four right dentaries 1145/296–299.

Locality and horizon—Solnechnodolsk (Stavropol Region, southwestern Russia); upper Miocene, MN 13.

Osteological description

Premaxilla. The premaxilla is a triradiate element (Fig 2A–2C). The nasal process is moderately broad and has a lanceolate form. Unfortunately, the apex of this process is broken off. The preserved portion of the internal surface bears the facet for the nasal on each side. Between these facets, a distinct ridge is developed. The external surface of the nasal process bears ornamentation. The portion below the nasal process is roughly triangular in shape. The maxillary processes are well developed, but short. On their lateral edges, they bear a wedge-shaped facet for the external ramus of the premaxillary process of the maxilla on each side. The dental portion bears nine tooth positions (eight teeth are still attached). The supradental shelf forms a short, slightly bilobed incisive process in its mid-region. The vomerine processes is well developed.

Maxilla. The description is based on the specimen GIN 1145/271 (Fig 2D–2F), which represents a right maxilla. It bears 16 tooth positions—all teeth are still attached. However, the posterior portion of the maxilla is broken off, so the tooth number of the complete tooth row is

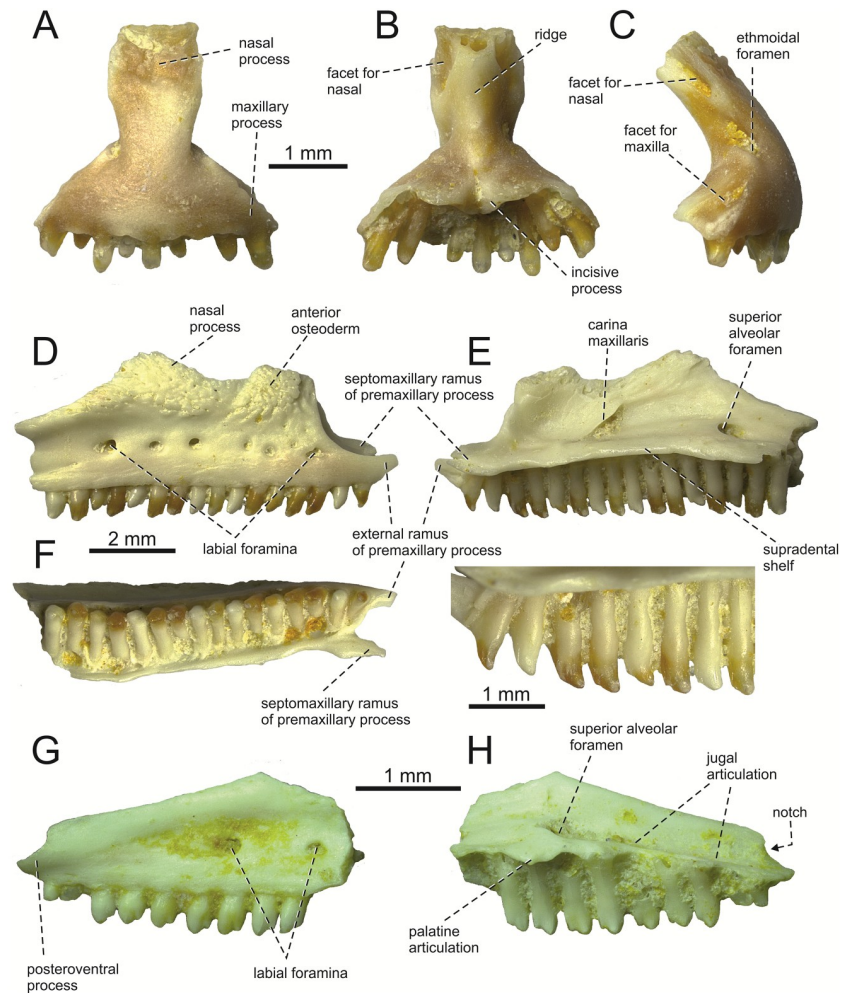


Fig 2. *Lacerta cf. trilineata* from the late Miocene of the Solnechnodolsk locality. Premaxilla GIN 1145/270 in external (A), internal (B), and lateral views (C). Maxilla GIN 1145/271 in lateral (D), medial (E) with a detail of teeth, and ventral views (F). Maxilla GIN 1145/272 in lateral (G), and medial views (H).

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certainly slightly higher. The suprudental shelf (sensu Rage & Augé [40]) is thin, well expanded medially and slightly dorsally convex. The anterior extremity of the maxilla is divided into a short external ramus, the premaxillary process, and a broader, more medially oriented and slightly more dorsally developed septomaxillary (internal) ramus. The orientation of the septomaxillary ramus is anterior rather than being dorsally curved as it is in *Timon lepidus* or *Zootoca vivipara* [41]. An oval premaxillary fenestra is present between these rami. Immediately dorsally to this fenestra, a small foramen is present, the anterior opening for the superior alveolar canal. The nasal process is broad, but its dorsal portion is damaged. The medial surface of this process bears the carina maxillaris (sensu Müller [42]; this structure passes between the vestibulum and the cavum nasi, see [43]), which starts to rise posterodorsally from the level of the 6th tooth position (counted from anterior). The superior alveolar foramen is located at the level between of the 13–14th. tooth positions (counted from anterior). If we use this position as a reference point in the specimen GIN 1145/272, the complete posterior portion of a maxilla (Fig 2G and 2H), we can estimate 18–19 tooth positions in the complete tooth row.

The lateral face of the maxilla is pierced by 6 larger labial foramina arranged in a single line and several smaller, scattered in the anterior region. The posteriormost one of the larger

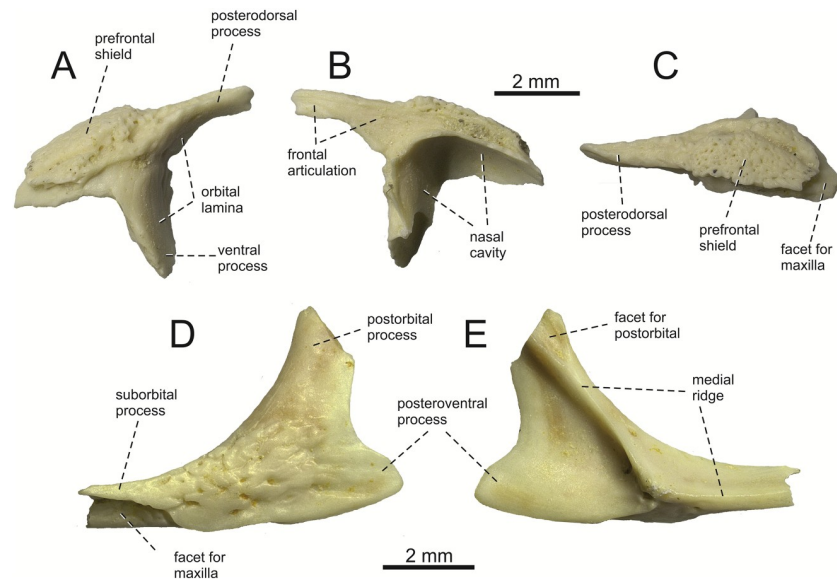


Fig 3. *Lacerta cf. trilineata* from the late Miocene of the Solnechnodolsk locality. Left prefrontal GIN 1145/286 in lateral (A), medial (B), and dorsal views (C). Left jugal GIN 1145/289 in lateral (D), and medial views (E).

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series is located at the level between the 13th and 14th tooth position (counted from anterior) in 1145/271, or at the level of 7th tooth position (counted from posterior) in 1145/272. The nasal process bears attached osteodermal shields. At least two well separated osteoderms fused to lateral side of the ventral portion of the nasal process of maxilla can be identified here. They are separated by a sulcus. This sulcus has a posteroventral course and virtually points to the 4th labial foramen (counted from anterior). The sculpture of these osteoderms consists of densely spaced grooves, pits and ridges. The anteriorly located osteoderm is large. The length of its ventral margin forms 1/3 of the entire length of the sculptured region. The posteroventral process of maxilla does not gradually narrow to its end, but it is stepped. The notch located between the dorsal and ventral portions of the posteroventral process is shallow, weakly developed (Fig 2H). The posteroventral process rises anteriorly, gradually continues to the nasal process. In their contact, only small dorsal curvature is present (it indicates the posterior end of the nasal process). On the internal side, the posterodorsal process bears a facet for the jugal.

Prefrontal. The left prefrontal is preserved (Fig 3A–3C). It is a roughly triradiate element. It has a long posterodorsal process, the ventral surface of which forms the anterodorsal margin of the orbit. In medial aspect, a facet for frontal can be observed. The ventral process, broader than the posterodorsal process, forms the anterior surface of the orbit. The dorsal surface of the bone possesses an ornamented osteodermal shield (the lateral portion of the prefrontal shield). The ornamentation consists of pits, grooves and small ridges. The internal surface is deeply excavated for the nasal capsule. The dorsal region forms the contact with maxilla.

Jugal. The best preserved, although incomplete, is the specimen GIN 1145/289 (Fig 3D–3E). It is a triradiate element. Only the ventral portion of the broad postorbital process is preserved—its dorsal termination is broken off. The posteroventral process is well defined. It is robust in lateral (or medial) aspect, roughly triangular in shape. The angle between the central line of the posteroventral and postorbital processes of the jugal is around 78°. The osteodermal shield is attached to the dorsolateral surface, mostly present in the suborbital process.

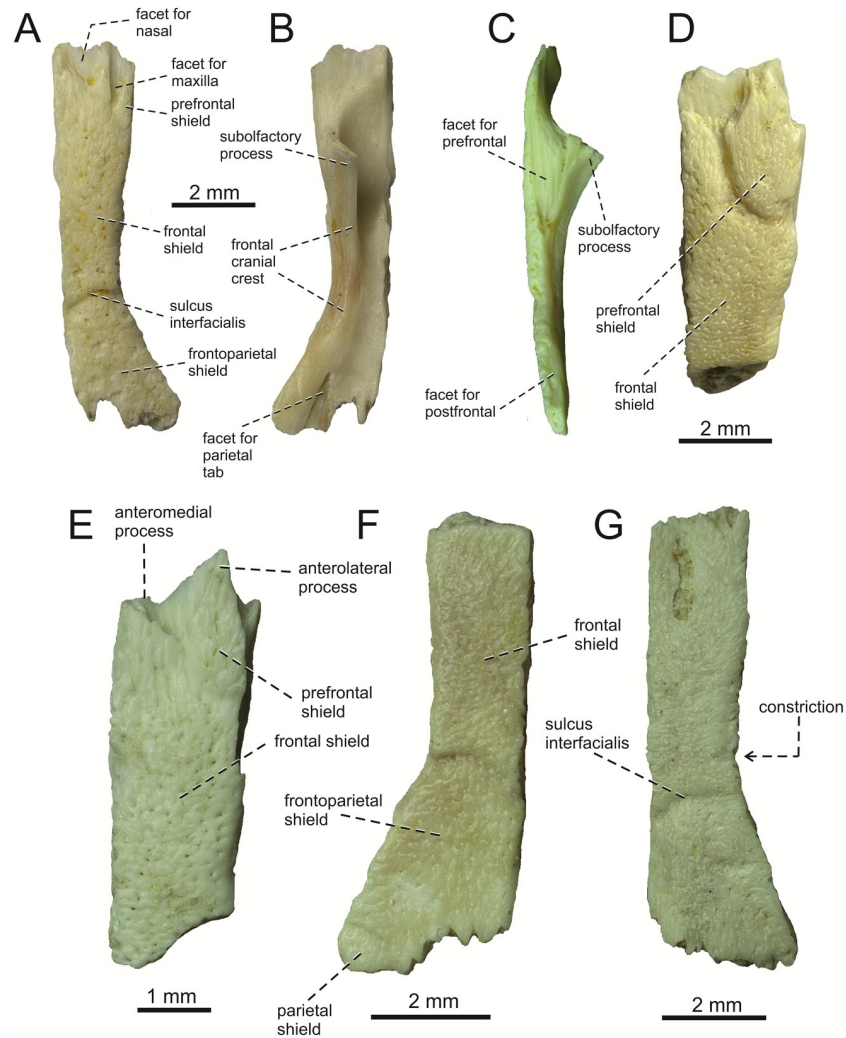


Fig 4. *Lacerta cf. trilineata* from the late Miocene of the Solnechnodolsk locality. Right frontals GIN 1145/277 (A-C), 1145/278 (D), 1145/279 (E), 1145/280 (G) and one left frontal 1145/282 (F) in dorsal (A, D, E, F, G), ventral (B), and lateral (C) views.

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Although the anterior portion of the suborbital process is not preserved, the posterior section of the facet for maxilla is visible in lateral aspect. In medial view, the medial ridge is present of the Type 1 in [44].

Frontal. There are six frontal bones preserved in the material. The description is mainly based on almost complete specimen GIN 1145/277 (Fig 4A–4C), which represents the right frontal. It is an anteroposteriorly elongate element, roughly rectangular in shape, with the posterior section being laterally expanded. The whole dorsal surface is covered by ornamented osteodermal shields, which are fused to the bone. Only exception is present in the anterior region, where a broad semi-elliptical smooth surface is located. It forms the articular facet for nasal. Laterally to it, a wedge-shaped smooth surface is located, representing the facet for the posterodorsal portion of the nasal process of the maxilla. The ornamentation of the osteodermal shields is identical to that of the prefrontal and maxilla. It should be noted that in the specimen 1145/277, the prefrontal shield is less defined, although it is possible to distinguish it from the frontal shield. The anteroposterior maximum length of this frontal is 10 mm. The

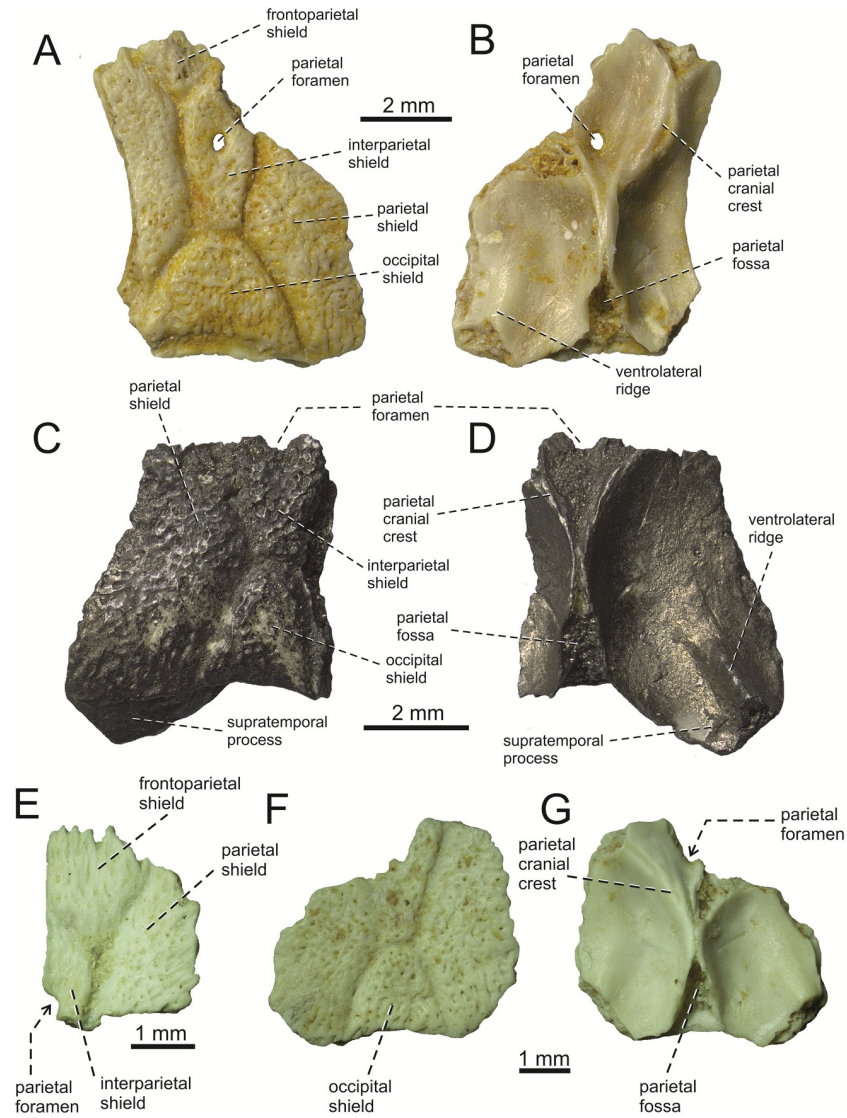


Fig 5. *Lacerta cf. trilineata* from the late Miocene of the Solnechnodolsk locality. Parietals GIN 1145/283 (A, B), 1145/284 (C, D), 1145/284, 1145/285 (E), and 1145/304 (F, G) in dorsal (A, C, E, F) and ventral (B, D, G) views.

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ornamentation is not so strongly developed as it is in larger specimens and thus we suggest that it represents a younger (immature) individual. In the specimen 1145/278 (Fig 4D), the oval prefrontal shield can be easily recognized. The anterior end of the frontal is more-or-less completely preserved in GIN 1145/279. Here, the pointed anterolateral process is prominent, triangular in shape (Fig 4E). Although only the base of the anteromedial process is preserved, it can be estimated (based on the size of the preserved portion) that it did not reach the level of the anterolateral process anteriorly. The sulcus interfacialis is well developed in several specimens, being slightly convex anteriorly. It forms a border between the frontal and frontoparietal shields. The lateral margin is slightly constricted anteriorly to the sulcus. The anterior region of the frontal in front of the sulcus interfacialis is much longer than the posterior region. It forms almost 2/3 of the entire anteroposterior length of the element. The contact with the parietal is interdigitated. The posterior region is especially well developed in 1145/282, where even

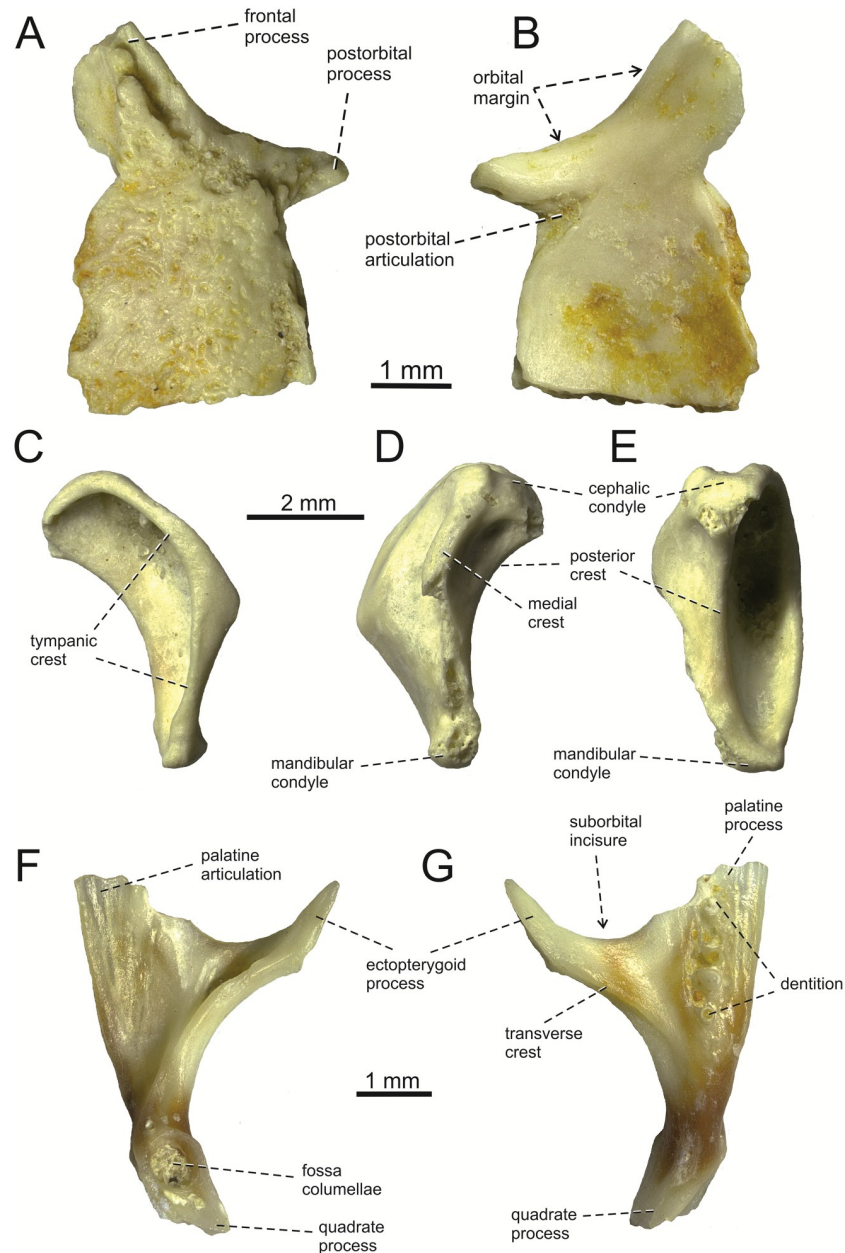


Fig 6. *Lacerta cf. trilineata* from the late Miocene of the Solnechnodolsk locality. Postfrontal GIN 1145/290 in external (A), and internal (B) views. Right quadrate GIN 1145/292 in lateral (C), medial (D), and posterior (E) views. Right pterygoid in dorsal (F), and ventral (G) views.

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the frontal portion of the parietal shield is preserved (see Fig 4F). It occupies a small area on the posterolateral corner of the frontal.

In lateral aspect, a wedge-shaped broad facet for the prefrontal and a thin one for the postfrontal are not in contact, leaving the frontal exposed on the orbital margin. On the ventral side, the frontal cranial crest is developed. It possesses two foramina in the posterior half of its length. The cranial crest expands anteriorly into a deep and well-developed subolfactory process. On the posterior margin, a well-developed triangular facet for the parietal tab is present.

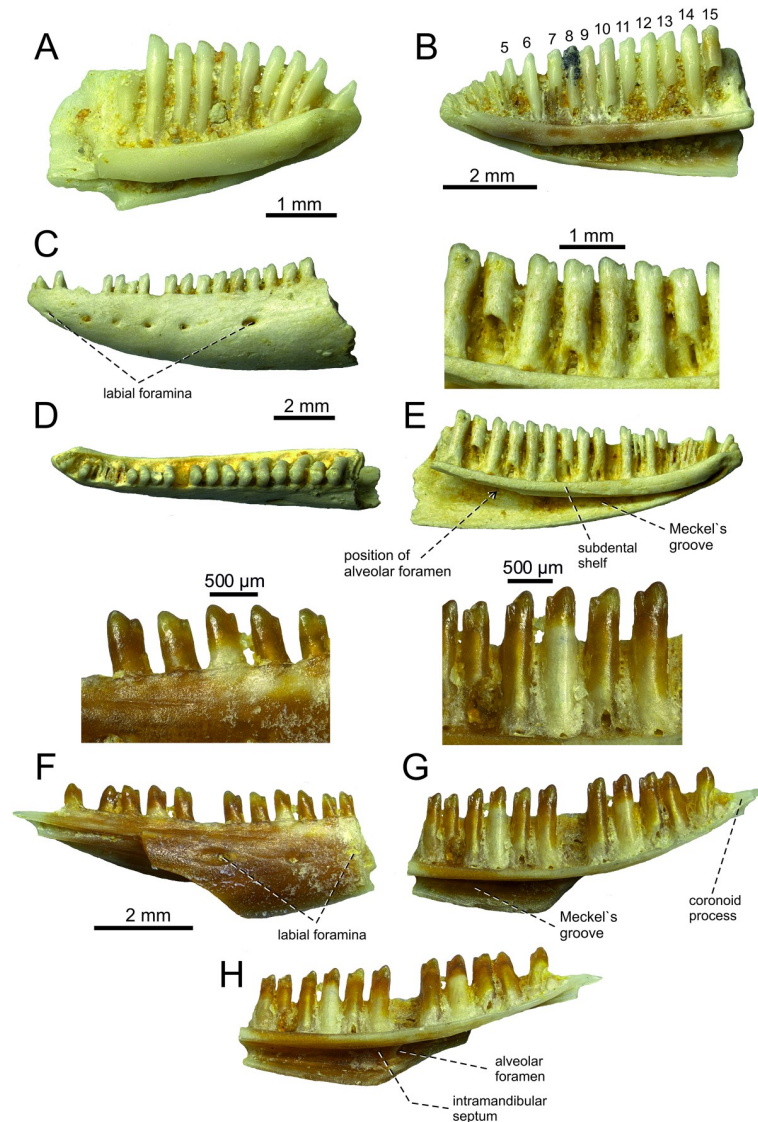


Fig 7. *Lacerta cf. trilineata* from the late Miocene of the Solnechnodolsk locality. Left dentary GIN 1145/294 in medial (A) view. Right dentary GIN1145/296 in medial (B) view. Left dentary GIN 1145/295 in lateral (C), dorsal (D) and medial (E) with detail of teeth. Right dentary GIN1145/297 in lateral (F) with detail of teeth, medial (G) with detail of teeth and ventromedial (H) views.

