

A lizard from Baltic amber (Eocene) and the ancestry of the crown group lacertids

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An almost complete lizard specimen discovered from the Baltic amber of middle Eocene age is described and considered conspecific with the first Baltic amber lizard *Succinilacerta succinea* (Boulenger, 1917). The new specimen demonstrates that the typical lacertid morphotype was fully developed by the middle Eocene. This is in conflict with a possible derivation of all the extant lacertids from a common ancestor of no earlier than Oligocene age based on the recent albumin-immunological and karyologic analyses using molecular clock methodology. Outgroup analysis of the lacertid pileus characters is applied to reconstruct the order and rate of appearance of character states during the pre-Oligocene section of phylogeny of the lacertid clade theoretically beginning by about the Late Jurassic. Two synapomorphies are proposed for the whole lacertid clade, including Eocene *Plesiolacerta*: frontoparietal scales largely overlapping the parietal table with a corresponding central position of the interparietal, and presence of the occipital. *Plesiolacerta* is the only stem lacertid known. *Succinilacerta* is considered a member of the crown lacertids on the basis of two other synapomorphies: an integration of parietal scales and a development of early ontogenetic control of the pileus pattern. Parietal integrity is suggested to be sensitive to animal size. Pileus fragmentation may be primary or secondary.

Key words: Amber inclusions, Eocene, Lacertidae, Scincomorpha, Squamata, *Succinilacerta*.

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Introduction

The specimen described herein is the second almost complete lizard specimen ever discovered from the Baltic amber. Three other fragmentary specimens have been an-