<https://doi.org/10.1371/journal.pone.0216191.g007>

Remarks: The facet for the posterodorsal portion of the nasal process of the maxilla deserves a comment here. The specimen GIN 1145/277 is smaller than other frontal elements from Solnechnodolsk available here. Thus, it most likely represents a juvenile (or subadult) individual. This is also supported by the apparent presence of somewhat stronger degree of mid-constriction (a juvenile character for *Lacerta*, but present in adults of other lacertid species). The facet for the maxilla is well-developed here and reaches even further posteriorly than the facet for the nasal. This is not present in other Solnechnodolsk specimens, where this facet is reduced. The facet for the maxilla in GIN 1145/277 forms a similar condition to that in adult individuals of extant species *L. pamphylica* studied herein and to the frontals described from the lower Miocene of the Czech Republic [18]. The frontals of extant European species of *Lacerta* usually have either a reduced or absent articulation facet for the maxilla (in dorsal

aspect, the bony septum is absent). However in some cases, this facet can have a similar morphology to that of GIN 1145/277, e.g. the left frontal of *L. viridis* NHMV 40137. For this reason, we regard this difference between GIN 1145/277 and other Solnechnodolsk fossil frontals as a result of individual and/or ontogenetic variation.

Parietal. All parietals are incompletely preserved (Fig 5). The description is mainly based on the specimens GIN 1145/283 (Fig 5A and 5B) and 1145/284 (Fig 5C and 5D). The parietal table is covered by several osteodermal shields. The centrally located interparietal shield is pierced by a parietal foramen in its anterior half. The interparietal shield is large, anteroposteriorly prolonged and pentagonal in shape. It is longer than a posteriorly located trapezoidal occipital shield. The occipital shield is, however, wider. It is twice as wide relative to the interparietal shield in GIN 1145/283 (although it can slightly vary in other specimens, see Fig 5). The occipital shield occupies a large area of the posterior portion of the parietal table (but not so large as in extant *Timon*). Laterally located parietal shields appear to be large, however they are not completely preserved. Only the right one shows the lateral margin, which appears to be slightly concave medially. The frontoparietal shields are only partly preserved on the left side in 1145/283. However, this region is better preserved in 1145/285, showing that the interparietal shield was entirely restricted to the parietal bone (Fig 5E). The ornamentation of shields in parietals is identical to that of prefrontal and frontal. Only the base of the left supratemporal process is preserved in the specimen 1145/284. It is markedly broad.

On the ventral surface, parietal cranial crests are well-developed. They originate from the anterolateral corners of the parietal and converge posteromedially. The best preserved region bearing an anterior section of the parietal cranial crest can be seen in 1145/283 (Fig 5B). Its course is not straight but it suddenly turns more medially approximately at the level of the anterior margin of the parietal foramen. Further posteriorly, the cranial crests merge posteriorly. They diminish posteriorly but continue to the end of the bone. A parietal fossa is located between them on the posterior midline (Fig 5G). The ventrolateral ridge is developed in the lateral half of the supratemporal process here. It gradually disappears anteromedially. As mentioned, only the base of the supratemporal process is preserved and so the morphology of its distal portion is unknown.

Postfrontal. It is sub-rectangular and anteroposteriorly elongated, but its posterior section is damaged in both specimens (Fig 6A and 6B). It bears anteroventral and anterodorsal expansions formed by the narrow, pointed postorbital process and a broad and blunt frontal process. This latter process bears a readily observed frontal articulation. The external surface of the postfrontal is mostly covered by an osteodermal shield. The internal surface is smooth, having a wedge shaped facet for an articulation with the postorbital.

Quadrate. The quadrate is dorsoventrally elongated, narrow rather than robust (Fig 6C–6E). In lateral aspect, the quadrate is anteroposteriorly narrow, with an anteriorly expanded anterior margin. The anterior section is bordered by a laterally expanded sharp ridge: the tympanic crest. This crest is continuous from the cephalic to the mandibular condyle. The crest is angled approximately in the mid-region. The dorsal surface of the cephalic condyle protrudes slightly posteriorly. The ventral half of the quadrate gradually markedly narrows ventrally. Thus the ventral portion is much narrower than the dorsal portion. This ventral region ends with the saddle-shaped mandibular condyle. It is slightly smaller than the cephalic condyle. The medial surface possesses a distinct medial crest, however, only its dorsal section is completely preserved, whereas the ventral section is damaged.

Pterygoid. The incomplete right pterygoid is preserved (Fig 6F and 6G). It is a tri-radiate, nearly letter “y”-shaped element. The ectopterygoid process is well developed, thin with a pointed anterior end. On the ventral surface, there is a transverse crest that runs along the base of the ectopterygoid process. The palatine process is broader, but its anterior end is broken off.

The palatine process bears teeth on its ventral side, located in a single line (only the posterior three teeth are preserved). On the dorsal side, the palatine articulation is present. Between the palatine process and the ectopterygoid process, there is a broad area—the suborbital incisure. Only a small portion of the quadrate process is preserved. The fossa columellae (= epipterygoid fossa) is large, well defined by its rounded margin.

Dentary. Several dentaries are preserved, but all only incompletely (Fig 7). The specimens GIN 1145/294 and 1145/296 represent only the anterior portions of the dentaries (see Fig 7A and 7B). The most completely preserved specimen is 1145/295 (Fig 7C–7E). In this specimen, 21 tooth positions (15 teeth are still attached) are preserved. In medial aspect, the subdental shelf (sensu Rage & Augé [40]) is rounded, dorsally concave. It gradually narrows posteriorly, mostly caused by the presence of the splenial here (the articulation with the splenial is still visible on the ventromedial side of the shelf, reaching the level of the 9th. tooth position if counted from anterior). Meckel's groove is largely widely open, especially in the posterior direction. The alveolar foramen is located at the level between the 18th–19th tooth positions (counted from anterior in the specimen 1145/295, or 7th tooth position counted from posterior in 1145/297; see Fig 7H). The symphyseal region is dorsally elevated and the symphysis is small, rectangular in shape.

The otherwise smooth labial surface is pierced by six labial foramina, with the posteriormost foramen being the largest one. They are located in a single line located in the upper half of the dentary rather than being in the mid-region.

Dentition. Tooth implantation in maxillae and dentaries is pleurodont. Teeth are tall, overarched the dental crest by the 1/3 of the tooth length. The tooth size slightly rises posteriorly. The anteriormost dentary teeth are monocuspid, becoming bicuspid starting from the 6th–7th tooth. There is a dominant cusp and an anteriorly located accessory cusp. The small interdental gaps are present. Most of the tooth bases are pierced by resorption pits. The pterygoid teeth are small and conical. They are slightly posteroventrally inclined.

Lacerta* group of ? *L. trilineata

Fig 8

Material—Three vertebrae GIN 1145/300, 302, 303.

Locality and horizon—Solnechnodolsk (Stavropol Region, southwestern Russia); upper Miocene, MN 13.

Osteological description

Dorsal vertebra. Three dorsal vertebrae are preserved, of which the specimen GIN 1145/300 is almost completely preserved (Fig 8). In lateral aspect, the neural spine is tall, posterodorsally oriented and trapezoidal—narrows posterodorsally. It slightly exceeds the condyle posteriorly. In dorsal aspect, the ascending region of the neural spine is laterally enlarged whereas the anteriorly located portion is thin. The interzygapophyseal constriction is weakly developed. The prezygapophyses bear oval articulation surfaces. Postzygapophyses bear roughly triangular articulation surfaces, being more posteriorly oriented rather than laterally. Zygosphenes-zygantrum accessory intervertebral articulations are present, but only incipient, weakly developed as small facets located laterally at the base of the neural arch and continuous with pre- or—postzygapophyseal articulations (character 468, state 2 in [45]). The neural canal is large, pentagonal in shape. The synapophysis is present in the anterior half of the vertebrae, being large and ovoid shaped. The posterior centrosynapophyseal lamina (sensu Tschopp [46]) is present posteriorly to the synapophyses. The cotyle and condyle are rounded. In ventral aspect, the centrum bears a low ridge in its mid-region. In lateral aspect, the ventral margin of the centrum is concave.

Remarks: The dorsal vertebrae of green lizards have tendency to uniform morphology, which encourages caution in assigning isolated vertebrae to particular species. The dorsal

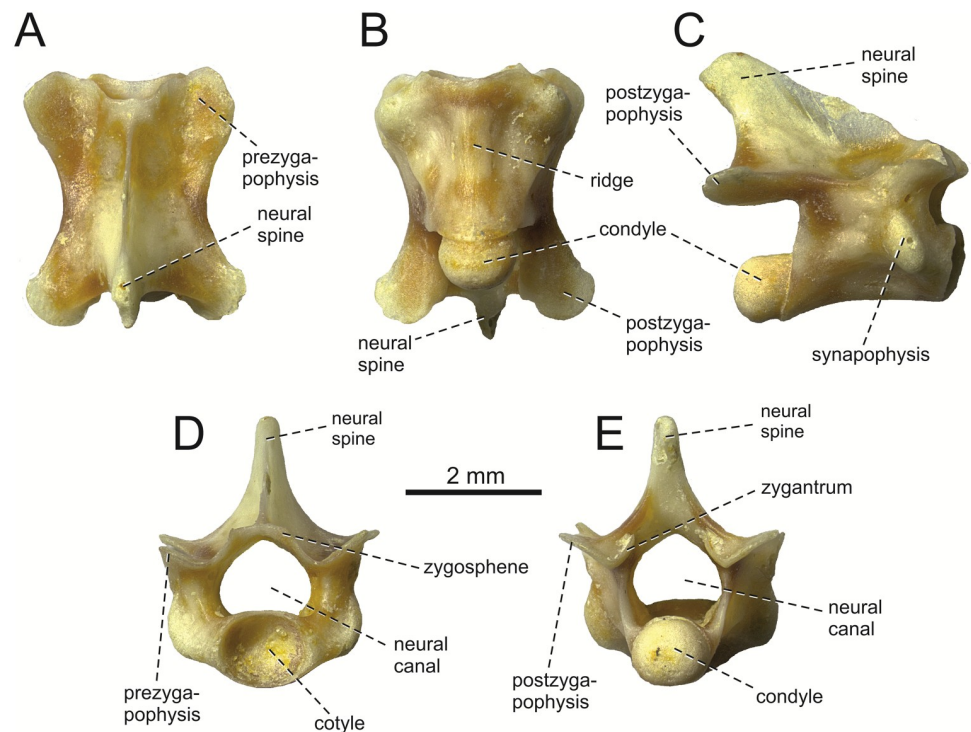


Fig 8. *Lacerta* group of ? *L. trilineata* from the late Miocene of the Solnechnodolsk locality. Dorsal vertebra GIN 1145/300 in dorsal (A), ventral (B), lateral (C), anterior (D) and posterior (E) views.

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vertebrae from Solnechnodolsk show a high similarity to that of *L. trilineata*, rather than to e.g. *L. strigata*. The posterior centrosynapophyseal lamina is absent in *L. strigata* and the synapophysis here is small (for vertebra of *L. trilineata* and *L. strigata*, see [46]). There are no characters that would prevent this vertebra from being assigned to *L. trilineata*, but strong support for such statement is absent. For this reason, we allocate this material here only potentially to the *L. trilineata* group.

Discussion and comparison

Affinities with green lizards

All fossil bones described here can be allocated to Lacertidae without doubt. They exhibit the following synapomorphies of Lacertidae, e.g., sulcus dentalis, lateral overlap of the posterodorsal margin of the dentary by the coronoid, maxilla-frontal contact, closure of the supratemporal fenestra, interparietal shield is restricted on parietal bone, and parietal cranial crests meet medially [37, 45]. Thus, reference to Lacertidae is strongly supported.

The fossil elements are assigned to a single species (except of vertebrae, see above) on the basis of dentition, sculpture of osteodermal shields and great similarity with the morphology presented by the extant green lizards (see below). Moreover they are comparable in size and come from a single site. Green lizards form a uniform group of lacertids. Their fossil record is rather poor (see Introduction), what is caused by two factors: (a) the low number of known fossil elements with a proper diagnostic features; (b) the lack of comparative studies focused on the detailed comparison of osteological elements in this group. For a proper identification of the Solnechnodolsk fossils, it was necessary to present such a study here. Although *Lacerta agilis* is traditionally called the sand lizard, it has been shown that this taxon branches within the green lizards [16, 26]. For this reason, it is included here and the complete list of green lizards

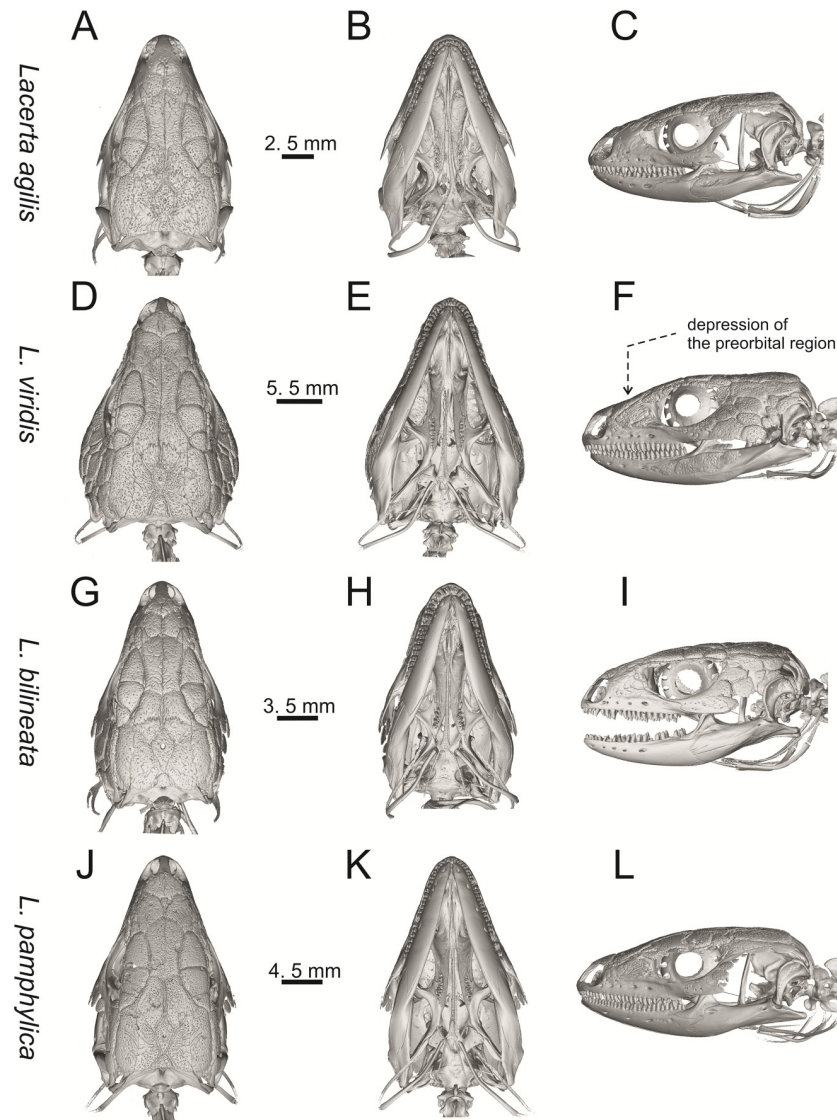


Fig 9. Skulls of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599–1 and *L. pamphylica* ZSM 939/2005 in dorsal (A, D, G, J), ventral (B, E, H, K) and lateral (C, F, I, L) views (continued).

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studied here includes *L. agilis*, *L. viridis*, *L. bilineata*, *L. pamphylica*, *L. strigata*, *L. schreiberi*, *L. trilineata* and *L. media* (see Figs 9–33). *Timon lepidus* was used for outgroup comparison (Figs 34 and 35). But because *T. lepidus* has a lot of unique features among extant lacertids (see below) and, moreover, to record the distribution of some character states, we also used *P. muralis* (Fig 36), *Zootoca vivipara* (Fig 37), *Takydromus sexlineatus* (Fig 38A–38F), *Meroles ctenodactylus* (Fig 38G–38I), *Psammodromus algirus* (Fig 39) and *Gallotia stehlini* (Fig 40).

Solnechnodolsk lacertid material can be allocated to green lizards without doubts. This can be supported by the combination of several features, e.g.:

(1) The frontal bone. The anterior region in front of the sulcus interfacialis is long, forming more-or-less 2/3 of the anteroposterior length of the frontal. In *Timon lepidus*, this anterior region of the frontal is short and the ratio of the anteroposterior length of the frontal shield vs. frontoparietal shield on frontal is approximately 1:1 (see [18]; or Fig 34A here).

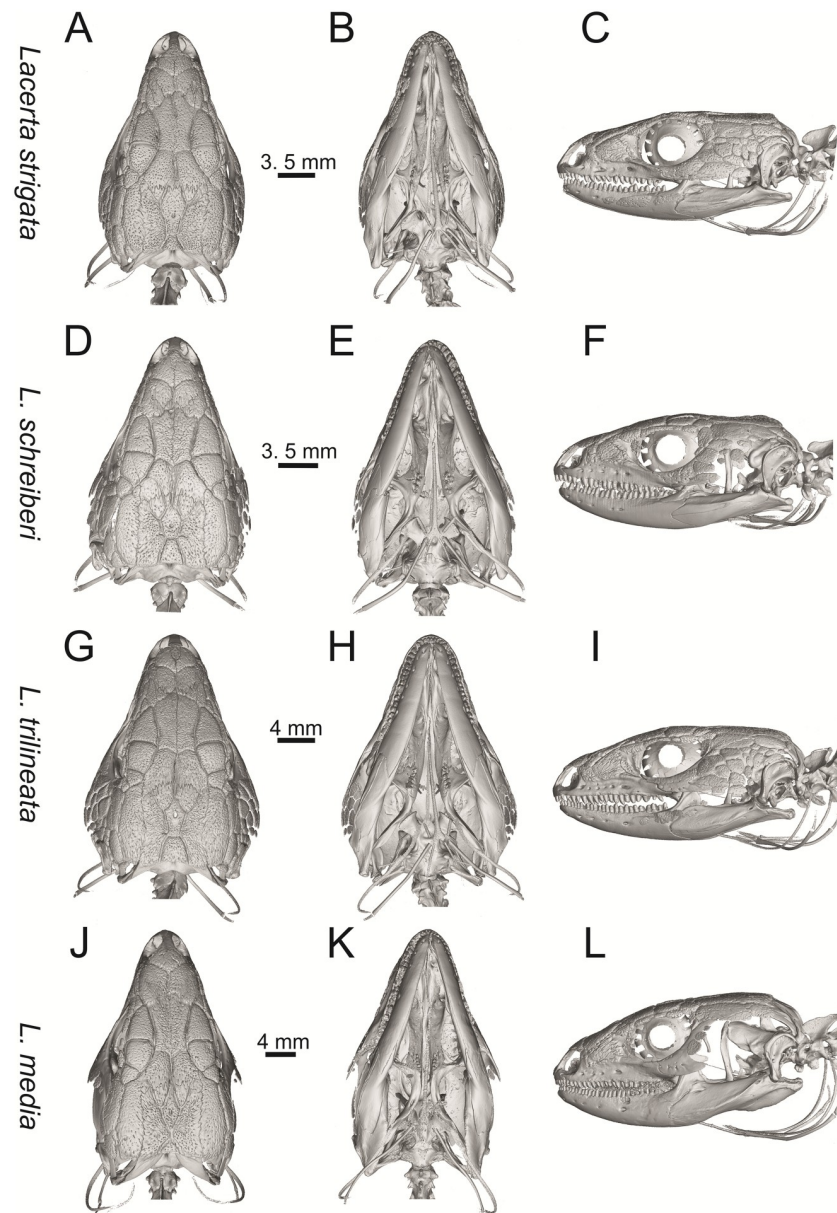


Fig 10. Skulls of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in dorsal (A, D, G, J), ventral (B, E, H, K) and lateral (C, F, I, L) views.

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(2) Premaxilla bears nine teeth. This is true for all green lizards (present in a juvenile as well, Fig 31A and 31B) and nine teeth can be observed in the Eocene taxon *Pl. lydekkeri* [8]. Among 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* [47, 48]. However, such a tooth count can be observed in *Gallotia* as well [11, 41, 49], whereas in *Psammodromus* and Lacertini, the premaxillary tooth count is higher—nine or more [11]. *Gallotia* deserves a comment here. In the specimen NHMV 11031–1 (Fig 40) the premaxilla bears nine rather than the usual seven teeth. This shows the presence of some occasional variety in this character. Moreover, the premaxillary tooth count in the specimen NHMV 35860–2 of *L. bilineata* is ten (Fig 29A and 29B), so these tooth numbers are not strictly absolute.

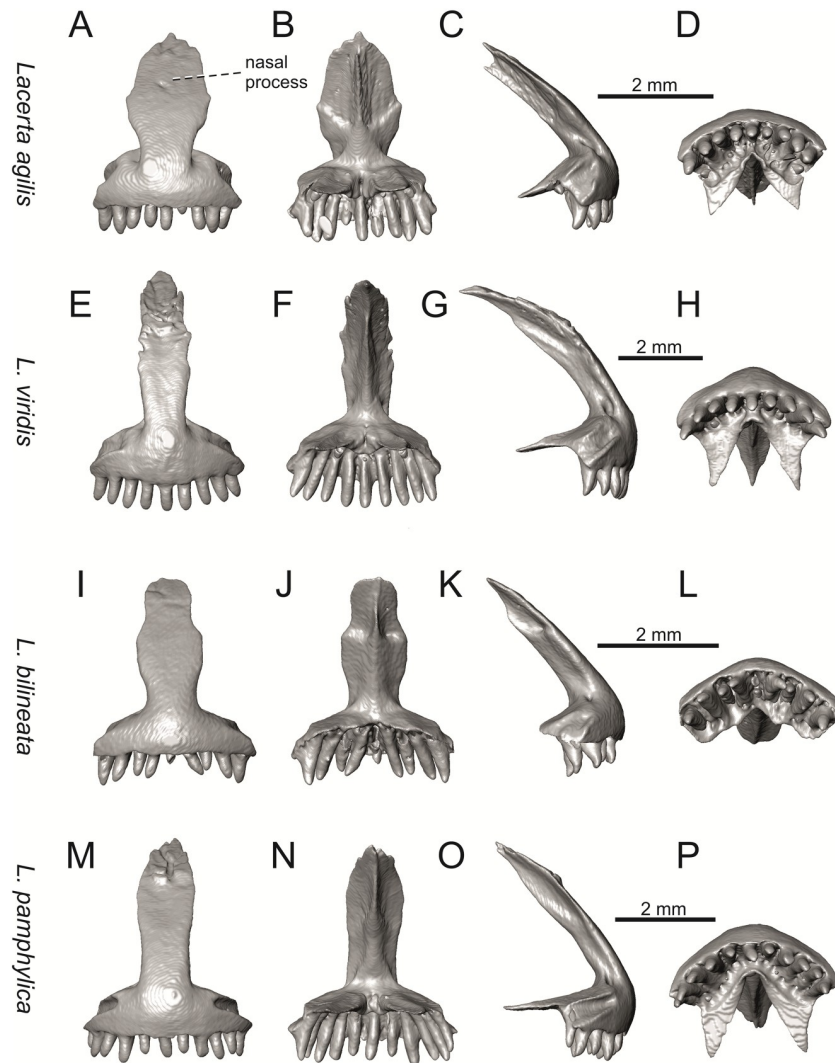


Fig 11. Premaxillae of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599–1 and *L. pamphylica* ZSM 939/2005 in anterior (A, E, I, M), posterior (B, F, J, N), lateral (C, G, K, O) and ventral (D, H, L, P) views (continued).

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(3) Parietal fossa. This structure in the posterior ventral section of the parietal forms an area where the ascending process of the supraoccipital fits into a groove (parietal fossa; see, e.g., [50]). In some taxa, the posterior margin of the parietal does not reach the anterior edge of the supraoccipital [49], leading to the absence of a connection, which also occurs frequently in eremiadine lacertids [12]. The shape and size of the parietal fossa can be variable and can change during ontogeny (see Fig 30 for *L. pamphylica*). In *T. lepidus*, the parietal fossa has a somewhat peculiar morphology, with an additional posterior constriction of the parietal fossa. This gives a lens shape to this structure (see Fig 35E; see also [51]). Moreover, these two lineages differ in body-size [52, 53]. Similar morphology as present in *T. lepidus* can be seen in Eocene *Pl. lydekkeri*. This taxon also exhibits a fragmented parietal shield [8, 54]. Note that the additional constriction of the parietal fossa can be found in some specimens of green lizards as well, here *L. bilineata* NHMV 35860–2 (Fig 29L) and *L. schreiberi* NHMV 10808–1 (32F). However, it

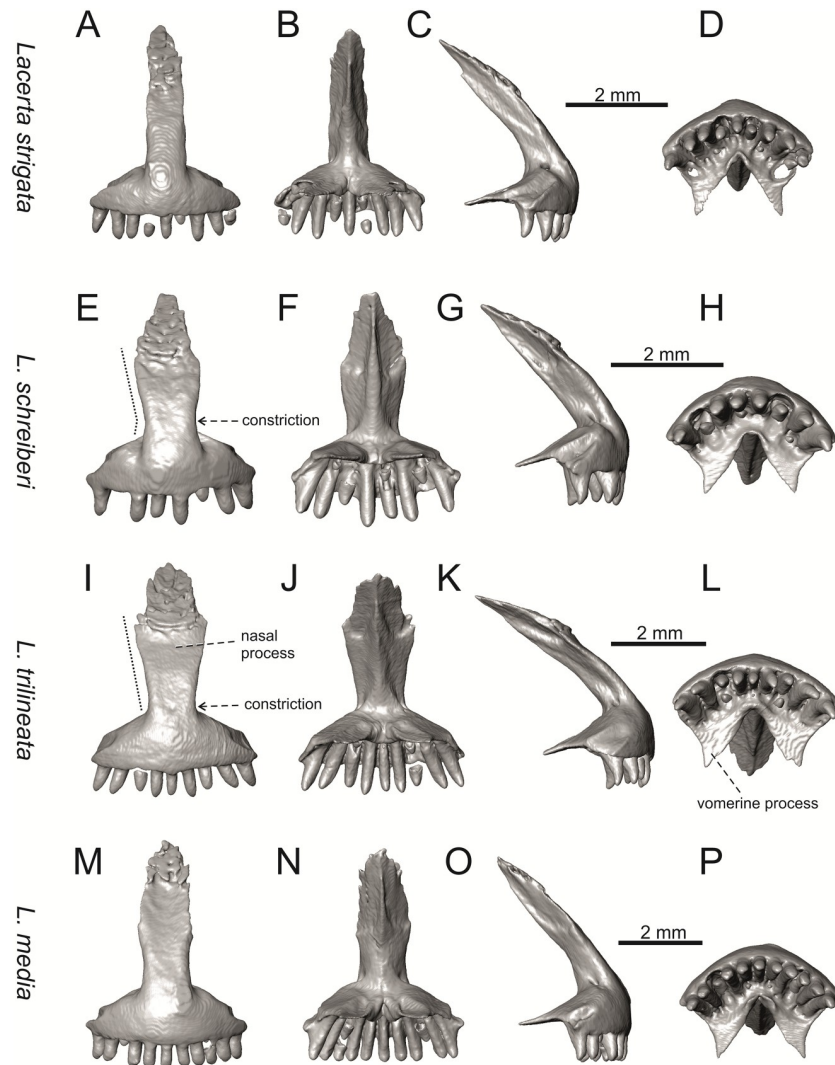


Fig 12. Premaxillae of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in anterior (A, E, I, M), posterior (B, F, J, N), lateral (C, G, K, O) and ventral (D, H, L, P) views. The dotted lines indicate a lateral margin of the nasal process and a position of constriction in *L. schreiberi* and *L. trilineata*.

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never reaches such a strong degree as in *T. lepidus* (the lateral margins, which frame the parietal fossa, do not contact each other posteriorly in those green lizards and thus, the fossa is not fully closed in this region by this additional constriction). Very unique morphology can be seen in the Oligocene durophagous lacertid specialist *Dracaenosaurus croizeti*, where the fossa is absent. In contrast, a parietal flange is present here [12].

(4) Medial expansion of the frontal process of the postfrontal, forming a broad area with a contact to frontal, is present. This is present in all green lizards, but is not unique to them [41]. It is also present in *T. lepidus* or *G. stehlini*, but absent in *Po. muralis*, *Z. vivipara*, *T. sexlineatus* and *M. ctenodactylus*.

(5) Pterygoid dentition. Teeth on the pterygoid are often found in species of *Lacerta*, *Timon*, *Anatololacerta*, *Gallotia*, and *Psammodromus algirus* [49, 55]. Among taxa studied here, pterygoid dentition is absent in *Po. muralis* and *Z. vivipara*. Among green lizards, the

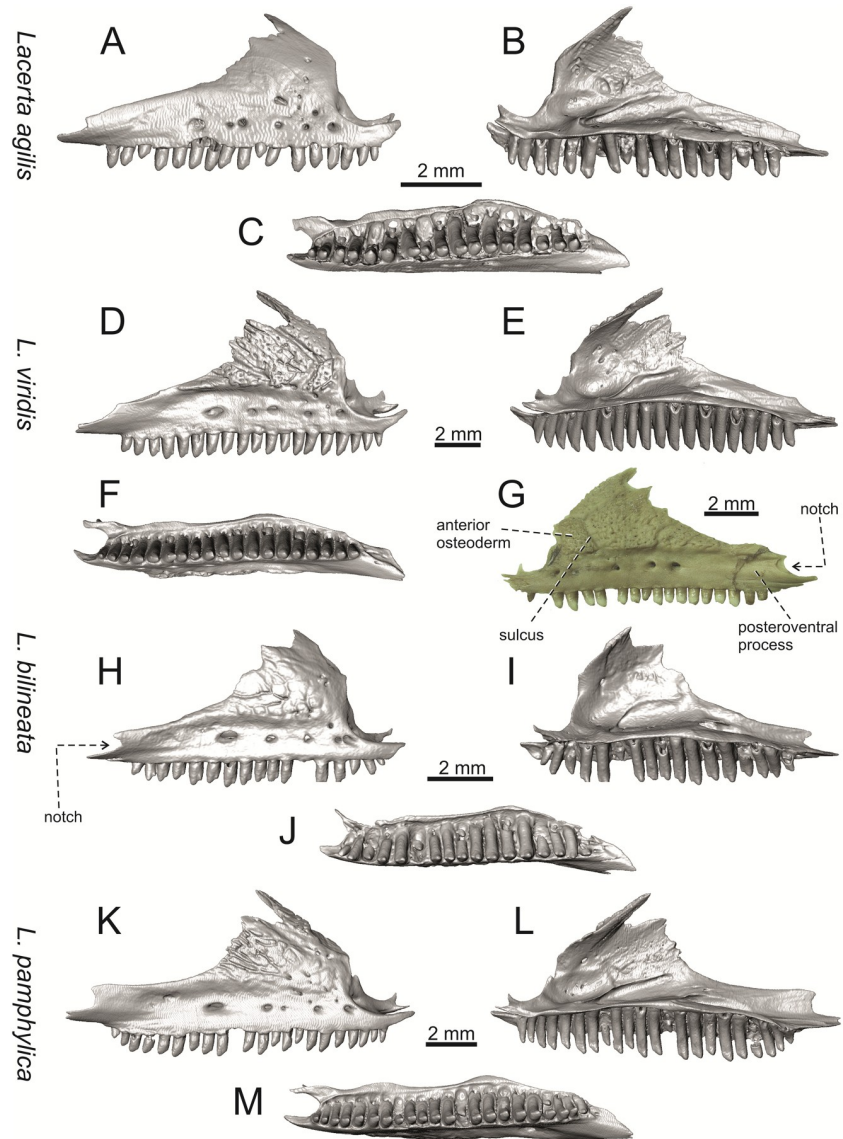


Fig 13. Maxillae of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* (right maxilla NHMV 40137; left maxilla DE 51), *L. bilineata* NHMV 18599-1 and *L. pamphylica* ZSM 939/2005 in lateral (A, D, G, H, K), medial (B, E, I, L) and ventral (C, F, J, M) views (continued).

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pterygoid teeth show several arrangements. The teeth on the Solnechnodolsk pterygoid are arranged strictly in a single line. This is present in several specimens of green lizards studied here. In others, teeth are arranged in the elliptical area, where the central region is wider; here at least two teeth can be found next to each other (in medio-lateral plane). Therefore, these two conditions seem to be a matter of individual (or ontogenetic) variations rather than being taxonomically important among green lizards. The second condition is also present in the specimens of *T. lepidus* and *G. stehlini* available to us. In *Ps. algirus*, teeth on pterygoid are arranged in a wide area and not in a single line. Because the clade Gallotiinae is sister to Laceratinae [6, 56], we regard the presence of pterygoid dentition as plesiomorphic among Laceratinae. Teeth on the pterygoid are also present in eolacertids [9, 57].

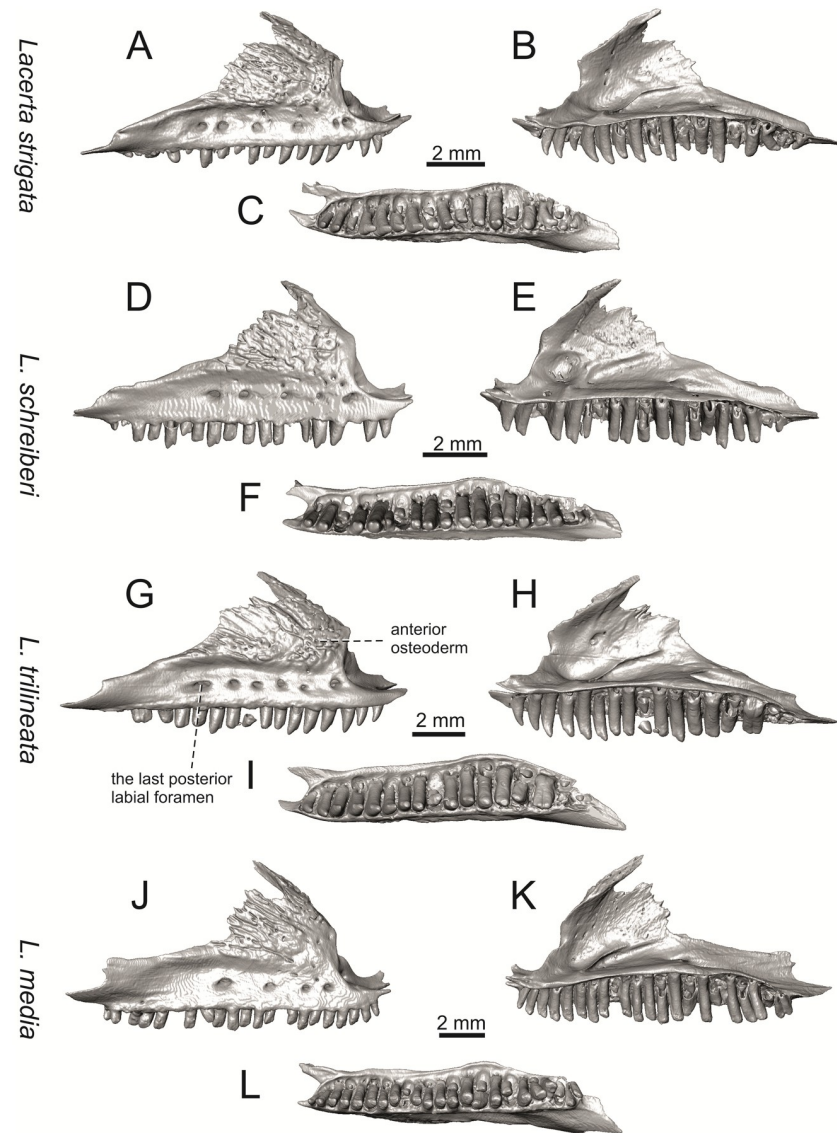


Fig 14. Right maxillae of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in lateral (A, D, G, J), medial (B, E, H, K) and ventral (C, F, I, L) views (continued).

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General comparison of green lizards

In the following section, osteological differences which cannot be observed in the Solnechnodolsk fossils, but are present among green lizards, are discussed:

(1) Lateral expansion of cheeks in adults. In dorsal view, *Lacerta viridis* and *L. trilineata* (when the osteoderms covering the cheeks laterally are present) have distinctly laterally expanded cheeks relative to other taxa (see Figs 9, 10 and 26). This is also present in *Timon lepidus* (Fig 34A).

(2) Osteoderms covering cheeks laterally (see Figs 9 and 10). In lateral view, cheeks are not covered by osteoderms in *L. agilis* (all specimens available to us, both male and female individuals), *L. pamphylica* (all specimens available to us, both male and female individuals) and *L.*

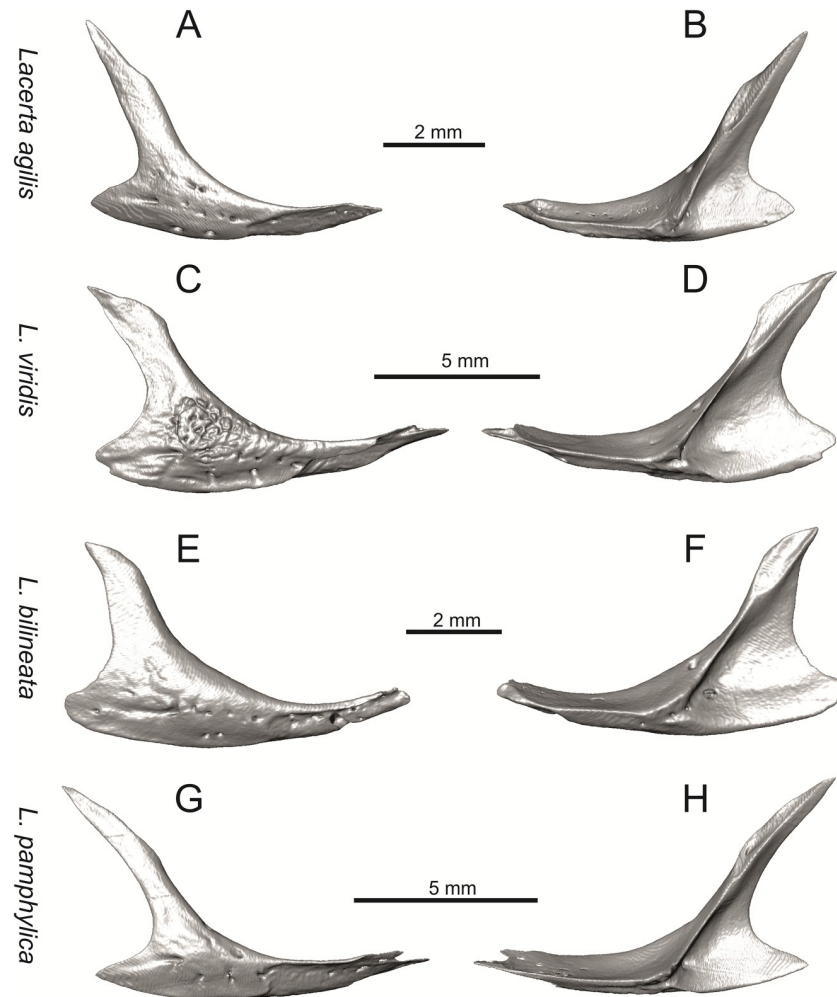


Fig 15. Right jugs of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599–1 and *L. pamphylica* ZSM 939/2005 in lateral (A, C, E, G) and medial (B, D, F, H) views (continued).

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media (all specimens available to us, see also Fig 33E and 33I). The example of *L. pamphylica* shows that this absence is stable during ontogeny (see Fig 30C, 30F and 30I). Although in adults, some small isolated osteoderms appear directly posterior to jugal in contrast to a juvenile, these do not cover the cheek. The cheeks are strongly covered by osteoderms in *L. viridis* (all specimens available to us, see Figs 9F and 26I), *L. bilineata*, *L. strigata* and *L. trilineata*. However, presence or absence of these osteoderms seems to be not absolute for several taxa. In *L. trilineata*, osteoderms are present in NHMV 27665 with the skull length of 25.6 mm (see Fig 10I). However, they are absent in NHMV 26524–1 with a skull length of 30.5 mm and NHMV 26524–2 with a skull length of 25.3 mm (Fig 27O and 27S). One possible explanation is a sexual dimorphism (at least for some of those species), where the adult males have wider, more robust heads than the adult females. However, the present data do not give a strong support to this. The specimen NHMV 27665 is male, whereas the NHMV 26524–2 is female. But the specimen NHMV 26524–1, with the longest skull among specimens of *L. trilineata* available to us, is male. If we exclude the possibility of an erroneous allocation of this museum specimen, the reason of its uncovered cheeks remains questionable. Based on available data, its presence or

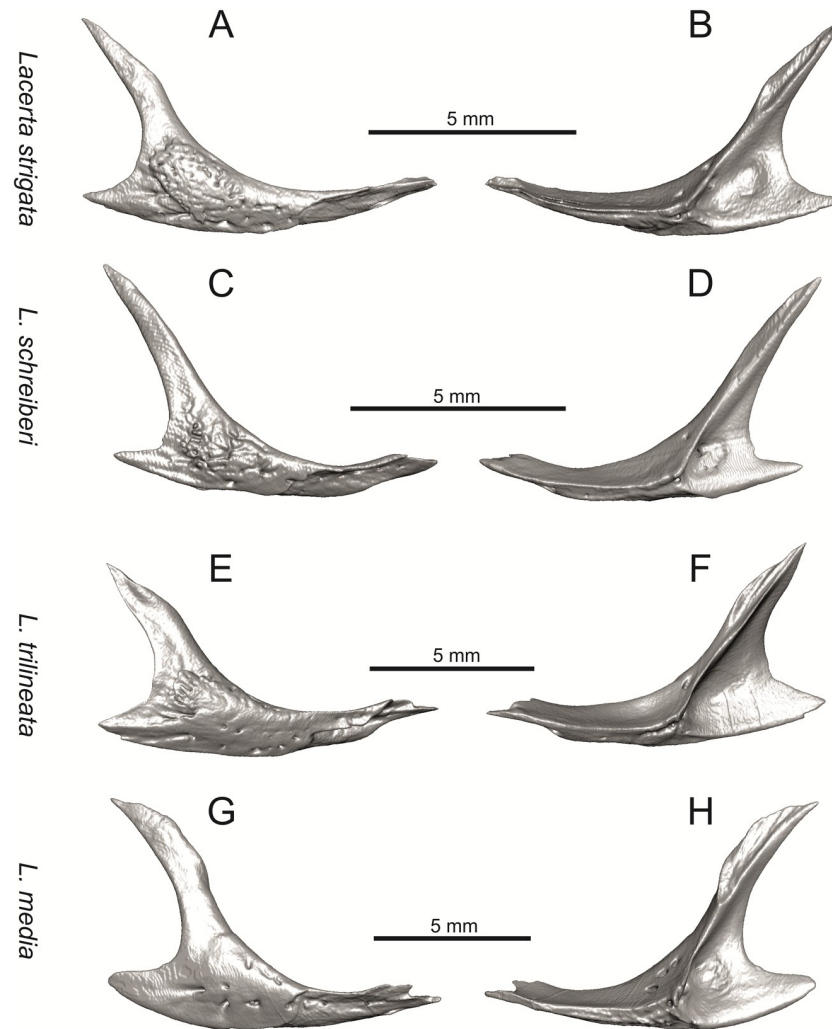


Fig 16. Right jugals of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in lateral (A, C, E, G) and medial (B, D, F, H) views.

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absence (two character states) in *L. trilineata* seems to be the case of individual variation. The presence of both character states could reflect the topology of *L. trilineata* within green lizards (see Fig 41A). But all these factors can be resolved only by further studies, where various ontogenetical series of males and females of this species will be CT-scanned.