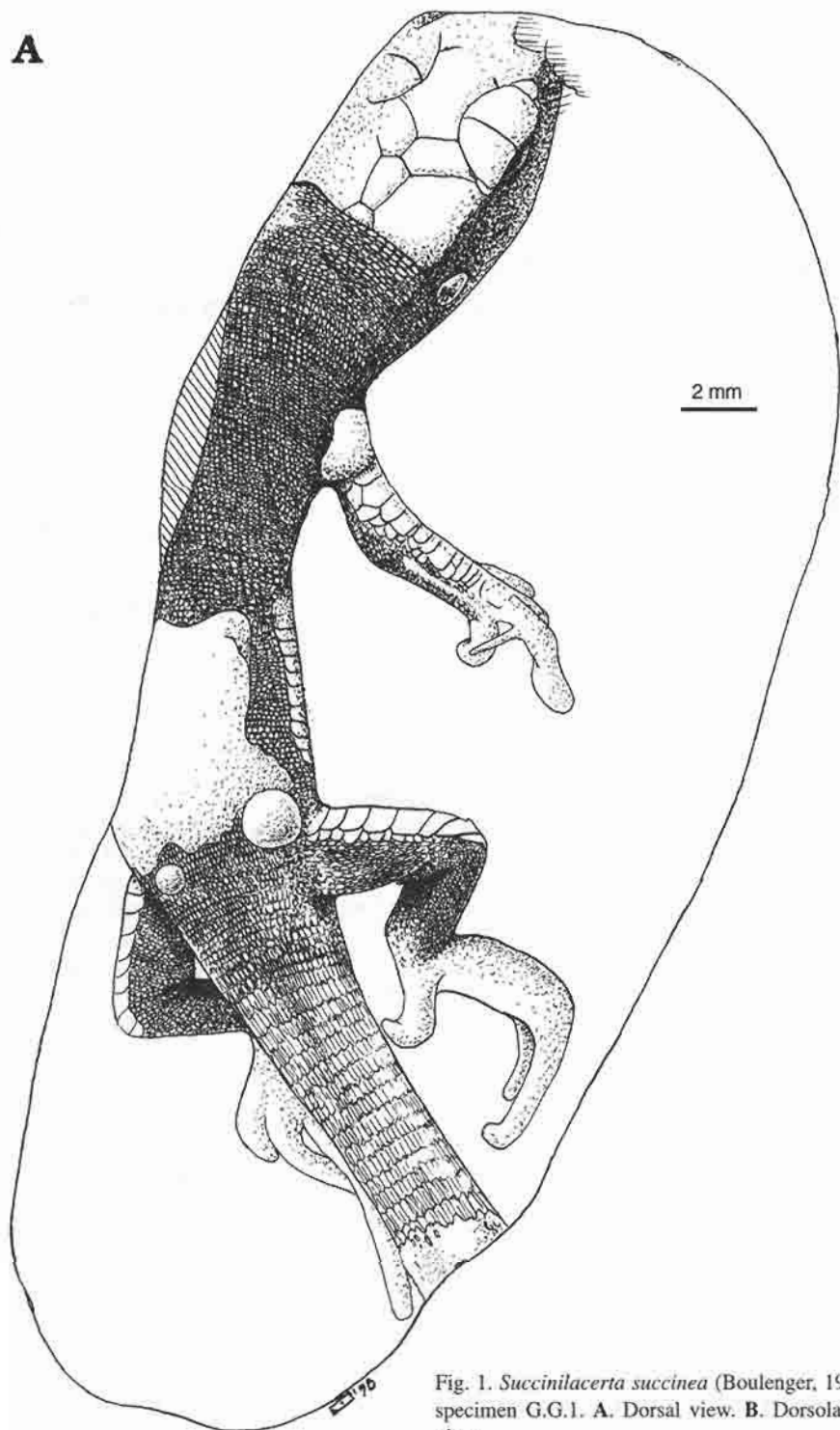


Fig. 1. *Succinilacerta succinea* (Boulenger, 1917), specimen G.G.1. A. Dorsal view. B. Dorsolateral view.



nounced recently (Böhme & Weitschat 1998). Baltic amber is a fossil resin occurring in those Paleogene deposits usually referred to as Blue Earth (Blaue Erde) and most abundant in Sambia. The Blue Earth, which is a glauconitic marine clayey sand, is now dated as latest Eocene (Kosmowska-Ceranowicz *et al.* 1997) or even earlier, middle Eocene (Lutetian after Ritzkowski 1997). So, the age of the inclusions in Baltic amber is estimated as about 40 MA.

Of the two more complete Baltic amber specimens, the first one was found in Sambia in 1891, and described by Klebs (1910) some 20 years later as *Nucras tessellata* (Smith, 1838), an extant African lacertid genus and species. Later on, it was assigned to a new species, *N. succinea* Boulenger, 1917. The specimen is housed in the Museum of Geology and Paleontology of the University in Göttingen, and has been redescribed by Böhme & Weitschat (1998, see also references therein and Ritzkowski in press), who assigned the species to a new genus *Succinilacerta* Böhme & Weitschat, 1998. According to these authors three other fragmentary specimens of lizards recently discovered from the Baltic amber are probably conspecific with *S. succinea*. Two of them, a partial body with posterior extremities, and a tail, both coming from Yantarnyj (= Palmnicken), were figured by Böhme & Weitschat (1998: pl. III: 1–3), while no information has been given on the third one. The present specimen is considered conspecific with the former Baltic amber specimens on the basis of distal finger scaling, and thus belongs to *Succinilacerta succinea* (Boulenger, 1917).

The specimen described herein was found by Mrs Gabriela Gierłowska in 1997 in Holocene beach sediments in Gdańsk-Stogi (about 1 km away from the shore), and belongs to her private collection. The piece of amber including the animal has been studied by means of infrared absorption spectrography (Kosmowska-Ceranowicz *et al.* 1997) to exclude forgery, and has displayed the IRS 468 curve typical of succinite of the Baltic amber.

Succinilacerta succinea is a representative of a lacertid clade that made its appearance about the late Paleocene according to Estes (1983). Still earlier, the pre-Tertiary origin of the clade is implied by the stratigraphic range of related groups (see discussion on p. 362).

According to Mayer & Benyr (1994), the extant lacertids (27 Old World lizard genera and 240 species) make up a monophyletic crown group Lacertidae rooted in the Oligocene. Though we realise that this date is hypothetical (Mayer & Benyr 1994: p. 628), we have tried to compare the data on fossil and extant lacertids with the Mayer & Benyr's (1994) hypothesis. The family Lacertidae Bonaparte, 1831 is here considered to include both crown and stem lacertids.

Most important references on the taxonomy of extant lacertids are papers by Boulenger (1920–1921), Arnold (1973, 1989), Bischoff (1990–1992), Darevsky (1967), and Mayer & Benyr (1994). Though the osteology of extant lizards has an abundant literature (Camp 1923, Estes *et al.* 1988 and references therein, as well as Klemmer 1957, and Arnold 1973, 1989 in the case of the Lacertidae) it is hardly applicable to a low level taxonomy. Many putative fossil lizards assigned to the genus *Lacerta* Linnaeus, 1758 on the basis of isolated bones, proved to be *nomina dubia*. The original materials of the late Oligocene *L. antiqua* Pomel, 1853, late Miocene *L. bifidentata* Lartet, 1851, and late Pliocene *L. crassidens* Gervais, 1859 have been inadequately described then lost (Estes *et al.* 1988). The name *L. eocena* Owen, 1884 was given to a fossil fish.

The studied lizard offers a state of preservation of the integument comparable to that of recent animals, but lacks any remains of the internal skeleton. On the other hand, the specimen is approximately synchronous with the earliest known fossil record of this lizard group. The pattern of scalation which is the primary taxonomic character in neoherpetology provides a direct basis for the familial affiliation of the lizards preserved as amber inclusions. This pattern is reflected by the underlying osteoderms, if they are present at all. The osteodermal covering which is preservable in fossil state, provides thus the first field of overlap of the two approaches, the paleo- and neoherpetological one. Unfortunately, lacertids lack body osteoderms, and thus, only the osteodermal skull covering remains to be compared. It may display the traces left by the scale covering of the dorsal surface of the head referred to as the pileus.