In *L. schreiberi*, fragmented discontinuous osteoderms in cheeks are present in NHMV 10809 (Fig 10F) with the skull length of 21 mm and in NHMV 10808–4 (Fig 27L) with a skull length of 20.3 mm. However, the cheeks are strongly covered by osteoderms in NHMV 10808–1 with a skull length of 24.2 mm (Fig 27I). Therefore it appears that it in the taxa in which osteoderms cover the cheek laterally, the degree of covering reflects the size of the individual (and its age). Thus, it is plausible that the covering might appear only later during ontogeny. This can be supported by the specimens of *L. bilineata* available to us. In the smallest specimen—NHMV 18599–1 with a skull length of 18.8 mm, the osteoderms cover the lateral cheek but are not in a strong mutual contact (in fact, a free space is present between the osteoderms; see Fig 9I). However in larger specimens—NHMV 35860–1 (skull length 28.5 mm)

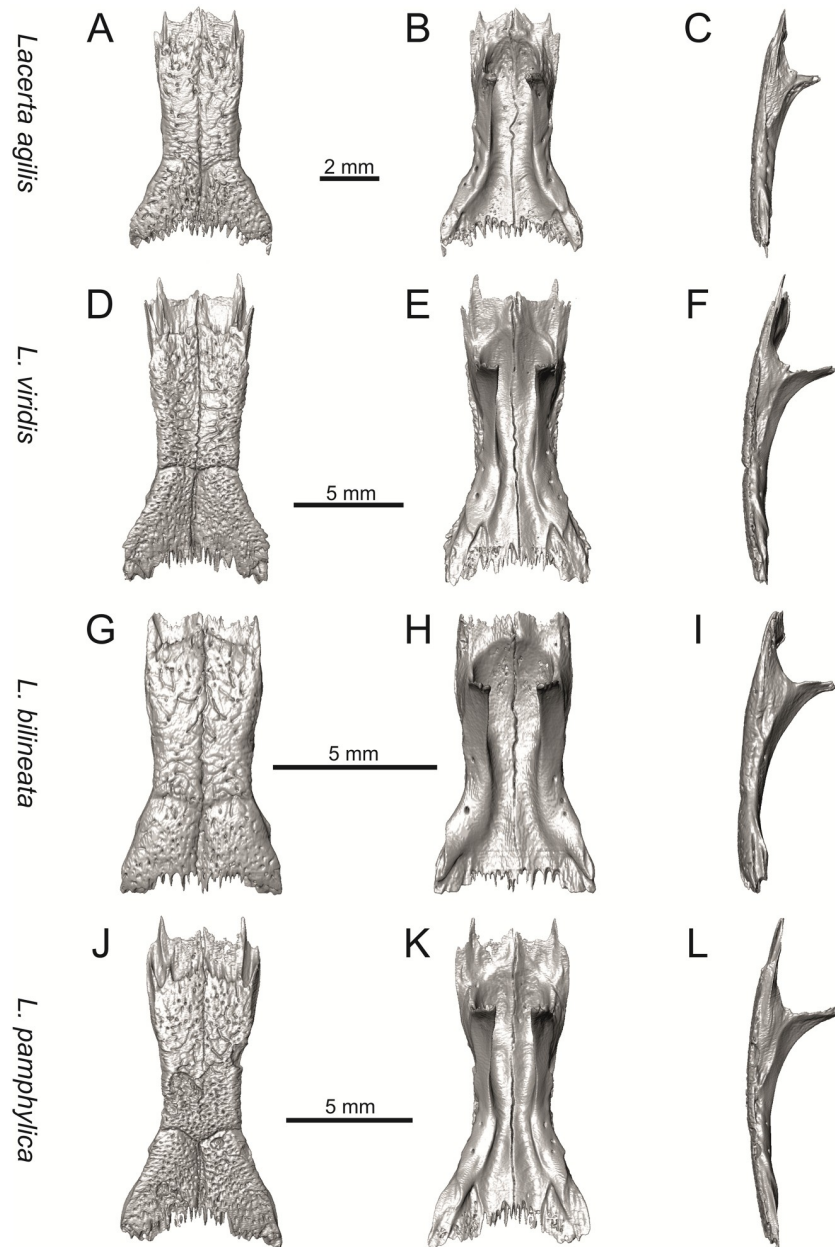


Fig 17. Frontals of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599–1 and *L. pamphylica* ZSM 939/2005 in dorsal (A, D, G, J), ventral (B, E, H, K) and lateral (C, F, I, L) views (continued).

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and NHMV 35860–2 (skull length 28.5 mm), the osteoderms are very close to each other, almost completely filling the free space (see Fig 26L and 26O).

The cheeks are strongly covered by osteoderms in *T. lepidus* (see Fig 34C), in contrast to *Podarcis muralis* (Fig 36C; also absent in male figured in [50]) and *Zootoca vivipara* (Fig 37C). In Gallotiinae, both states are present. Cheeks are strongly covered by osteoderms in *Psammodromus algerius* (Fig 39C), but they are absent in *Gallotia stehlini* (Fig 40C). However, it should be noted that these osteodermal coverings have been identified in the mummified specimen BM-2 of the subfossil species *G. goliath* [58]. The character optimization in Mesquite supports

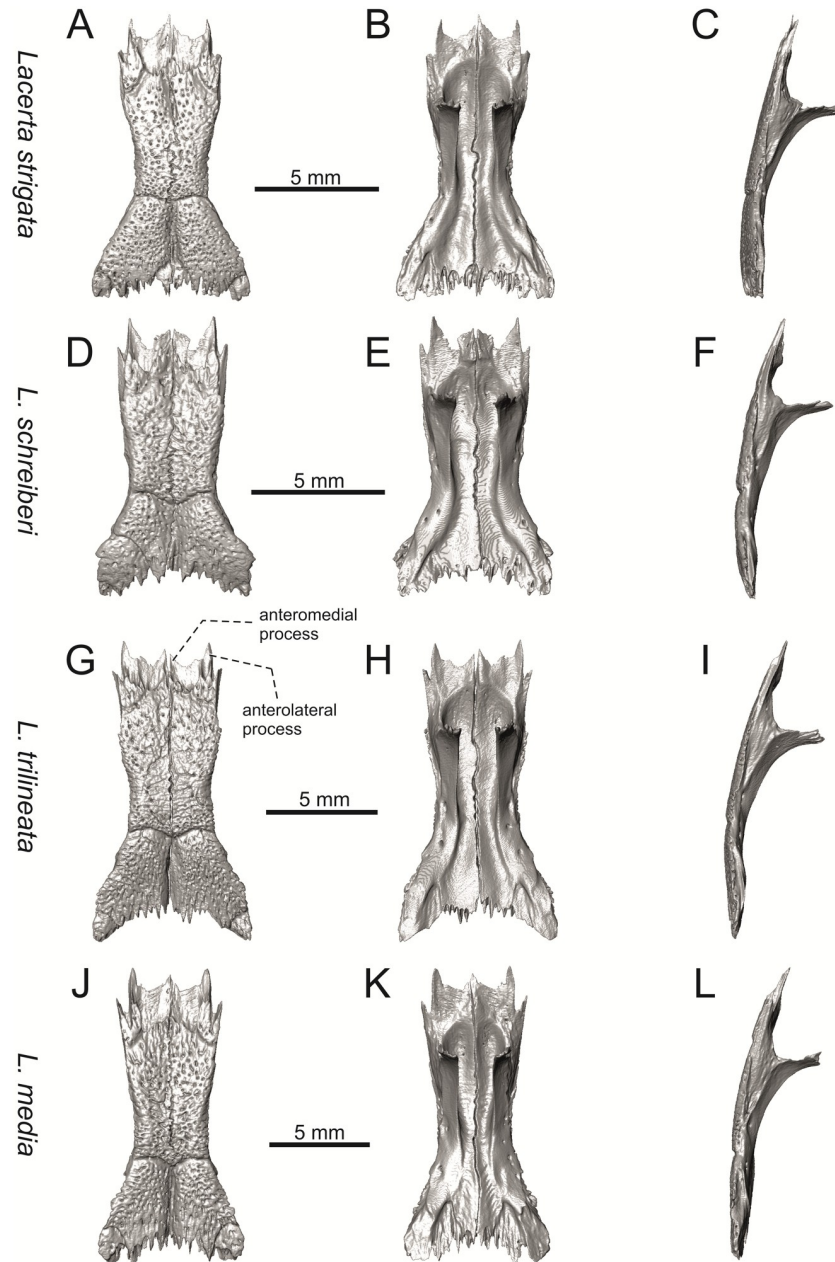


Fig 18. Frontals of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in dorsal (A, D, G, J), ventral (B, E, H, K) and lateral (C, F, I, L) views.

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the absence of the osteodermal covering on cheeks as being the condition at the basal node of the clade Lacertidae. Character optimization in Mesquite (Fig 41A) shows that the presence is the condition at the basal node of the clade *Timon* + *Lacerta*, whereas covering the cheeks in *Ps. algirus* (Gallotiinae) evolved independently. Its absence in *L. agilis*, *L. pamphylica* and *L. media* is regarded as reversal.

(3) In dorsal view, the supraoccipital in adults is highly exposed (its posterior section is not overlapped by parietal; see Figs 9 and 10) in *L. agilis* (Figs 9A, 26A and 26D), *L. pamphylica* (Fig 9J), *L. strigata* (Figs 10A, 27A and 27D) and *L. schreiberi* (in NHMV 10809 and 10808–4,

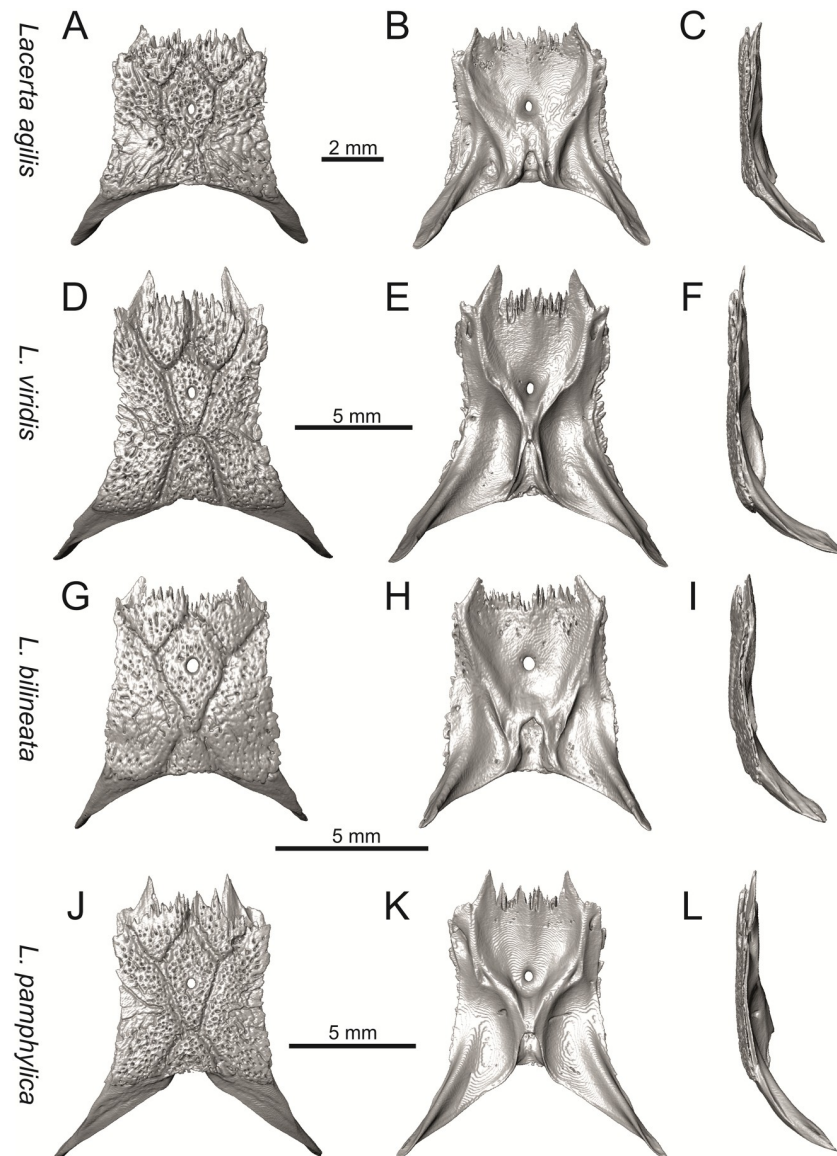


Fig 19. Parietals of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599–1 and *L. pamphylica* ZSM 939/2005 in dorsal (A, D, G, J), ventral (B, E, H, K) and lateral (C, F, I, L) views (continued).

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but not in NHMV 10808–1, see Figs 10D, 27G and 27J). Only a small posterior portion of the supraoccipital is visible in *L. viridis*, *L. bilineata* (in NHMV 35860–1 and 35860–2, note that the supraoccipital is well exposed in smaller specimen NHMV 18599–1) and *L. media*. In *T. lepidus* (Fig 34A) and *G. stehlini* (33A), the supraoccipital is completely covered by the parietal in dorsal view. In contrast to that, it is highly exposed in *Po. muralis* and *Z. vivipara*. Regarding the posterior region of the parietal, the *Z. vivipara* + *Ta. sexlineatus* clade can be characterized by the presence of a smooth area of the parietal table posterior to the ornamented region and by the presence of a short bilobed, posteriorly located process in the posterior mid-region.

(4) The width of the supratemporal processes of the parietal (Figs 19 and 20): In dorsal aspect, broad supratemporal processes can be found in *L. media*, whereas they are rather

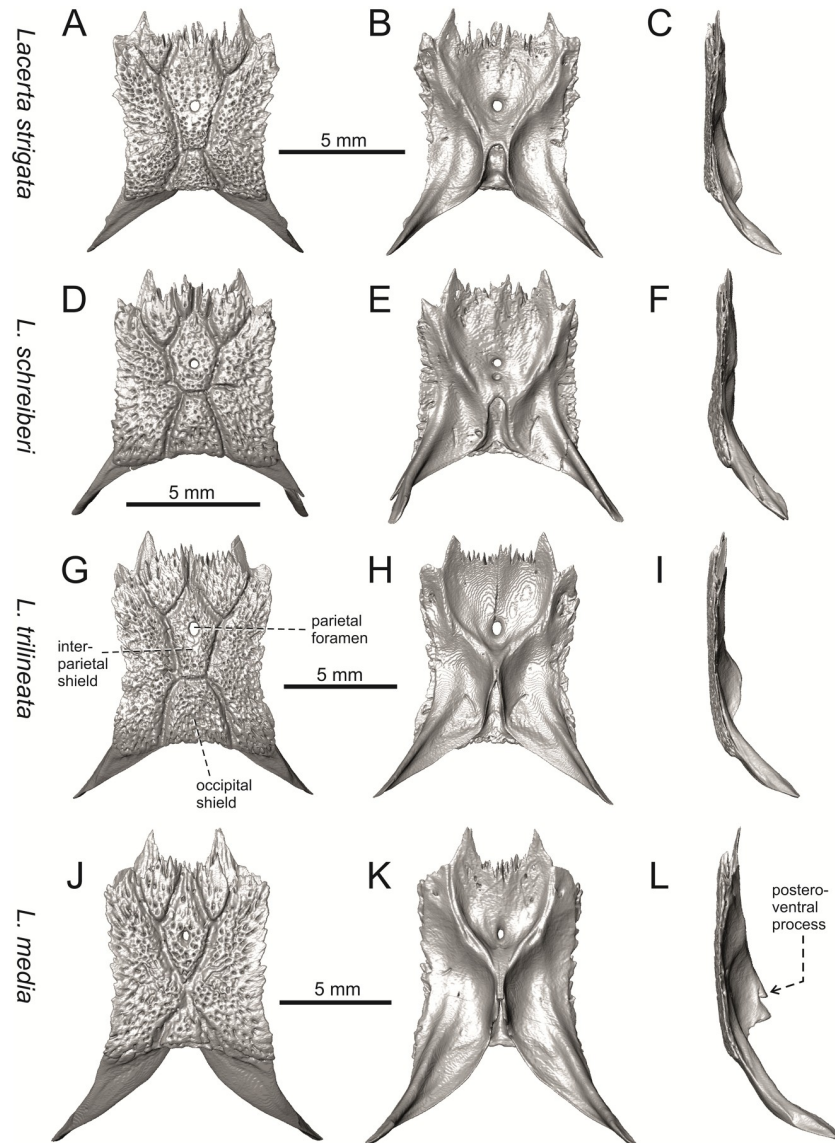


Fig 20. Parietals of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in dorsal (A, D, G, J), ventral (B, E, H, K) and lateral (C, F, I, L) views.

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narrow in some specimens of *L. schreiberi* and *L. agilis* (although moderate size in other specimens, see Fig 28F). In other green lizard taxa, the width spans to moderate range of width as well as in *T. lepidus* (Fig 35D and 35E). Thus this state appears to be plesiomorphic among green lizards. The most ventral inclination of the supratemporateral process among lacertids studied here is present in *G. stehlini* (Fig 40).

(5) In lateral view, the skull is slightly depressed in the preorbital region, so the premaxillary region is slightly stepped (Figs 9 and 10) in *L. viridis* (marked by arrow in Fig 9F; for this species, see also Fig 261), *L. pamphylica* (Fig 9L; even in juvenile, Fig 30C), *L. strigata*, *L. schreiberi*, *L. trilineata* and *L. media*. In contrast, the dorsal margin of the preorbital region is more-or-less rounded in *L. agilis* (Fig 9C), as well as in the smaller specimen NHMV 18599–1 of *L. bilineata* (Fig 9I). However, in larger specimens (NHMV 35860–1 and 35860–2) of *L. bilineata*,

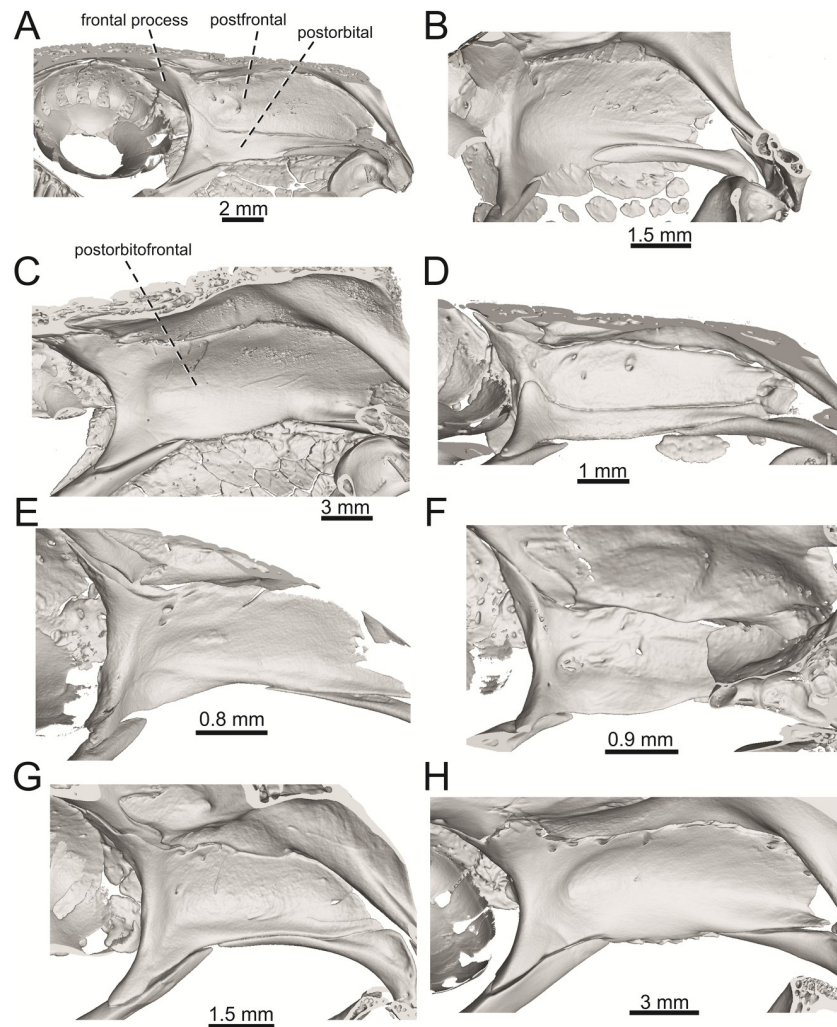


Fig 21. Right postfrontals + postorbitals located in the skulls in internal views in *Lacerta viridis* NHMV 40137 (A), *L. schreiberi* NHMV 10809 (B), *Timon lepidus* NHMV 10921–1 (C), *Podarcis muralis* NHMV 39359–1 (D), *Zootoca vivipara* NHMV 32438–1 (E), *Takydromus sexlineatus* DE 134 (F), *Meroles ctenodactylus* NHMV 31376 (G), *Gallotia stehlini* NHMV 11031–1 (H).

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this depression is developed (Fig 26L and 26O). The preorbital depression is present in *T. lepidus* (Fig 34C). The depression is absent in *Ps. algirus* (Fig 39C) and weakly developed in *G. stehlini* (Fig 40C).

(6) The position of the anterior mylohyoid foramen on the splenial relative to the anterior inferior alveolar foramen. The anterior mylohyoid foramen is located ventrally to the anterior inferior alveolar foramen, but its position varies (Figs 24 and 25): it is posteroventral to the centroid of the alveolar foramen in *L. trilineata*, *L. media*, *L. pamphylica* (but anteroventral in a juvenile specimen NHMV 35861; Fig 31M) and *L. schreiberi*, whereas it is located directly below the centroid of the anteroposterior length of the alveolar foramen in *L. viridis*, *L. bilineata*, *L. agilis* and *L. strigata* (in NHMV 10917–2, see Fig 32 C; but note that it is more anteroventrally located relative to the centroid of the alveolar foramen in NHMV 39765, see Fig 25B). As for the outgroup, it is posteroventral in *T. lepidus*, *Po. muralis*, and *G. stehlini*, but directly below in *Z. vivipara* as well as in *M. ctenodactylus*. It is located anteroventrally in our specimen of *Ps. algirus*.

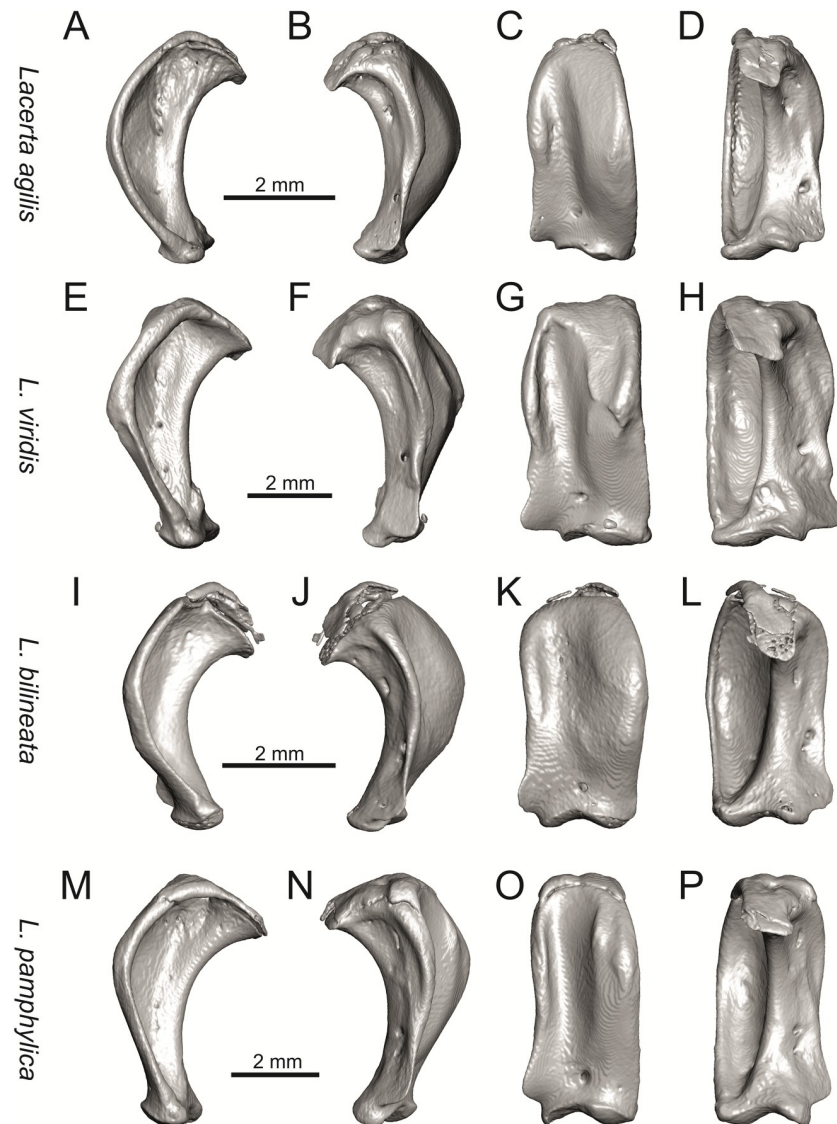


Fig 22. Left quadrates of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599-1 and *L. pamphylica* ZSM 939/2005 in lateral (A, E, I, M), medial (B, F, J, N), anterior (C, G, K, O) and posterior (D, H, L, P) views (continued).

<https://doi.org/10.1371/journal.pone.0216191.g022>

(7) The position of the posterior mylohyoid foramen on the angular relative to the top of the dorsal process of coronoid (Figs 24 and 25): posterior to the top of the dorsal process in *L. agilis*, *L. viridis* and *L. strigata*. It is located at the level of the dorsal process of coronoid or only slightly posterior to it in *L. bilineata*, *L. pamphylica*, *L. schreiberi*, *L. trilineata* and *L. media*. This second character state is also present in *T. lepidus*, whereas it is posteriorly located in *Po. muralis* and *Z. vivipara*, but anterior to the dorsal process of coronoid in *G. stehlini*.

(8) Among green lizards, the dentary of *L. media* in dorsal aspect (Fig 25L) is markedly narrower relative to the robust postdentary mandibular region. Moreover, the articular + prearticular element forms a large mediolateral keel (or flange; it is exposed even in lateral aspect, see Fig 25J). Although the posterior region is more robust relative to the dentary region in *T. lepidus*, this keel is not developed here (Fig 35K–35M).

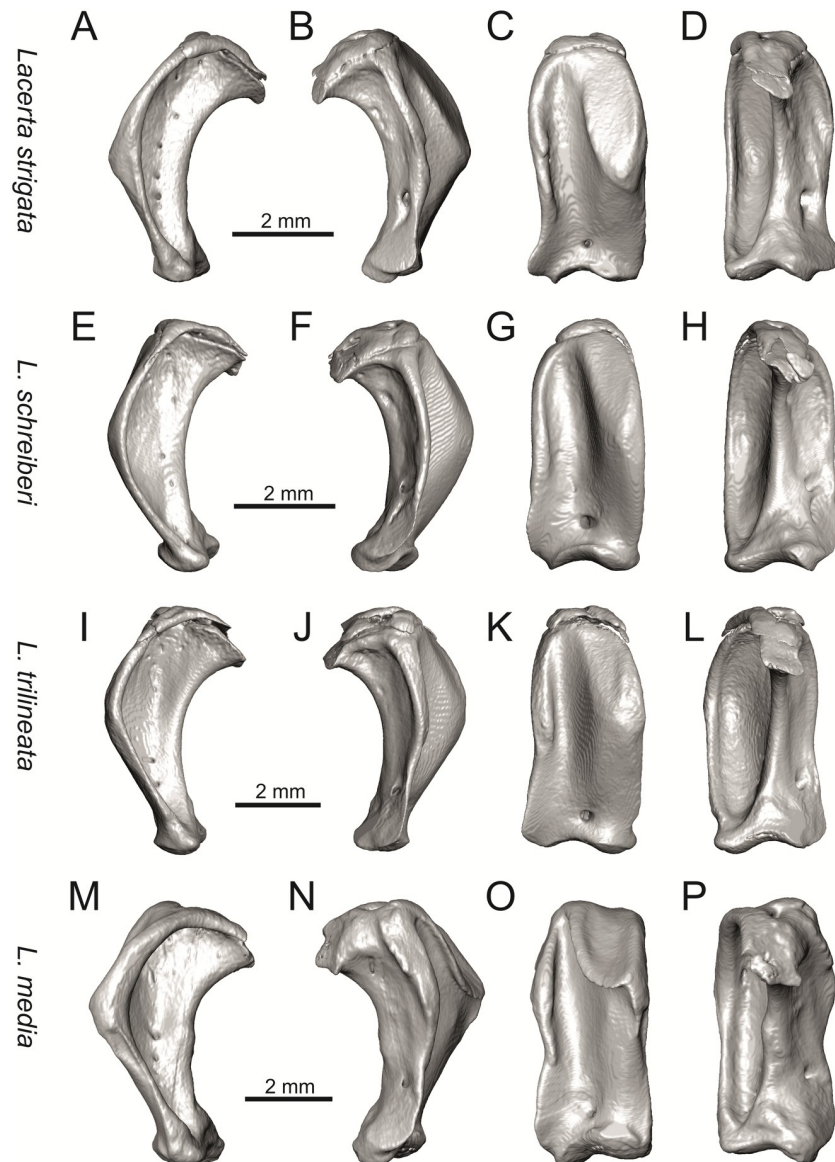


Fig 23. Left quadrates of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in lateral (A, E, I, M), medial (B, F, J, N), anterior (C, G, K, O) and posterior (D, H, L, P) views.

<https://doi.org/10.1371/journal.pone.0216191.g023>

The Miocene Solnechnodolsk fossils compared to the extant taxa

Today, the area to the east of the Black Sea (where Solnechnodolsk is located) is occupied by *Lacerta agilis*, *L. strigata* and *L. media*; whereas *L. viridis* is distributed in northern, western and southern regions (e.g., Turkey) of the the Black Sea [21, 59, 60]. Nowadays, *L. trilineata* can be found in southern and western areas around the Black Sea [21]. The lacertid material from the upper Miocene of the Solnechnodolsk locality shares a combination of a features that is found only in *L. trilineata* among extant species. However, caution is needed here, because the sample size here does not fully allow to discuss the patterns of ontogenetic and sexual variation that must be present in these lizards and which would introduce more variation. For this

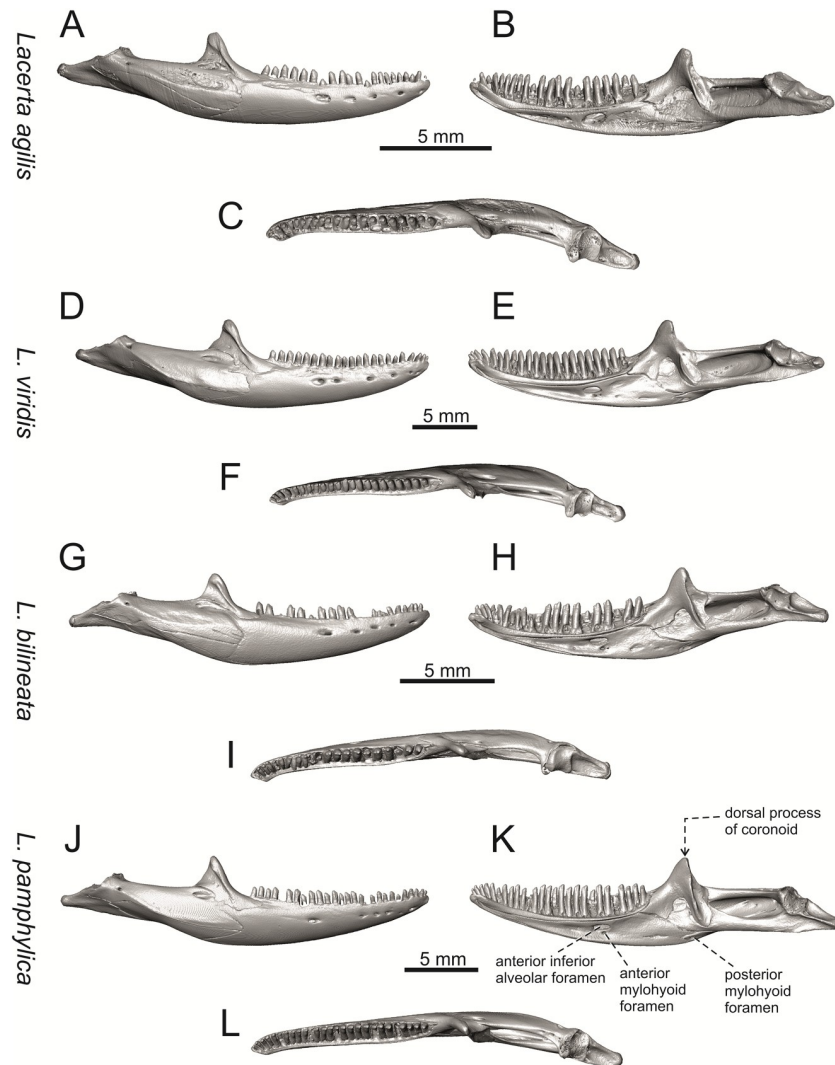


Fig 24. Right mandibles of extant green lizards *Lacerta agilis* NHMV 39028, *L. viridis* NHMV 40137, *L. bilineata* NHMV 18599–1 and *L. pamphylica* ZSM 939/2005 in lateral (A, D, G, J), medial (B, E, H, K) and dorsal (C, F, I, L) views (continued).

<https://doi.org/10.1371/journal.pone.0216191.g024>

reason, we decided to allocate this material as *L. cf. trilineata*. This combination of features is as follows:

Premaxilla. (1) The nasal process of premaxilla is moderately wide, gradually expanding laterally from its base in a posterodorsal direction. This is identical to that of *L. trilineata*. The process is very broad in *Lacerta agilis* (Fig 11A; in some cases having a stepped lateral expansion, see Fig 28A and 28B), whereas it only slightly expands laterally in posterodorsal direction (although small variation can be present), being thus rather narrow (relative to others) in *L. viridis*, *L. strigata*, *L. pamphylica*, or *L. media* (see Figs 11, 12, 32B and 33K). The condition in *L. schreiberi* and *L. bilineata* (but only in the specimen NHMV 35860–2 here, Fig 29A) is similar to that of *L. trilineata*. However in *L. schreiberi* (present in all specimens available to us), the base of the process is already slightly expanded laterally, so the lateral margins of the mid-region of the process are slightly concave (a mid-constriction is present here above the base of the nasal process, rather than gradual expansion from the base; see Fig 12). In *Timon lepidus*,

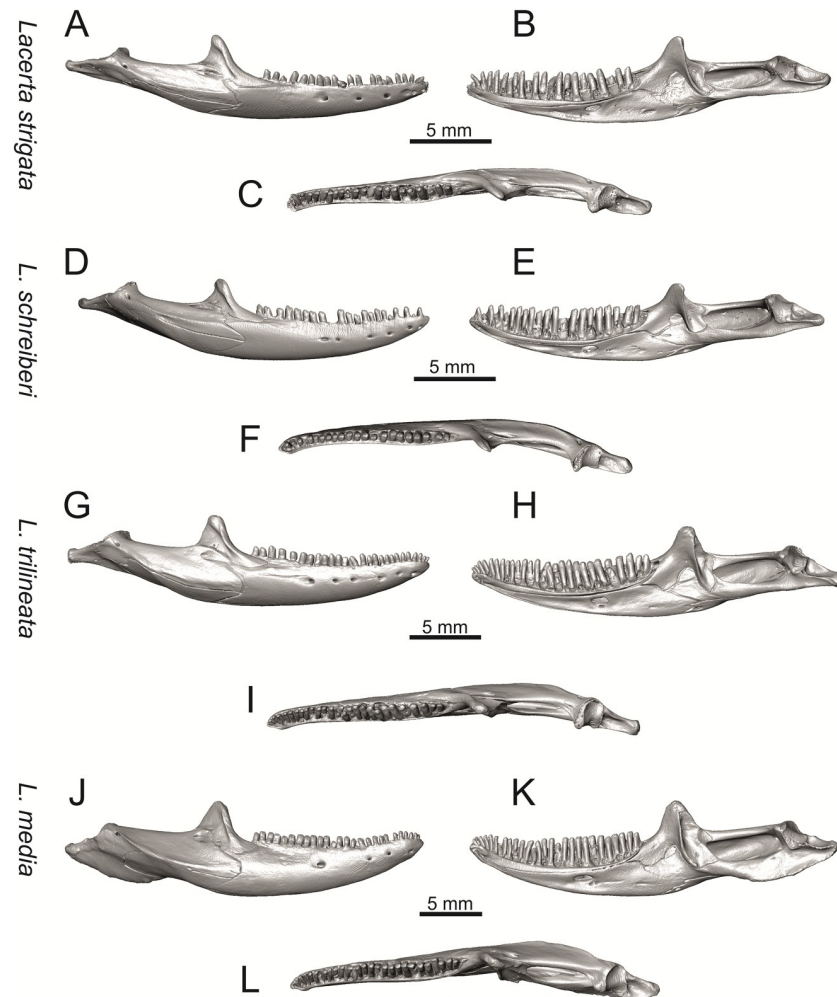


Fig 25. Right mandibles of extant green lizards *Lacerta strigata* NHMV 39765, *L. schreiberi* NHMV 10809, *L. trilineata* NHMV 27665 and *L. media* NHMV 34808 in lateral (A, D, G, J), medial (B, E, H, K) and ventral (C, F, I, L) views (continued).

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the nasal process of the premaxilla is broad in the ventral region, but is posterodorsally stepped—the posterodorsal termination is usually suddenly narrow (see Fig 34D and 34E). A distinctly thin nasal process, which gradually narrows posterodorsally, can be observed in *Gallotia stehlini* (here, a small lateral step can be present at the half-way point of the posterodorsal length of the process, see Fig 40D and 40E). Moreover, the maxillary processes are reduced in this taxon [11]. The narrow nasal process of the premaxilla is present in members of the Eolacertidae [9]. The broad process among lacertids can be therefore most likely regarded as derived. Character optimization in Mesquite evaluated this change in two equally parsimonious ways (Fig 41B): as the condition at the basal node in the the tribe Lacertini with an additional reversal in *T. sexlineatus* and, independently, *L. strigata*, or as the condition at the basal node of the clade formed by *Podarcis* + *Timon* + *Lacerta*. The wide nasal process in *Psammodromus algirus* (it is narrow in *Ps. hispanicus* [41]) represents an independent derivation.

(2) The vomerine processes (formed by the posteriorly expanded supradental shelf of the premaxilla) are moderately long. They are small, not posteriorly expanded in the specimen NHMV 18599–1 of *L. bilineata* (see Fig 11L; the skull length 18.8 mm), although it should be

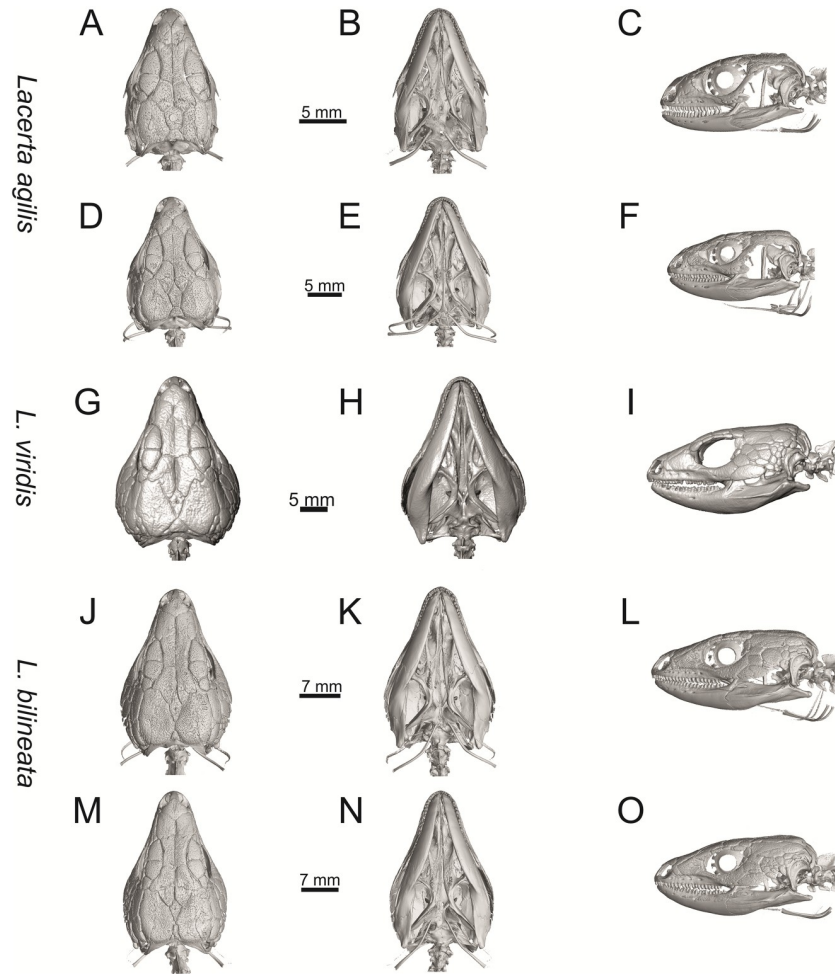


Fig 26. Skulls of extant green lizards *Lacerta agilis* NHMV 30885–1 (A–C) and 36392–1 (D–F), *L. viridis* UF 65017 (G–I), and *L. bilineata* NHMV 35860–1 (J–L) and 35860–2 (M–O) in dorsal (A, D, G, J, M), ventral (B, E, H, K, N) and lateral (C, F, I, L, O) views (continued).

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noted that in other individuals, these processes are well developed (Fig 29D; skull length 28.5 mm, see also [41]). Therefore, this can be related to the size (and changes during ontogeny) of individuals. The extremely long processes are present in *L. pamphylica*. In this taxon, well developed long processes are already present in a juvenile (Fig 31D).

Maxilla. (3) The posteroventral process of the maxilla is stepped as it is in all green lizards studied here (Figs 13 and 14). However, the notch between the dorsal portion and ventral portion is only weakly developed in the Solnechnodolsk fossil. A similar condition is present in *L. trilineata* (see Fig 14G; note that the notch is wide in NHMV 27665 and NHMV 25524–2, but not anteriorly deep) and *L. agilis* (in all specimens available to us). However, the notch appears to be fully absent in *L. strigata* (only weakly developed in NHMV 10917–1), and *L. schreiberi* (all specimens available to us). A strong notch is developed in *L. pamphylica*. The notch is usually shallow in *L. media* (in this species and in *L. pamphylica*, the dorsoventral height of the termination of the posteroventral process is large, see Figs 13K and 14); for *L. media*, see also [61]). This character state appears to be stable in all studied specimens of *L. trilineata* and *L. pamphylica* (juvenile and adults, see Fig 30). However, *L. viridis* and *L. bilineata* deserve a

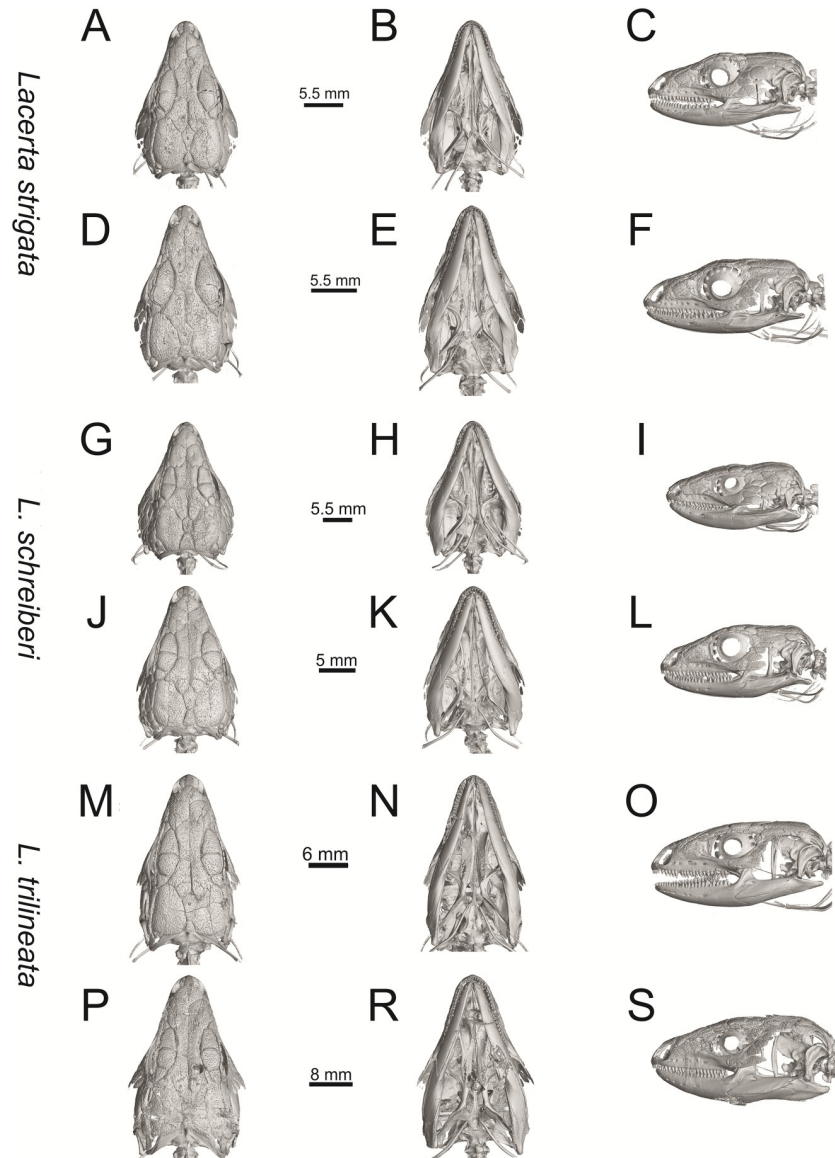


Fig 27. Skulls of extant green lizards, *Lacerta strigata* NHMV 10917-1 (A-C) and 10917-2 (D-F), *L. schreiberi* NHMV 10808-1 (G-I) and 10808-4 (J-L), *L. trilineata* NHMV 26524-2 (M-O) and NHMV 26524-1 (P-S) in dorsal (A, D, G, J, M, P), ventral (B, E, H, K, N, R) and lateral (C, F, I, L, O, S) views.

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comment here. The notch is almost absent in NHMV40137 (see Fig 13D and 13E), but is present in other specimens, as DE 51 (Fig 13G; for other see Digimorph.org [62]). Therefore it seems to be reasonable to expect that usually the notch is well-developed in *L. viridis*. In *L. bilineata*, the strong notch is present in NHMV 18599-1 (Fig 13H), but not in NHMV 35860-1 and 35860-2 (Fig 26L and 26O). This shows that caution is needed here, because in some cases, this character state can vary among individuals.

In contrast, the termination is not stepped in *T. lepidus* (Fig 34H and 34I) and Eocene *Pl. lydekkeri* [8] and it is absent in *Meroles* or *Eremias* [48]. The termination is not stepped in the Paleogene clade Eolacertidae [9, 63]. Thus the presence of this step appears to be a derived character state among Lacertidae. The character optimization in Mesquite (see Fig 41C)

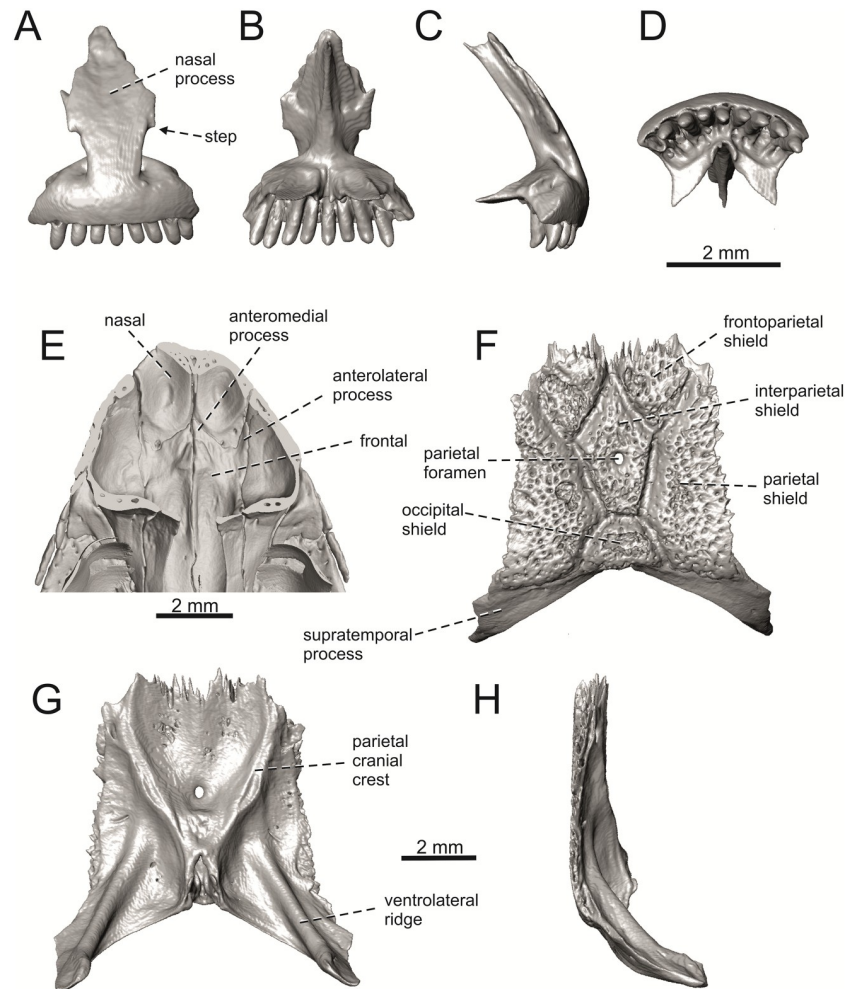


Fig 28. Selected cranial elements of *Lacerta agilis*—The specimen NHMV 36392–1 (male). Premaxilla in anterior (A), posterior (B), lateral (C) and ventral (D) views. Frontals + nasals located in the skulls in internal view (E). Parietal in dorsal (F), ventral (G) and lateral (H) views.