The second field of overlap of the two approaches is given by the shape of the whole body and that of its parts. Among others, the proportions of the extremities, and the number, length and shapes of the digits included, indicate the locomotory adaptation of the animal, and thus may bear on its generic and/or specific affiliation.

In herpetological literature, the pileus pattern has rarely been considered in detail in terms of morphocline polarity. Some features, but mostly those of the anterior pileus, were included in the osteological character analysis of lacertids by Arnold (1989: characters 8, 9, 11, 39–41, and 32–44). More broadly, the pileus pattern was analysed in the Cordyliformes (Lang 1991). In both cases, cladistic analysis using the PAUP programme was applied. The objective of the present paper is not to check existing cladograms of squamate relationships or to construct new ones, but just to propose the morphocline polarity of some pileus characters by comparing the data available from fossil and recent material with the best supported cladograms.

For the sake of brevity, the names of extant taxa referred to in the text are listed *in extenso* in the Appendix (p. 380) whereas authors' names and dates are usually omitted in the text.

Methods

The outgroup analysis of some characters of the posterior part of the lacertid pileus (preserved in the amber specimen) has been applied to infer their morphocline polarity according to cladistic methodology.

The best supported and most recent hypotheses of general relationships within squamates (Estes *et al.* 1988; Evans & Chure 1998) and of those within the lacertids (Mayer & Bischoff 1996) have been used as a basis for this analysis. The results have been combined with stratigraphic data on fossil lacertids and contrasted with the results of molecular data from the literature.

We follow Jefferies (1979) in his understanding of the terms 'crown group' and 'stem group'. The crown group as defined by this author contains 'the latest common ancestor of the living (we add: at a given moment of geological time) members of a monophyletic group, plus all descendants of this ancestor'. Stem groups are (usually) fossil taxa that share some but not all synapomorphies of the crown group. We find this concepts very useful while studying the problem of the taxonomic range of the Lacertidae.

Institutional abbreviations: G.G., The private collection of Mrs. Gabriela Gierłowska, Gdańsk, ul. Szara 9 m. 50; GPIK, Institut für Geologie und Paläontologie, Königsberg; KBUK, Königliche Bernsteinsammlung der Universität Königsberg; MGPU, Museum für Geologie und Paläontologie der Universität in Göttingen; MNHN, Muséum d'Histoire Naturelle, Paris; MZ, Museum of the Earth, Polish Academy of Sciences, Warsaw; ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw; ZFMK, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn; SMF, Senckenberg Museum, Frankfurt a.M.

Other abbreviations: s-v, snout-vent length; Rh index, relative head size index (= pileus to snout-vent length).

Systematic Part

Squamata Merrem, 1826

Scincomorpha Camp, 1923

Lacertidae Bonaparte, 1831

Succinilacerta Böhme & Weitschat, 1998

Succinilacerta succinea (Boulenger, 1917)

Emended generic and specific diagnosis. — Small lacertid. Estimated adult s-v length about 70 mm. Head robust. Pileus length is about 32% of s-v length. Parietal scales large without any traces of subdivision, not reaching the lateral edges of parietal table, bordered by three supratemporal scales, the second one much elongated. Temporal region covered by small scales. Tiny spindle-shaped intercalary scale squeezed between the frontoparietal and supraocular III, symmetrically on both sides. Dorsal body scales tiny, juxtaposed, unkeeled to slightly keeled. Six rows of almost rectangular and slightly imbricated belly scales. Sharp transition of dorsal scaling into true caudal whorls of elongated and keeled scales occurs at the distance of about 2/3 femur length from the sacrum. Some alternation in length of successive scale whorls in the proximal part of the tail. Digits provided with protruding subunguicular scales.

Note. — The genus is monotypic. A discrimination between specific and generic characters is impossible.

Material. — Five specimens have so far been discovered, all of them from the middle Eocene Baltic amber: (1) G.G.1, the specimen described herein from Gdańsk, Poland; (2) KBUK then GPIK, now MGPU 12664, from Sambia, Lithuania, the holotype; (3)–(5) three fragmentary specimens from Lithuania (Böhme & Weitschat 1998: pl. III: 1–3 and pp. 210, 211), private collections, no cat. numbers.

State of preservation. — The specimen G.G.1 is preserved almost whole (Figs 1, 2) except for the front part of the head (anterior to the orbit), the left side of the trunk along with the left anterior limb (except the hand), and the posterior part of the tail. The damage to the trunk resulted in washing out of the tissues, so that the fossil is almost empty. The colour of the specimen has not been preserved.