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supports the presence of a stepped process as being the condition at the basal node of the green lizards, whereas this character state in *Po. muralis* evolved independently. The tendency to form a dorsal step appears to be present in the basal node of the tribe Lacertini.

(4) The posteroventral process rises anteriorly, gradually continuing to the nasal process. Where the two processes contact, only a small dorsal curvature is present (it indicates the posterior end of the nasal process). In *L. media*, the posteroventral process is of almost uniform height along its length, only slightly higher anteriorly than posteriorly. The contact with the nasal process in this species is clear, the posterior margin of the ventral portion of the nasal process is almost vertical to the posteroventral process of maxilla. In *L. pamphylica*, the posteroventral process is also uniformly high and its dorsal margin flows anteriorly into the nasal process, the two forming a smooth concave margin.

(5) The presence of well separated osteoderms fused to the lateral side of the ventral portion of the nasal process of maxilla and the ratio of the anteroposterior length of the anterior osteoderm relative to the posteriorly located sculptured region. The anteriorly located osteoderm is large. The sulcus which separates the anterior osteoderm from the posteriorly located

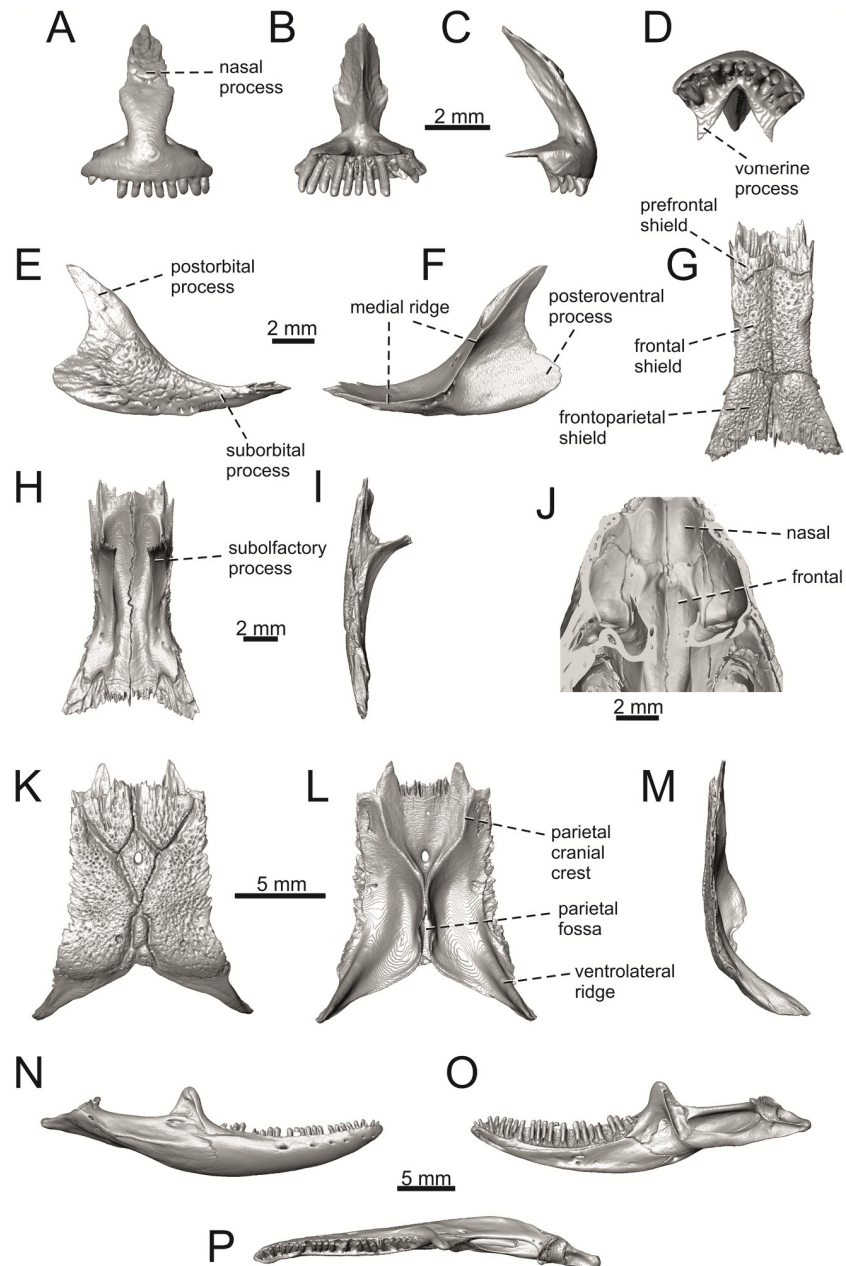


Fig 29. Selected cranial elements of *Lacerta bilineata*—The specimen NHMV 35860–2 (A–I, K–P) and 35860–1 (J). Premaxilla in anterior (A), posterior (B), lateral (C) and ventral (D) views. Jugal in lateral (E) and medial (F) views. Frontals in dorsal (G), ventral (H) and lateral (I) views. Frontals + nasals located in the skulls in internal (J) view. Parietal in dorsal (K), ventral (L) and lateral (M) views. Mandible in lateral (N), medial (O) and dorsal (P) views.

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sculptured region, has a posteroventral course virtually pointed to the 4th labial foramen (counted from anterior). The anteroposterior length of its ventral margin forms 1/3 of the entire ventral margin of the sculptured region. Such a condition is present in *L. trilineata*, but not in *L. media*, *L. schreiberi*, *L. pamphylica*, *L. bilineata*. The separation of the anterior osteoderm by a sulcus is present in *L. strigata* and *L. viridis* as well. However, the anterior osteoderm in these species is distinctly smaller in comparison to the dominant posterior osteoderm. In *L.*

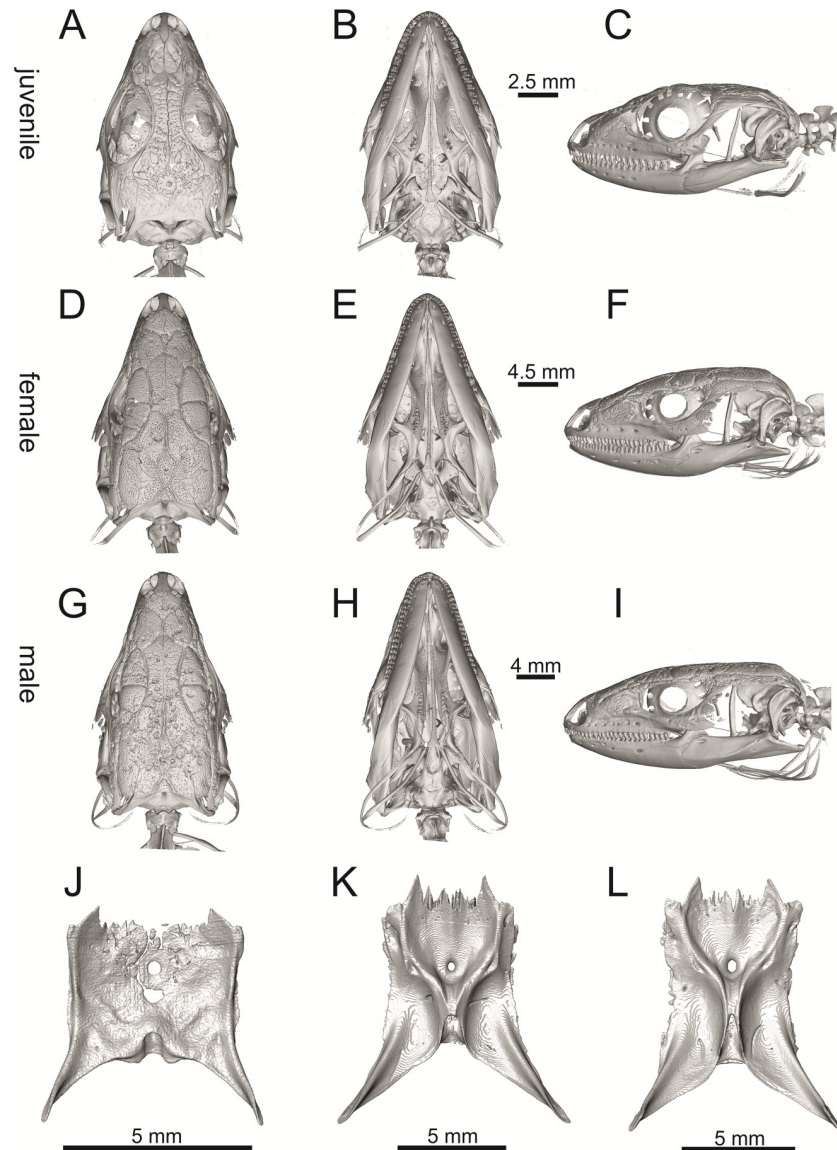


Fig 30. Ontogenetic and sexual variation of *Lacerta pamphylica* (juvenile NHMV 35861 A-C, J; female ZSM 939/2005 D-F, K and male ZSM 1047/2005 G-I, L): Skulls in dorsal (A, D, G), ventral (B, E, H) and lateral (C, F, I) aspects. Parietals in ventral (J, K, L) views.

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agilis, there is usually an absence of fused osteoderms (see Fig 13A; see also [64]; present here only in the specimen NHMV 36392–1, see Fig 26F). In *T. lepidus*, the anterior osteoderm is small (Fig 34H).

(6) The last labial foramen is located at the level of the 7th tooth position (counted from posterior). This is present in adults of *L. trilineata*, *L. viridis* and *L. bilineata*. It is located at the level of around the 4th–5th tooth position in adults of *L. strigata*, 6th in *L. agilis* (but at the 7th tooth position in NHMV 36392–1, see Fig 26F), around the 7th–8th in *L. schreiberi*, around the 8th–9th in *L. pamphylica* and around the 8th–10th in *L. media*. It should be noted that this character is not absolute and can be different in at least some juveniles, because the posterior-most labial foramen is present at the level of the 6th position in a juvenile specimen of *L. pamphylica* studied here.

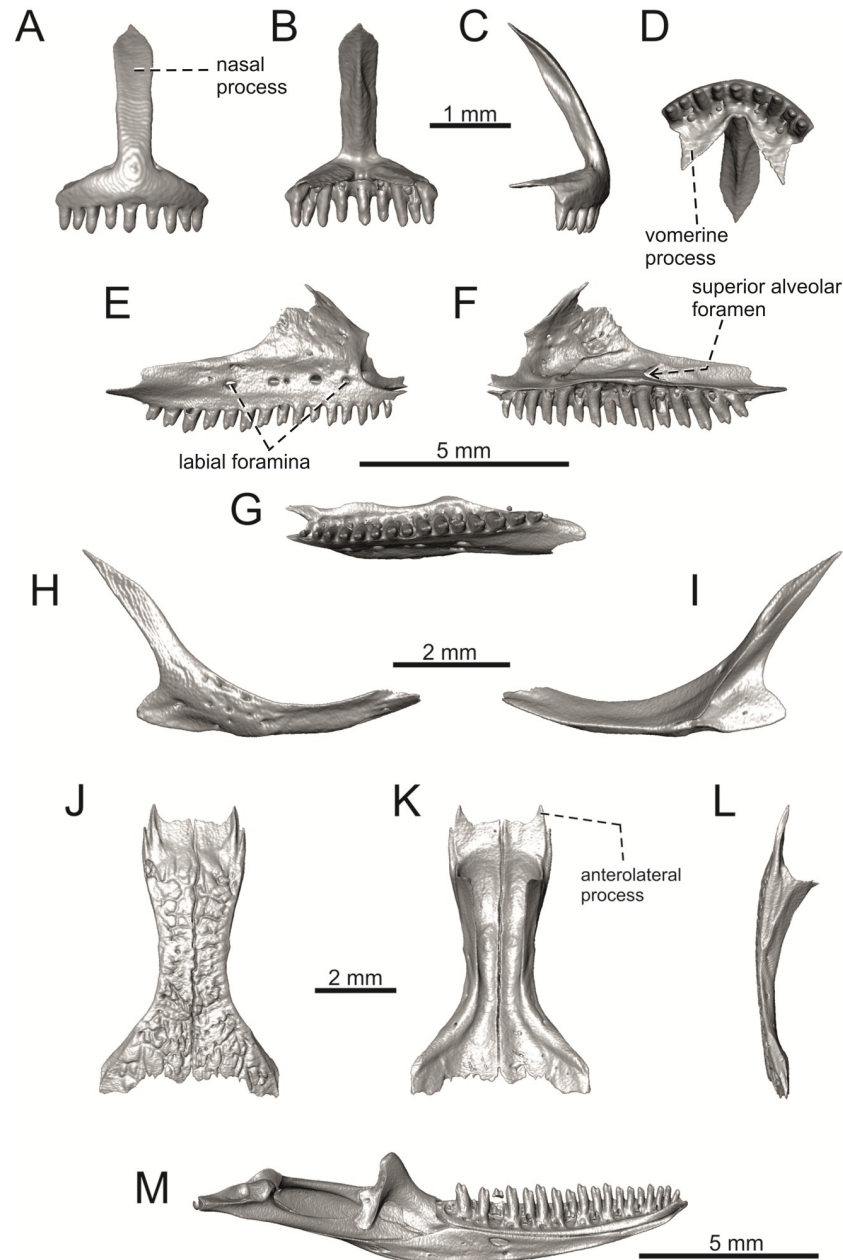


Fig 31. Selected cranial elements of a juvenile specimen NHMV 35861 of *Lacerta pamphylica*. Premaxilla in anterior (A), posterior (B), lateral (C) and ventral (D) views. Maxilla in lateral (E), medial (F) and ventral (G) views. Jugal in lateral (H) and medial (I) views. Frontals in dorsal (J), ventral (K) and lateral (L) views. Mandible in medial (M) view.

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(7) The septomaxillary (internal) ramus of the premaxillary process of the maxilla is larger and more robustly developed than the external one. This condition is present in *L. trilineata*, *L. schreiberi*, *L. media* and *L. agilis*. The opposite condition can be found in *L. bilineata* and *L. strigata*. These two rami are almost equally developed in *L. viridis* and *L. pamphylica*. In *T. lepidus*, the septomaxillary ramus of the premaxillary process is more robust relative to the external one.

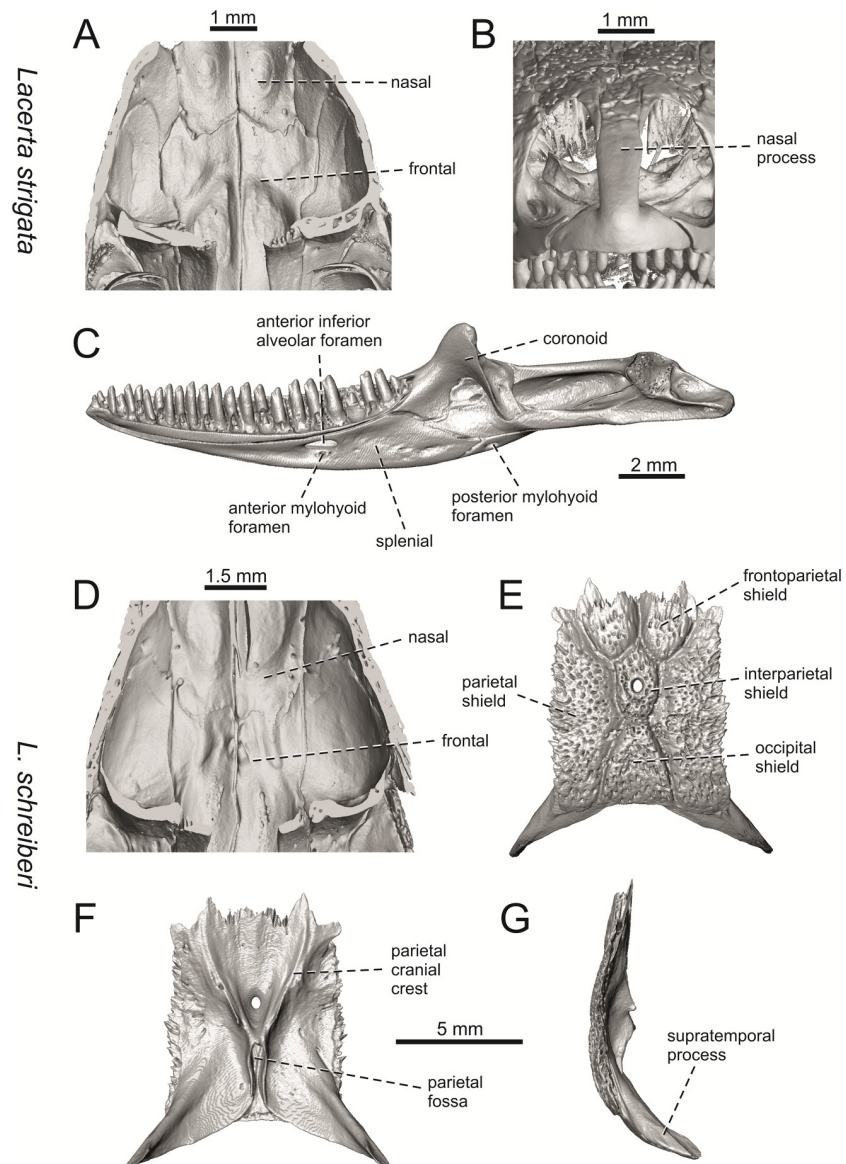


Fig 32. Selected cranial elements of *Lacerta strigata* NHMV 10917-2 (A-C) and *L. schreiberi* NHMV 10808-1 (D-G). Frontals + nasals located in the skulls in internal (A, D) views. Premaxilla located in the skull in anterior (B) view. Mandible in (C) medial view. Parietal in dorsal (E), ventral (F) and lateral (G) views.

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Jugal. (8) The angle between the central line of the posteroventral and postorbital process of jugal is around 78° in both the fossil taxon and *L. trilineata*. It is around 75° in *L. bilineata*. 70° can be found in *L. media* and *L. viridis*, whereas it is 67° in *L. strigata* and *L. agilis*, 65° in *L. pamphylica* and 60° in *L. schreiberi*. It is 60° in *T. lepidus*. It should be noted that the morphology of the Solnechnodolsk jugal slightly resembles that in the specimen NHMV 18599-1 of *L. bilineata* (Fig 15E and 15F), but not in two other ones, where the posteroventral process is much broader (see Fig 29E and 29F). In *L. bilineata*, the posteroventral process appears to be shorter, less defined and bluntly ended if compared to that in other green lizards (Fig 15E and 15F; see also [65]). The posteroventral process in Solnechnodolsk specimen appears to be better defined, not having such concave dorsal margin. Moreover, in some specimens of *L.*

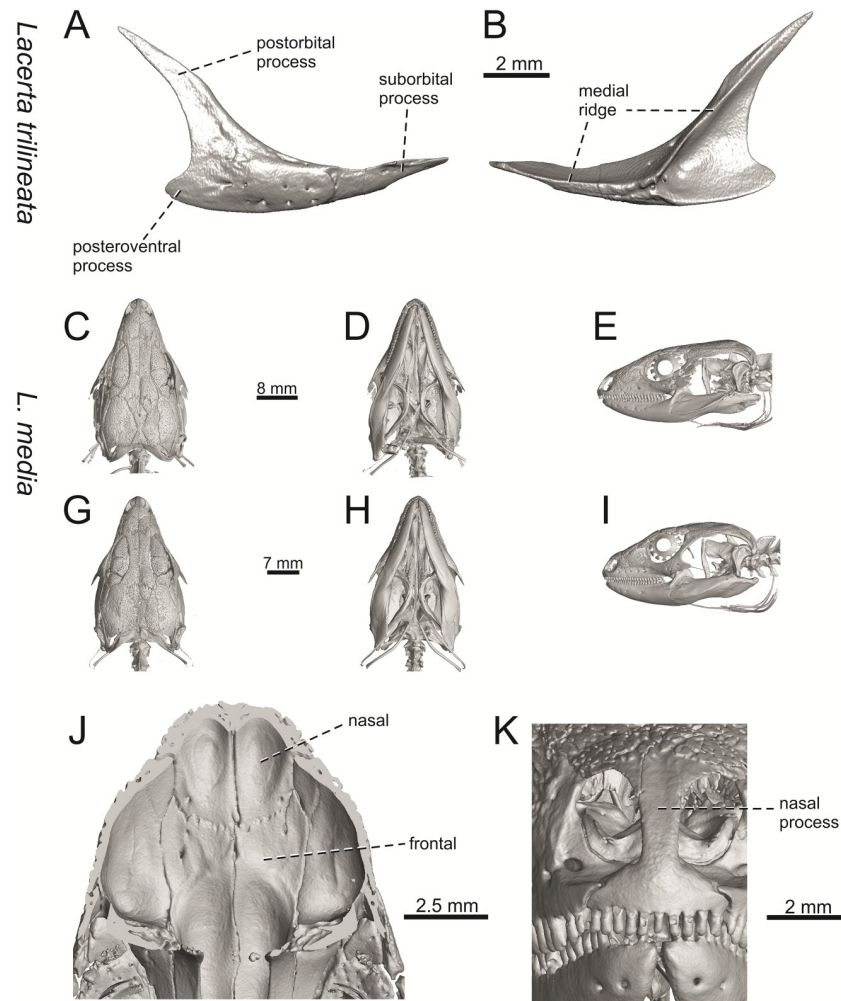


Fig 33. *Lacerta trilineata* NHMV 25524–2 (A–B) and *L. media* NHMV 18956–1 (C–E, J, K) and 18956–2 (G–I). Jugal in lateral (A) and medial (B) views. Skulls in dorsal (C, G), ventral (D, H) and lateral (E, I) views. Frontals + nasals located in the skulls in internal (J) view. Premaxilla located in the skull in anterior (K) view.

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trilineata, the posteroventral process can be somewhat blunt (see Fig 33A and 33B) and this condition strongly resembles that seen in the Solnechnodolsk specimen (Fig 3D and 3E). A condition similar to that seen in the Solnechnodolsk fossil is also present in *L. schreiberi* (Fig 16C and 16D), but here the posteroventral process of the jugal is narrow and more dorsally inclined (slightly dorsally inclined process is also present in *L. media*). In *T. lepidus*, the posteroventral process is broad and well developed (see Fig 34K and 34L).

(9) Width of postorbital process relative to posteroventral process: The postorbital process is wide in the fossil material studied here. The wide postorbital process is present in *L. trilineata*, *L. viridis*, *L. bilineata*, but is somewhat narrow in *L. schreiberi*, *L. strigata*, *L. media*, *L. pamphylica*. In *L. agilis*, the postorbital process is moderately narrow if compared to others. In *T. lepidus*, the postorbital process is wide.

Frontal. (10) The length of the anterolateral process relative to the anteromedial process. Although only the base of the anteromedial process is preserved in the fossil material, it can be estimated that it did not reach the level of the anterior end of the anterolateral process, thus was shorter in comparison to the anterolateral process. This is identical to that of *L. trilineata*.

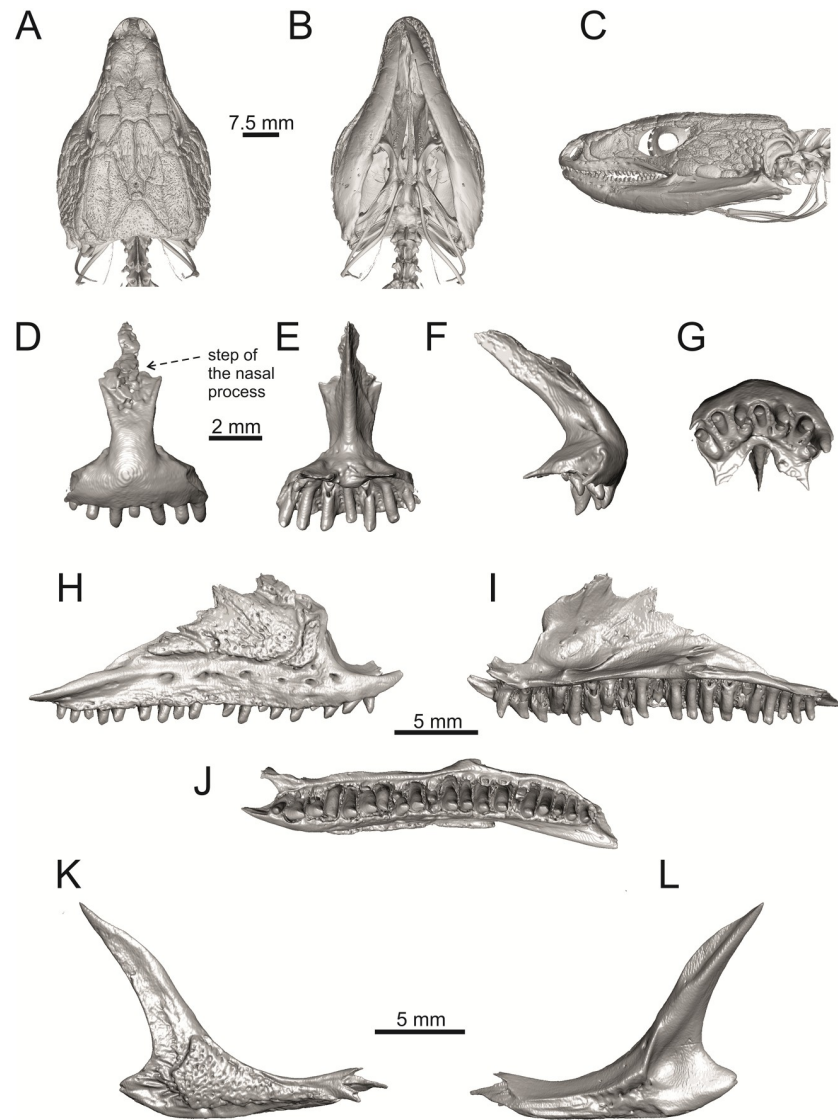


Fig 34. Skull and selected cranial elements of extant *Timon lepidus* NHMV 10921–1. Skull in dorsal (A), ventral (B) and lateral (C) views. Premaxilla in anterior (D), posterior (E), lateral (F) and ventral (G) views. Maxilla in lateral (H), medial (I) and ventral (J) views. Jugal in lateral (K) and medial (L) views (continued).

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The relative length of these two anterior processes varies among species: a) the anterolateral processes are long whereas the anteromedial ones are indistinct in adults of *L. viridis*, *L. bilineata* and *L. pamphylica*. *L. bilineata* deserves a comment here—both processes are weakly developed and reach more-or-less the same level anteriorly in NHMV 18599–1 (see Fig 17G). However in the larger specimens NHMV 35860–1 and 35860–2, the anterolateral process is much longer (see Fig 29G, 29H and 29J), whereas the anteromedial one is indistinct. Thus, it seems that this can vary in some individuals of this species and might be affected by the size (the anterolateral process grows more anteriorly later in ontogeny). In contrast, the juvenile specimen NHMV 35861 of *L. pamphylica* exhibits the same character state as adults and thus this seems to be not affected by ontogeny in this species (see Fig 31J and 31K); b) the anteromedial process is developed, but shorter than anterolateral one in *L. schreiberi*, *L. trilineata*

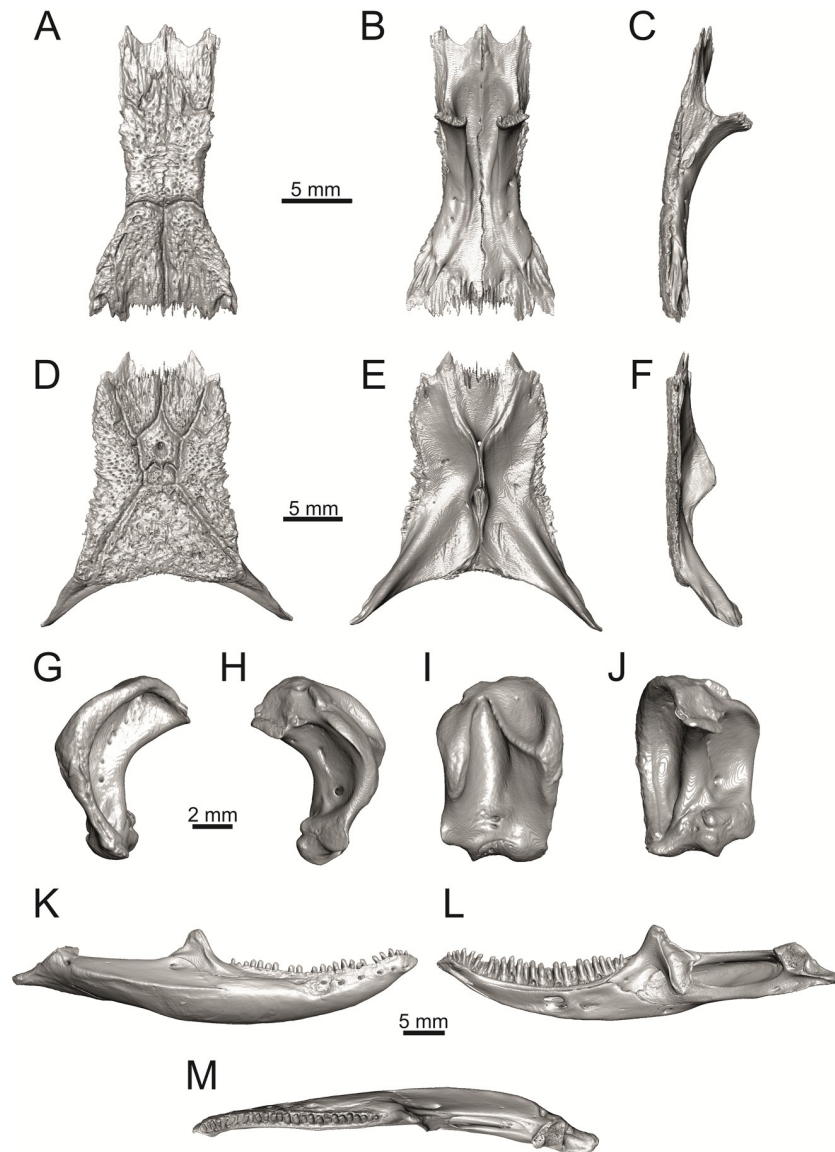


Fig 35. Skull and selected cranial elements of extant *Timon lepidus* NHMV 10921–1. Frontal in dorsal (A), ventral (B) and lateral (C) views. Parietal in dorsal (D), ventral (E) and lateral (F) views. Quadrate in lateral (G), medial (H), anterior (I) and posterior (J) views. Mandibles in lateral (K), medial (L) and dorsal (M) views.

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and *L. media* (in the latter taxon, the anteromedial process can be indistinct in some individuals, see Fig 33J); c) both reach more-or-less the same level anteriorly in *L. agilis* (Figs 17A, 17B and 28E) and *L. strigata* (Figs 18A, 18B and 32A). In *T. lepidus*, both processes reach approximately the same length. The same condition is present in *Po. muralis*. In *Ps. algirus* and *G. stehlini*, the lateral processes reach further anteriorly than the medial ones.

(11) The lateral mid-constriction of the frontal. The position and level of the constriction is identical to that of *L. trilineata*. The most pronounced mid-constriction of the frontals is present in *L. strigata* and a distinct constriction can be also found in *L. media*. The widest frontals relative to their antero-posterior length is present in *L. schreiberi* and *L. bilineata*. In *Timon lepidus* and *Zootoca vivipara*, frontals are wide, however, they are constricted in *Podarcis*

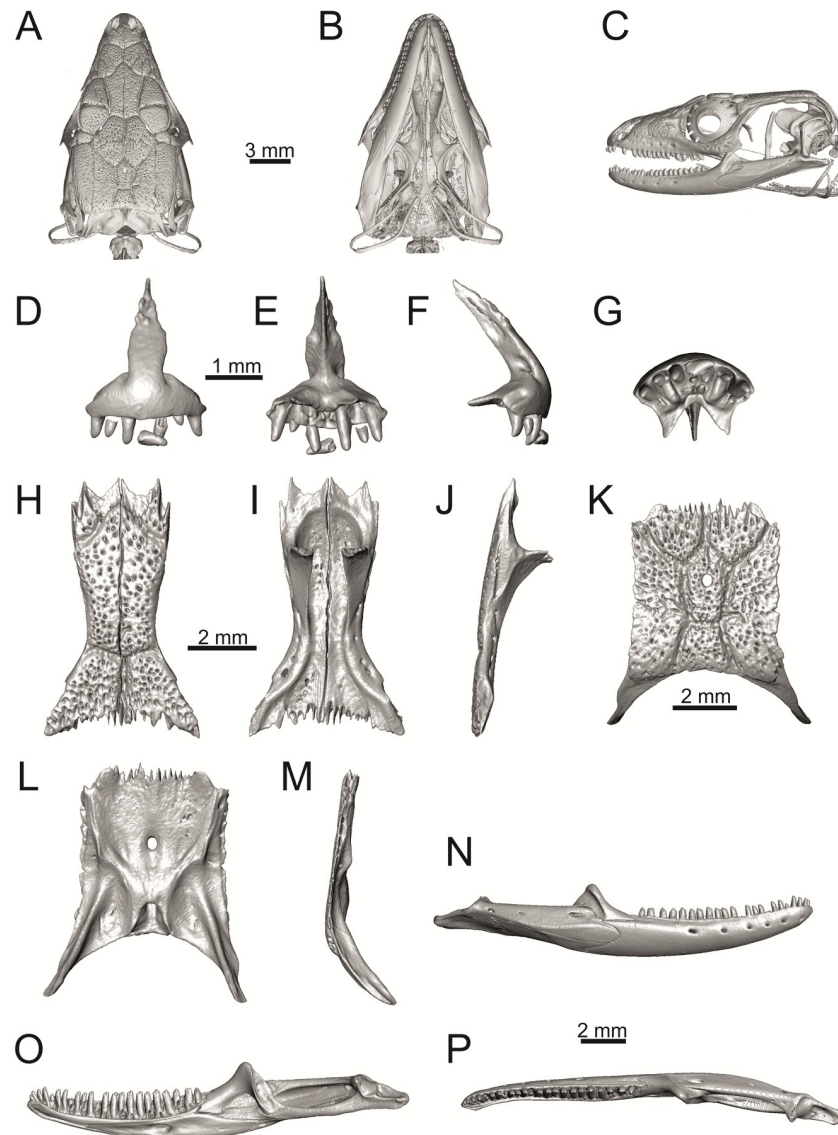


Fig 36. Skull and selected cranial elements of extant *Podarcis muralis* NHMV 39359–1. Skull in dorsal (A), ventral (B) and lateral (C) views. Premaxilla in anterior (D), posterior (E), lateral (F) and ventral (G) views. Frontal in dorsal (H), ventral (I) and lateral (J) views. Parietal in dorsal (K), ventral (L) and lateral (M) views. Mandible in lateral (N), medial (O) and dorsal (P) views.

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muralis. The marked constriction can be seen in *Meroles ctenodactylus* and a similarly strong constriction appears to be common in members of the tribe Eremiadini (for *Acanthodactylus erythurus*, see [41]).

Parietal. (12) On the dorsal surface of the parietal, the interparietal shield is pierced by the parietal foramen in the anterior half of its anteroposterior length. This is identical to *L. trilineata* (in all four specimens available to us). In all other green lizards (for all green lizards, see Figs 19 and 20), the position of the parietal foramen is located in the posterior half of the interparietal shield (*L. agilis*, *L. strigata*, *L. schreiberi*, *L. media*, *L. pamphylica*), or more or less in the mid-region (*L. viridis*, *L. bilineata*). One exception is the specimen NHMV 35860–2 of *L. bilineata*, where the parietal foramen is located anteriorly to the mid-length of the interparietal

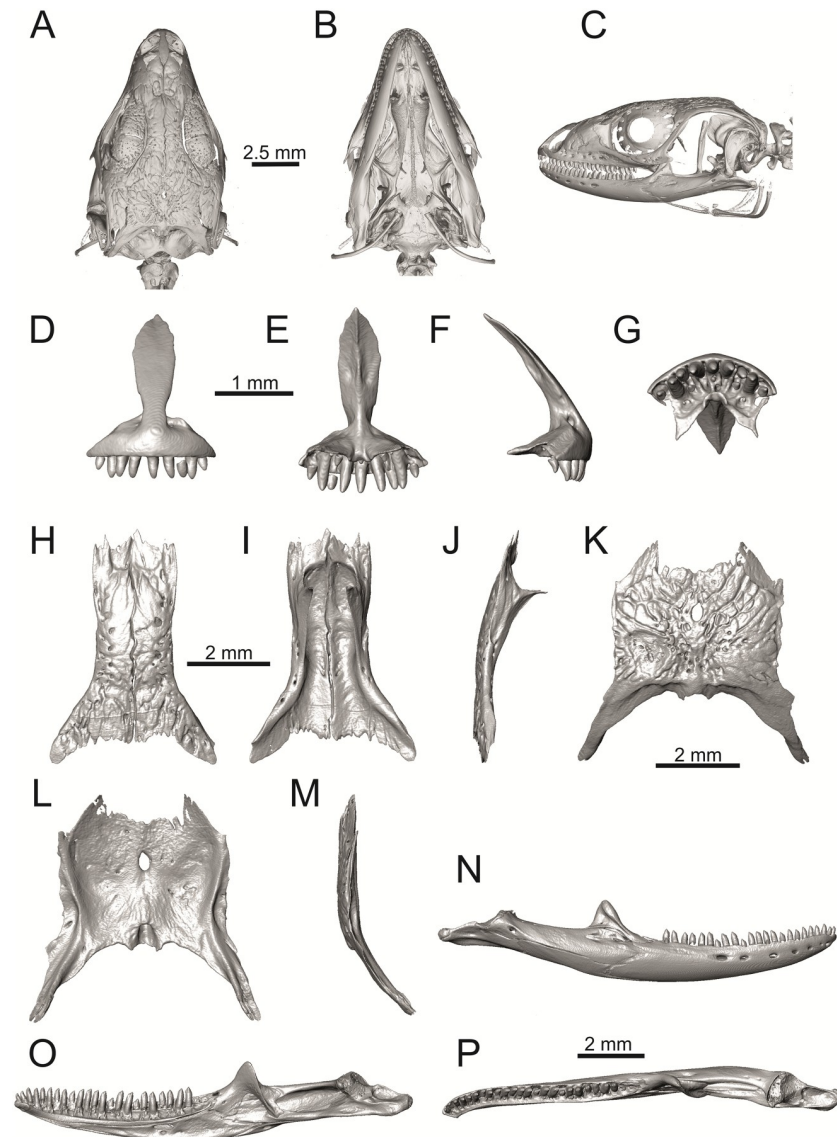


Fig 37. Skull and selected cranial elements of extant *Zootoca vivipara* NHMV 32438–1. Skull in dorsal (A), ventral (B) and lateral (C) views. Premaxilla in anterior (D), posterior (E), lateral (F) and ventral (G) views. Frontal in dorsal (H), ventral (I) and lateral (J) views. Parietal in dorsal (K), ventral (L) and lateral (M) views. Mandible in lateral (N), medial (O) and dorsal (P) views.

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shield. In *T. lepidus*, the interparietal shield is pierced in its anterior region (Fig 35D; see also [51]). An even more anterior location of the foramen can be observed in *Po. muralis*, *Takydromus sexlineatus*, and *G. stehlini* (as well as *Janosikia ulmensis* [11]). The interparietal shield is pierced more-or-less in the middle in *Z. vivipara* and the foramen is located in posterior region of the interparietal shield in *Ps. algirus*.

(13) In the Solnechnodolsk fossils, as well as in *L. trilineata*, *L. pamphylica*, *L. schreiberi* and *L. viridis*, the interparietal shield is entirely restricted to the parietal by the frontoparietal shields that meet to form a medial suture that interpolates between the anterior margin of the parietal shield and the suture with the frontal bone. In *L. agilis* and *L. bilineata* the frontoparietals are in point contact, but this can vary. In *L. bilineata*, the interparietal reaches the

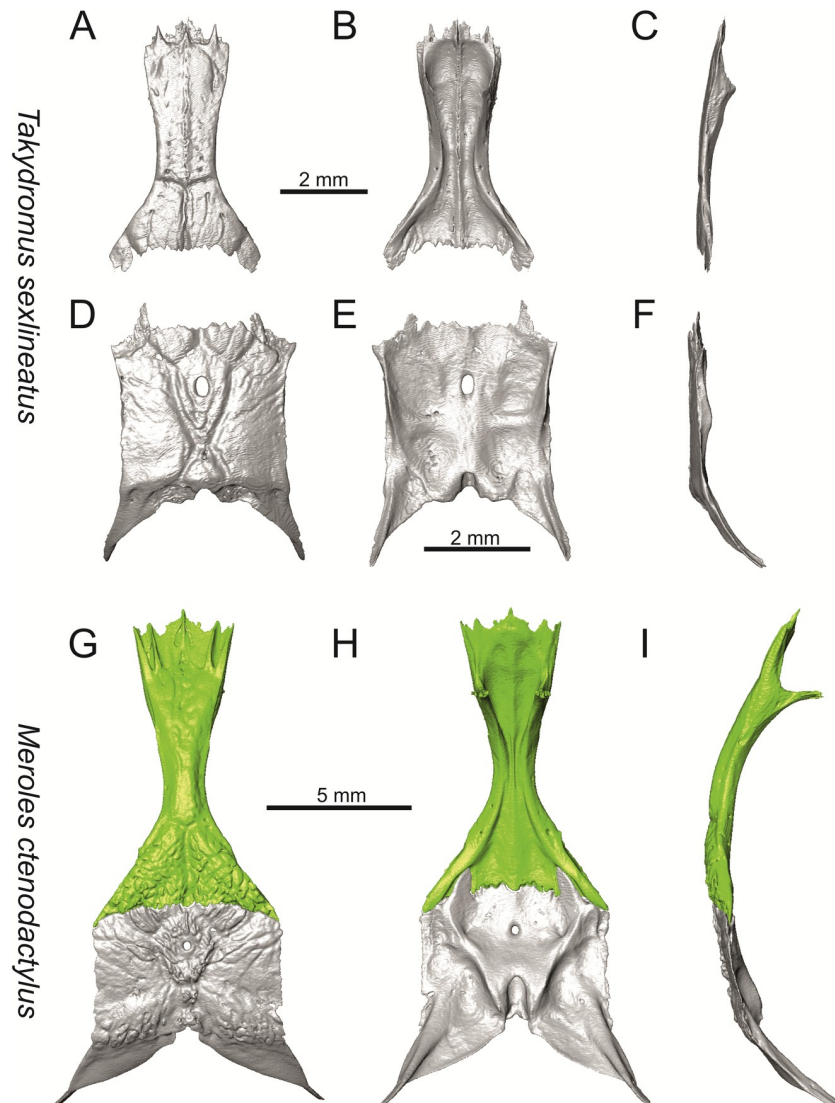


Fig 38. Frontals and parietals of extant *Takydromus sexlineatus* DE 134 (A-F) and *Meroles ctenodactylus* NHMV 31376 (G-I) in dorsal (A, D, G), ventral (B, E, H) and lateral (C, F, I) views.

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frontoparietal suture in NHMV 35860–1, whereas it is fully restricted to the parietal table in NHMV 35860–2 (see Fig 26J and 26M). In *L. media*, the frontoparietal shields do not meet on the parietal bone in the NHMV 34808, allowing the anterior margin of the parietal shield to contact the suture with the frontal (not present in NHMV 18956–2). In the NHMV 39765 of *L. strigata*, a small anterior portion of interparietal shield continues on the posterior mid-region of frontals. However, in two other specimens, NHMV 10917–1 and 10917–2, the interparietal shield is completely restricted to the parietal table.

(14) The occipital shield of the parietal in *L. trilineata* is moderately large, based on the specimen NHMV 27665 (Fig 20G), occupying the largest area of the parietal table (about 1/3 of the posterior width of the parietal table) among all green lizards (it is wider than the interparietal shield, although it should be noted that the anteroposterior length of the occipital shield is smaller than the length of the interparietal shield). The lateral margins of the occipital shield are convex laterally rather than having a straight course. The same condition is present in the

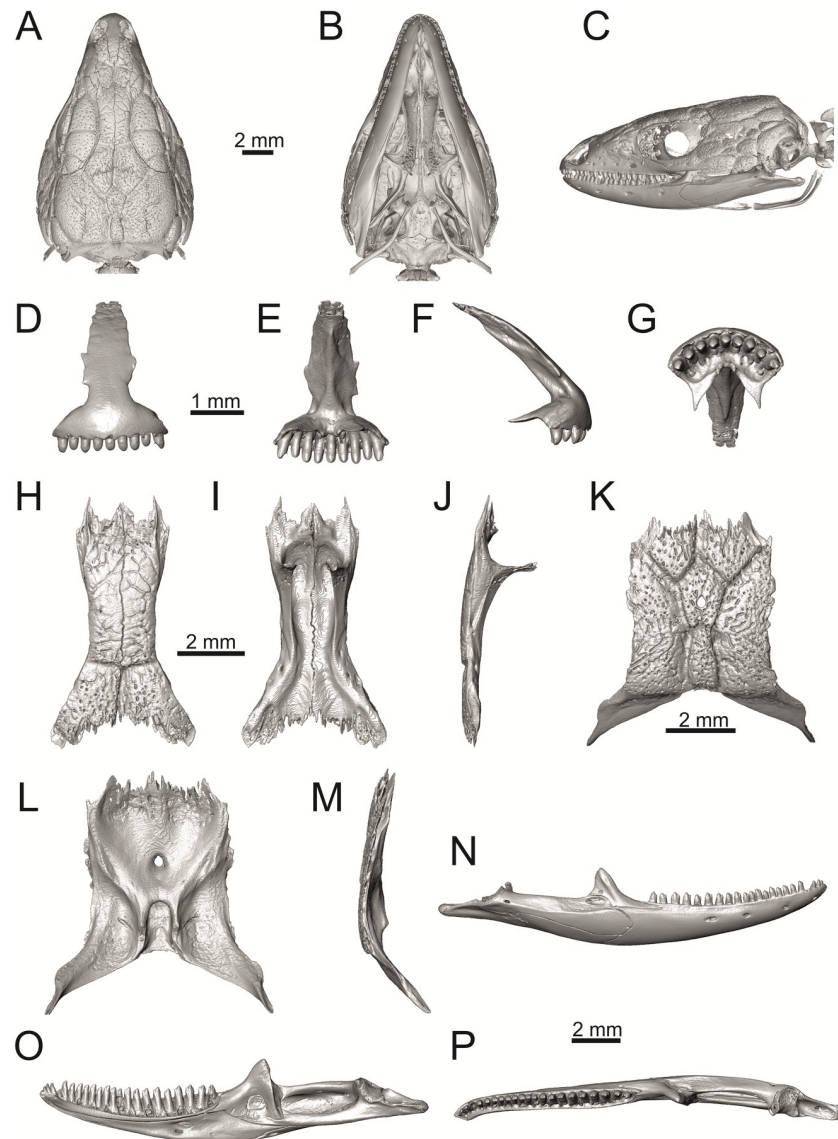


Fig 39. Skull and selected cranial elements of extant *Psammodromus algirus* NHMV36038-2. Skull in dorsal (A), ventral (B) and lateral (C) views. Premaxilla in anterior (D), posterior (E), lateral (F) and ventral (G) views. Frontal in dorsal (H), ventral (I) and lateral (J) views. Parietal in dorsal (K), ventral (L) and lateral (M) views. Mandible in lateral (N), medial (O) and dorsal (P) views.

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Solnechnodolsk specimen GIN 1145/283 (Fig 5A). The occipital shields of other fossil specimens seem to be not as large (Fig 5C and 5F). This can, however, vary among individuals of modern *L. trilineata* (see Figs 20G, 27M and 27P). The large occipital shield can be found, e.g., in the specimen NHMV 10808–1 of *L. schreiberi* as well (see Figs 27G and 32E). But the parietal of this specimen is different from the Solnechnodolsk fossils in many other aspects, e.g., the position of the parietal foramen, the course of the parietal cranial crests and the ratio of the anteroposterior length of the interparietal shields vs. occipital shield—the interparietal shield in the fossils and in individuals of *L. trilineata*, where the occipital is large, is longer than the occipital shield. In the specimen NHMV 10808–1 of *L. schreiberi*, the length of the interparietal shield is equal to the length of the occipital shield. Interestingly, the occipital shield is not in

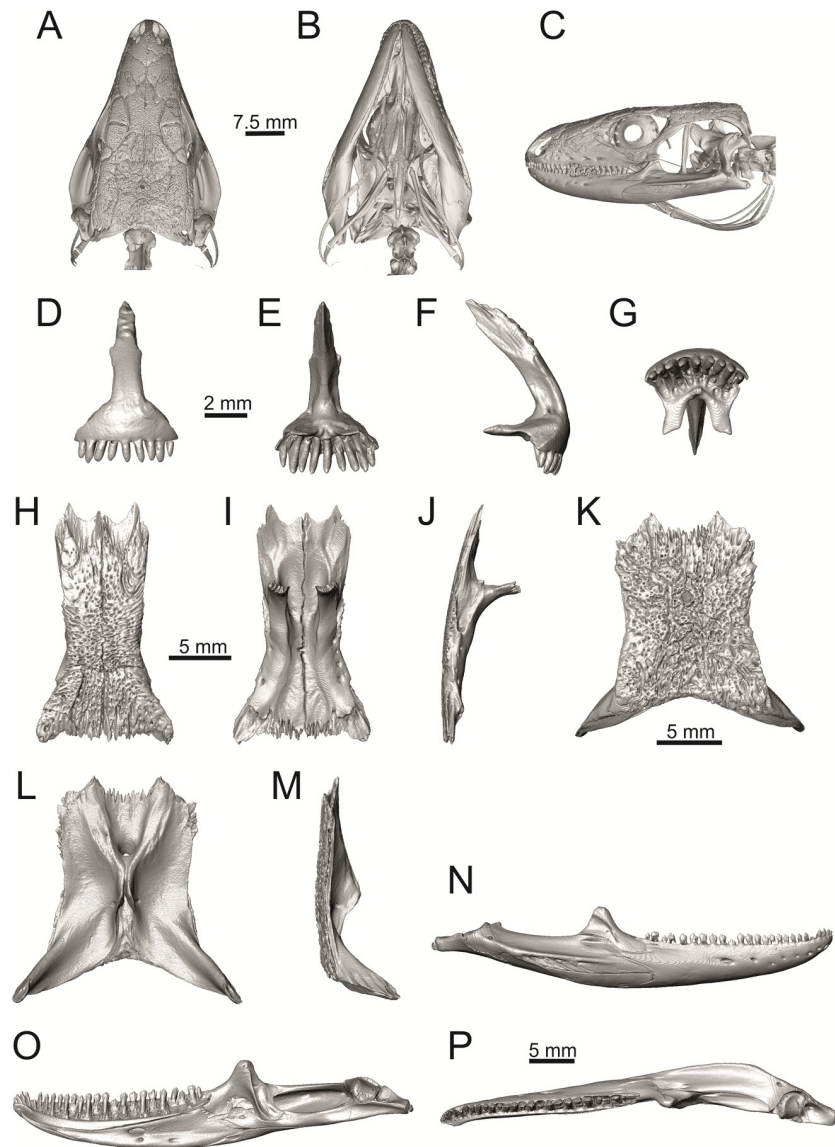


Fig 40. Skull and selected cranial elements of extant *Gallotia stehlini* NHMV 11031–1. Skull in dorsal (A), ventral (B) and lateral (C) views. Premaxilla in anterior (D), posterior (E), lateral (F) and ventral (G) views. Frontal in dorsal (H), ventral (I) and lateral (J) views. Parietal in dorsal (K), ventral (L) and lateral (M) views. Mandible in lateral (N), medial (O) and dorsal (P) views.

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contact with the interparietal shield in NHMV 35860–1 and 35860–2 of *L. bilineata* and thus, the right and left parietal shields are in a short contact here. Among the taxa studied here, the occipital shield is large in *G. stehlini* (for this character state see also [11]) and extremely large in *T. lepidus* (but also in *Pl. lydekkeri* [8]).

(15) The lateral margins of the parietal are not completely preserved and can be only estimated. However, they appear to have a lateral concave course similar to *L. trilineata*, *L. media*, *L. pamphylica* and *L. viridis*. In *L. trilineata* and *L. media*, the small mid-constriction is present and the posterior portion is equally wide as the anterior portion. Such constriction is also present in *L. viridis* and *L. pamphylica*, but here the posterior portion is slightly wider than the anterior one. In *L. agilis* (slightly concave margins) and *L. bilineata* (slightly convex margins or

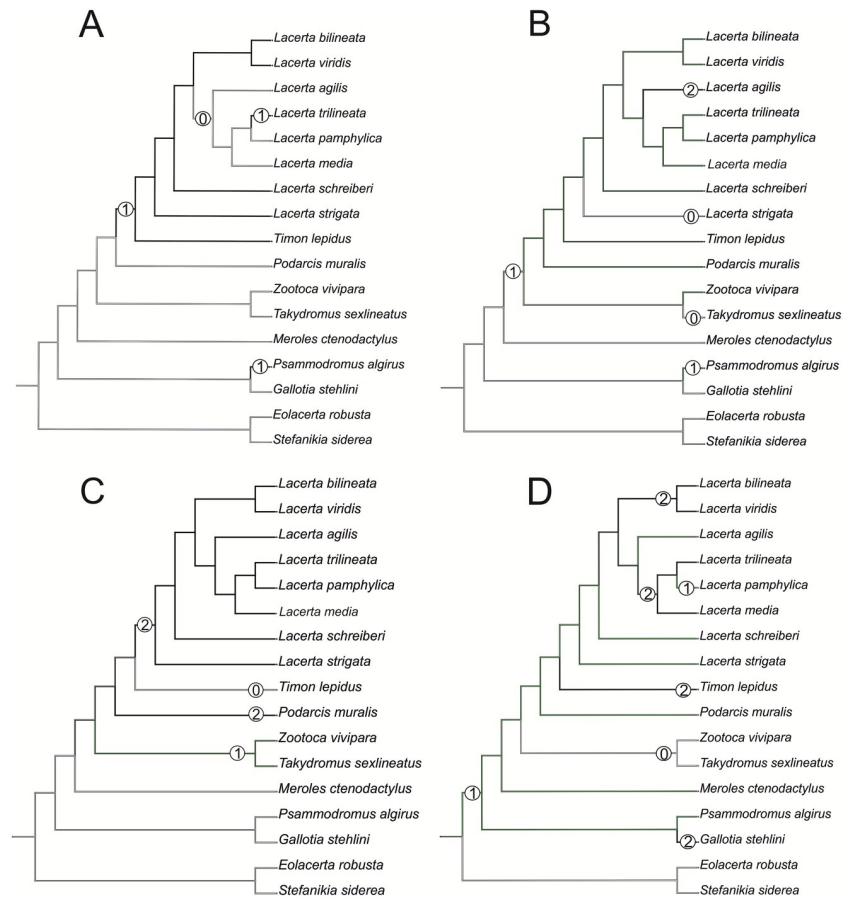


Fig 41. Trace character history analysis in Mesquite. (A) Cheeks covered laterally by osteoderms (absent 0, cheeks covered by osteoderms 1); (B) The width of the nasal process of premaxilla (narrow 0, wide 1, extremely wide 2); (C) The stepped posteroventral process of premaxilla (absent 0, weakly developed—initial condition 1, present, well developed 2); (D) Parietal cranial crest medial convergence (absent, 0; tendency to medial course present 1; crests meet medially 2).

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more or less straight margins), the whole parietal narrows anteriorly. In *L. schreiberi*, the lateral margins are more-or-less straight. In *L. strigata*, the lateral margins diverge laterally from each other anteriorly, thus the anterior portion appears to be usually slightly wider than the posterior one. In *T. lepidus*, the parietal table is anteroposteriorly long and slightly narrows anteriorly. The lateral margins of the parietal table are slightly concave in this taxon.

(16) On the ventral surface of the parietal in the Solnechnodolsk fossil lacertid, the parietal cranial crests converge strongly posteromedially, forming a distinct median crest slightly posterior to the parietal foramen (for this character see [23]). This is identical to adults of *L. trilineata*, *L. viridis* and *L. bilineata* and slightly similar condition can be observed in *L. media*. The difference here between *L. trilineata* and *L. viridis* is in the course of the parietal crest. In *L. viridis*, the crest on each side continues anterolaterally in a more or less straight course. Thus, the virtual line extending anteriorly from the posterior section of the branch would meet the anterolateral corner of the parietal (see also [9]). In *L. trilineata* (in all specimens available to us), the parietal crest on each side is angled approximately at the level of the anterior margin of the parietal foramen. Here, the parietal crest turns more anteromedial relative to its posterior section. Thus, the virtual line extending anteriorly from the posterior section (posteromedial

to this angle) would not meet the corner of the parietal table, but would finish on its anterolateral side. This is identical to the condition present in the Solnechnodolsk parietal GIN 1145/283 (see Fig 5B). The condition in the specimen NHMV 35860–2 of *L. bilineata* (Fig 29L) might slightly resemble this character state. However, closer observation shows that the angle is located further anteriorly (anterior to the parietal foramen) and both branches of the parietal cranial crests do not extend laterally to a strong degree (the central area framed by the crests is rather narrow). Moreover, the virtual line extending anteriorly from the posterior section of the parietal cranial crest (posteromedial to this angle) would meet the anterolateral corner of the parietal table. In other green lizards, an evident tendency to a medial course of the parietal crest is present, but not in the distinct form as it is in *L. trilineata*, *L. viridis* and *L. bilineata*. Moreover, this character state changes during ontogeny. It is absent in juveniles of green lizards, here supported by *L. pamphylica* (see Fig 30J). The tendency for medial convergence of the parietal crests is only present in the smallest specimen of *L. bilineata* available to us, NHMV 18599–1 (Fig 19H vs. Fig 29L). Among large adults, the cranial crests do not meet medially in *L. agilis* (see Figs 19B and 28G). The parietal crests converge in *T. lepidus* and *G. stehlini*. Only a tendency to more-or-less medial course can be observed in adults of *Po. muralis*, *M. ctenodactylus* and *Ps. algirus*. The tendency to a more or less medial course is absent in *Z. vivipara* and *T. sexlineatus*, and in known Paleogene members of the clade Eolacertidae (it is regarded here as absent, but members of this clade might appear to show somewhat an initial tendency [9]). The juveniles of green lizards therefore show the morphology of their ancestral lineage and the converging of the parietal crests can be regarded as derived among the Lacertidae. The character optimization in Mesquite (Fig 41D) supports the presence of a tendency to a medial course of the parietal crests as being the condition at the basal node of the clade Lacertidae (this is also supported by the presence of medially merged parietal crests in the Eocene *Pl. lydekkeri* [8]. Its absence in *T. sexlineatus* and *Z. vivipara* is regarded as reversal. Character optimization in Mesquite shows that the presence of the medially merged parietal crests in *G. stehlini*, *T. lepidus* and several members of *Lacerta* evolved independently. In the clade *L. trilineata* + *L. pamphylica* + *L. media*, character optimization in Mesquite evaluated this change in two equally parsimonious ways: as the condition at the basal node in this lineage with an additional reversal in *L. pamphylica*, or as representing independent derivations of the medially merged crests in *L. trilineata* and *L. media*.

(17) The ventrolateral ridge in the internal region gradually disappears anteromedially. This character state can be observed in *L. trilineata*, *L. viridis*, *L. bilineata*, *L. pamphylica*, *L. strigata* and *L. media*, but not in *L. agilis* (all specimens available to us; see also [9]) and in the specimen NHMV 10809 of *L. schreiberi*. Here, this ridge continues markedly almost to the parietal crests.

(18) Parietal fossa—in regard to the Solnechnodolsk parietals, we can exclude *L. media* here. This taxon is characterized by very narrow wedge shaped fossa, with an additional process located in the anterior end of the fossa (posteroventral process in Fig 20L). This process is directed posteroventrally.

Postfrontal. (19) In Solnechnodolsk fossils, the postfrontal and postorbital are separated individual elements. This is present in all specimens of green lizards (e.g., *L. viridis*; see Fig 21A) examined here except for two species. In *L. agilis*, partial fusion of these two elements has occurred, with traces of the suture being easily recognized. However in *L. schreiberi*, the fusion is present in a stronger degree, where traces of the suture can be recognized only in the posterior region of the postorbitofrontal element (Fig 21B). On its dorsal surfaces, two osteoderms are separated by a longitudinal sulcus. The fusion of the postorbital and postfrontal bones to form a postorbitofrontal can be seen in adults of *T. lepidus* (Fig 21C), but not in *Po. muralis* (Fig 21D). The fusion is present in *Z. vivipara* (Fig 21E) and in *T. sexlineatus* (Fig 21F), but

also in *M. ctenodactylus* (Fig 21G) and in members of Gallotiinae (Fig 21H; see also [11, 55]), as well as in the Eocene *Pl. lydekkeri* [8]. The postfrontal and postorbital are unfused in *Eremias* and *Mesalina* [48].

Quadrate. (20) The tympanic crest, which forms the anterolateral margin of the quadrate, is angled approximately in the mid-region. This is present in *L. trilineata*, *L. media*, *L. strigata*, *L. viridis*, *L. pamphylica* and *L. schreiberi* (Figs 22 and 23). This anterior margin is completely rounded in *L. agilis* and *L. bilineata*. The angle is also present in *T. lepidus*.

(21) In lateral aspects, the ventral half of quadrate (ventral to angulation of the tympanic crest) gradually markedly narrows ventrally. Thus this portion is much narrower than the dorsal portion. This condition is identical to that of *L. trilineata*, *L. viridis* and *L. media*. However in the latter taxon, the quadrate is more robustly built if compared to other taxa. This difference between the width of the dorsal and ventral portion is not so pronounced in other taxa. In *T. lepidus*, the whole quadrate is robust.

Dentary. (22) Number of unicuspid teeth. In the Solnechnodolsk material, bicuspidity sometimes starts with the 7th tooth, but this can be variable even in extant taxa. Kosma [66] stated that the first five anterior dentary teeth are unicuspid, whereas more posterior teeth are bicuspid in both *L. viridis* and *L. trilineata*. In contrast, unicuspidity is restricted only to the first two anterior teeth in *L. agilis* [66].

(23) The position of alveolar foramen in dentary at the level of the 7th tooth position (counted from posterior). Such condition is present in *L. trilineata* and *L. schreiberi*, whereas it is present at the level of the 6th tooth position in *L. bilineata*, *L. strigata*, *L. agilis*, *L. viridis*. The alveolar foramen is located further anteriorly, at the level of the 8th tooth position, in *L. pamphylica* and at the level between 9th-10th tooth positions in *L. media*. Although the location of the alveolar foramen can be informative, it should be noted that the positions of the alveolar foramen in lacertids, like virtually all lizards, should not be interpreted as absolute due to its variations.

***Lacerta cf. trilineata* in the late Miocene of Russia**

The detailed comparison above strongly supports an allocation of the Solnechnodolsk lizard fossil to *Lacerta cf. trilineata*—it shows that the Solnechnodolsk lacertid material shares the complete combinations of character states (also with regards of variations among individuals available to us) only with *L. trilineata*. According to Ahmadzadeh et al. [28], *L. trilineata* seems to have evolved and diverged in western Anatolia during the Pliocene or Early Pleistocene. Sagonas et al. [16] suggested a longer history of this taxon, with the first split occurred in the early Tortonian (9.55 Mya). Based on these authors, the split of *L. viridis* and *L. bilineata* is also dated to the late Miocene (6.78 Mya). This is in a strong contradiction with the recently published results of Kornilios et al. [27]. These authors suggested that the radiations of all major green lizard groups, including *trilineata+pamphylica*, occurred in parallel in the late Pliocene. All three studies used the same calibration points and the same data (mtDNA) for their time estimates, but differed in their inference methods. The Solnechnodolsk material shows support for the hypothesis of Sagonas et al. [16] and forms the first potential evidence of the occurrence of the lineage of *L. trilineata* already in the late Miocene.

Green lizards form a dominant component of the squamate paleofauna from the Solnechnodolsk locality (see also [3, 33]), showing their successful adaptation to the paleoenvironment of this area east of the Black Sea during the late Miocene. In this geological sub-epoch, the climate in Europe remained warm in the MN 13, however the mean annual temperature dropped when compared to the Miocene Climatic Optimum [1, 67]; the amplitude of the temperature drop varying geographically [68, 69]. This led to a more distinct climatic zonation on the

European continent and to the survival of thermophilic ectothermic animals only in southern regions [1, 3, 58, 70]. The rapid climatic changes during the Miocene (and the Cenozoic in general) most likely led to the broad radiation of lacertid lizards in Europe. In the late Miocene, major vegetation changes are documented in the southeastern areas of this continent. Based on paleobotanical data, Ivanov et al. [71] reported slight cooling and some drying at the beginning of the late Miocene, followed by cycling changes of humid/dryer and warmer/cooler conditions. The occurrence of *Varanus* sp. in Solnechnodolsk suggests a mean annual temperature not less than around 15 °C [3]. Today, *Lacerta trilineata* occupies Mediterranean-type shrubby vegetation, sandy shores, arable land, pastureland, plantations, and rural gardens. The diet of this taxon consists mainly of insects [72, 73]. In conclusion, the material of *Lacerta* together with previously-described lizard fossils [3, 33], exhibit an interesting combination of survivors and the dawn of modern species in the Solnechnodolsk locality. Thus, this locality forms an important evidence of a transition from an archaic Miocene world to the modern diversity of lizards in Europe.

Selected fossils in European deposits vs. extant taxa

Lacertids are often reported from the fossil record of Europe [18, 54, 74–77] and from areas adjacent to Solnechnodolsk (the Black Sea area), including lacertid material previously described from the early Pliocene of Turkey. However due to the fragmentary nature of the elements, they were allocated only to cf. *Lacerta* sp. [78]. A locality identical in age (MN 13) to the Solnechnodolsk locality is represented by the Ano-Metochi locality of northern Greece, where the clade Lacertidae has also been identified. However, due to the fragmentary nature of the material, only an allocation at the family level is supported without doubt [2]. It should be noted that a herpetological assemblage from the Romanian margins of the Black Sea, is described from slightly older sediments—MN 7+8 [79]. The lacertid material there consists only of jaws and frontal fragments and was identified as *Lacerta* sp.

In this section, previously described lacertid fossils from the European Cenozoic, which can may have strong affinities with modern lineages, are discussed. The Eocene taxon *Plesiolacerta lydekkeri* is regarded as in or close to the crown Lacertidae [8]. As was already recognized by Hoffstetter [80], this taxon resembles morphologically the extant *Timon lepidus* [81]. These shared features (some of them are potential synapomorphies) are as follows: (1) the shape of the nasal process of premaxilla (see above); (2) shape of the maxillary processes of the premaxilla; (3) presence of nine teeth on premaxilla; (4) posteroventral process of maxilla is not stepped; (5) the overall shape of the nasal process of maxilla; (6) the maxillary crest of the maxilla (the *carina maxillaris*) starts from the supradermal shelf at the level of the 4th tooth position; (7) the course of the maxillary crest—its anterior section runs posteriorly almost in a horizontal level (this gives the appearance to this section as being depressed). It starts to rise posterodorsally at the level of the 6th tooth position; (8) similar ratio of the anteroposterior length of the frontal and frontoparietal shields; (9) fragmentation of the interparietal shield (= presence of the transitional shield, see [8]; although it should be noted that not all individuals of *Timon* possess this character, see e.g. [37]); (10) large occipital shield; (11) a similar type of sculpture of osteodermal shields fused to cranial bones; (12) posterior constriction of the parietal fossa of the parietal; (13) the anteroposterior length of the parietal table greater than its width; (14) postfrontal and postorbital fused to form a postorbitofrontal; (15) markedly rounded subdental shelf of dentary; (16) the alveolar foramen on dentary located at the level of the 16th tooth position (counted from anterior) in our specimen of *T. lepidus*, whereas it is located at the level of the 17th tooth position in *P. lydekkeri*; (17) the size of the elements, indicating animals with a similar large body size.

These are not just shallow similarities, because some features e.g., additional posterior constriction of the parietal fossa, are present only in these two taxa and cannot be only a matter of a large size (this feature is not present in large members of *Gallotia*, e.g. *G. stehlini*). It seems to be more plausible that such similarities might reflect possible relationship rather than represent just homoplasies. *Plesiolacerta* is also known from late Oligocene deposits of Germany, where the species *P. eratothenesi* is described [8]. The molecular clock estimation of the evolutionary divergence between *Lacerta* and *Timon* dates back to 18.6 Mya [82], or 20.7 [27]. However, if *Plesiolacerta* has a close relationship to *Timon*, it would show a much longer evolutionary history of lineage. In comparison with other lizard lineages, this would be not so unusual- one example is the presence of the modern genus *Ophisaurus* (or morphologically identical elements) in the late Eocene [83]. This problem could be resolved if fossils proving the existence of *Timon* lineage were recognized in deposits close to the Oligocene/Miocene boundary.

The parietal (UMJGP 204.750) from the late middle Miocene of Gratkorn in Austria, allocated to Lacertidae *incertae sedis* by Böhme & Vasilyan [77] deserves a comment here. Based on the comparative study presented here, this parietal is almost identical to *Podarcis muralis* (for *Podarcis*, see also [50]). If the allocation of this parietal to *Podarcis* were correct, it shows the presence of this taxon already in the middle Miocene (for the fossil record of *Podarcis* and other lacertid lineages in Europe, see [84]). Therefore, this parietal requires a detailed revision.

Supporting information

S1 Dataset. Repository of computed tomography data. The CT data links for Figshare and Morphosource.
(DOCX)

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