The amber is opaque in some regions, so that the left side of the head, the collar and anal regions, as well as a presacral part of the dorsum are obscured. Ovoid bodies situated on the dorsal surface of the limb bases are here interpreted as pockets of decay gas caught by amber. The distal parts of the extremities are also covered by a sort of 'gloves', that in some cases (Fig. 1A, B) include small fragments of plant detritus. This cover makes the digits thicker and obscures their structure. Still, it is

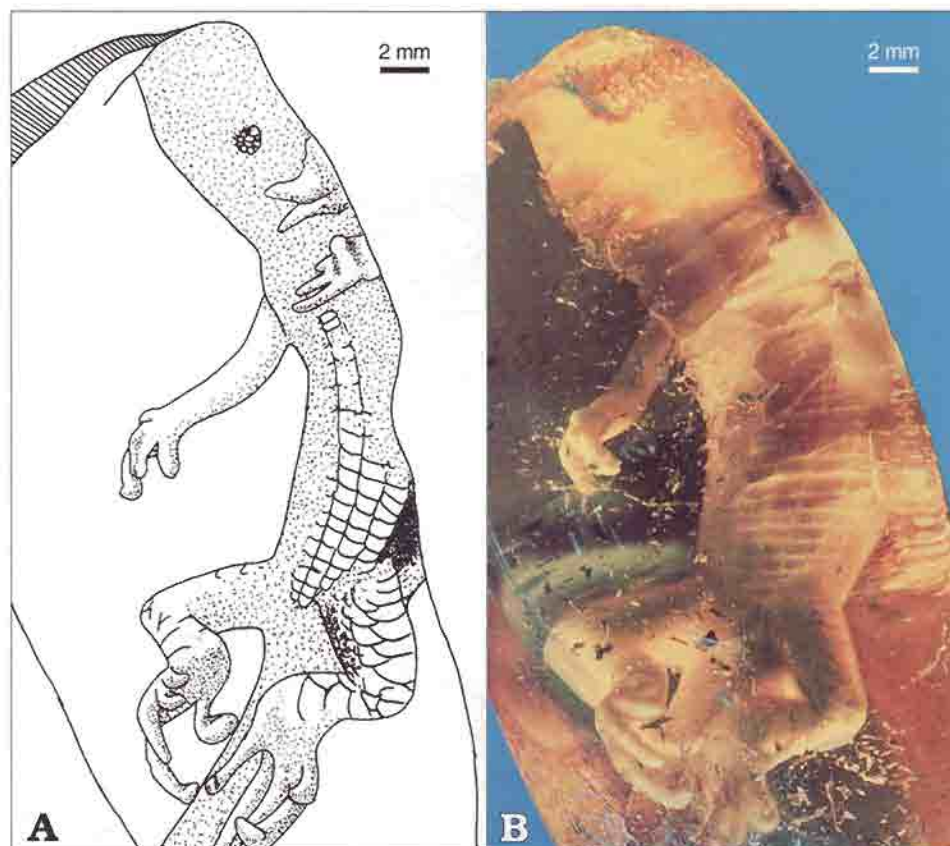


Fig. 2. *Succinilacerta succinea* (Boulenger, 1917), G.G.1. A. Slightly ventrolateral view. B. Ventral view.

slightly translucent at the very tips of the digits, thus allowing the reconstruction of the claw regions (Fig. 6A).

Description. — **Measurements:** The s-v length of specimen G.G.1 is about 27 mm, the head being almost one third of this length. The length of the tail, of which just a basal section (13 mm) is preserved, is not known. The head is stout and relatively short. Pileus width (6.7 mm) is $2/3$ of the estimated length. Posterior limbs are much stronger than the anterior ones. The estimated length of the posterior limbs (about 18 mm) attains 65% whereas that of the anterior ones (9.9 mm) is just 36% of the estimated s-v length.

Pileus: The preserved part of the pileus (Fig. 3A, B) is subrectangular in shape, the posterior width being equal to the orbital one (over the supraocular II). This shape results from the large posterior width of parietal scutes. This character along with a large size of frontoparietals, their long sagittal contact at the expense of the posterior part of the frontal, and their large posterior extension, is very much lacertid in pattern. Of the four pairs of supraocularia, the second and the third one reach approximately the size of the frontoparietals and produce an almost complete cover of the orbits. At both ends they are bordered by small supraoculars, the first and the fourth one respectively, and with a longitudinal series of tiny scutes along the outer margin. Two elongated supratemporal scutes, the first one three times longer than the second, follow the tiny scale bordering supraocular IV. The bordering of the pileus by small scutes adds to the lacertid character of the fossil. Posterior to the frontoparietals, there is a single interparietal (without any trace of a parietal foramen), and further back a

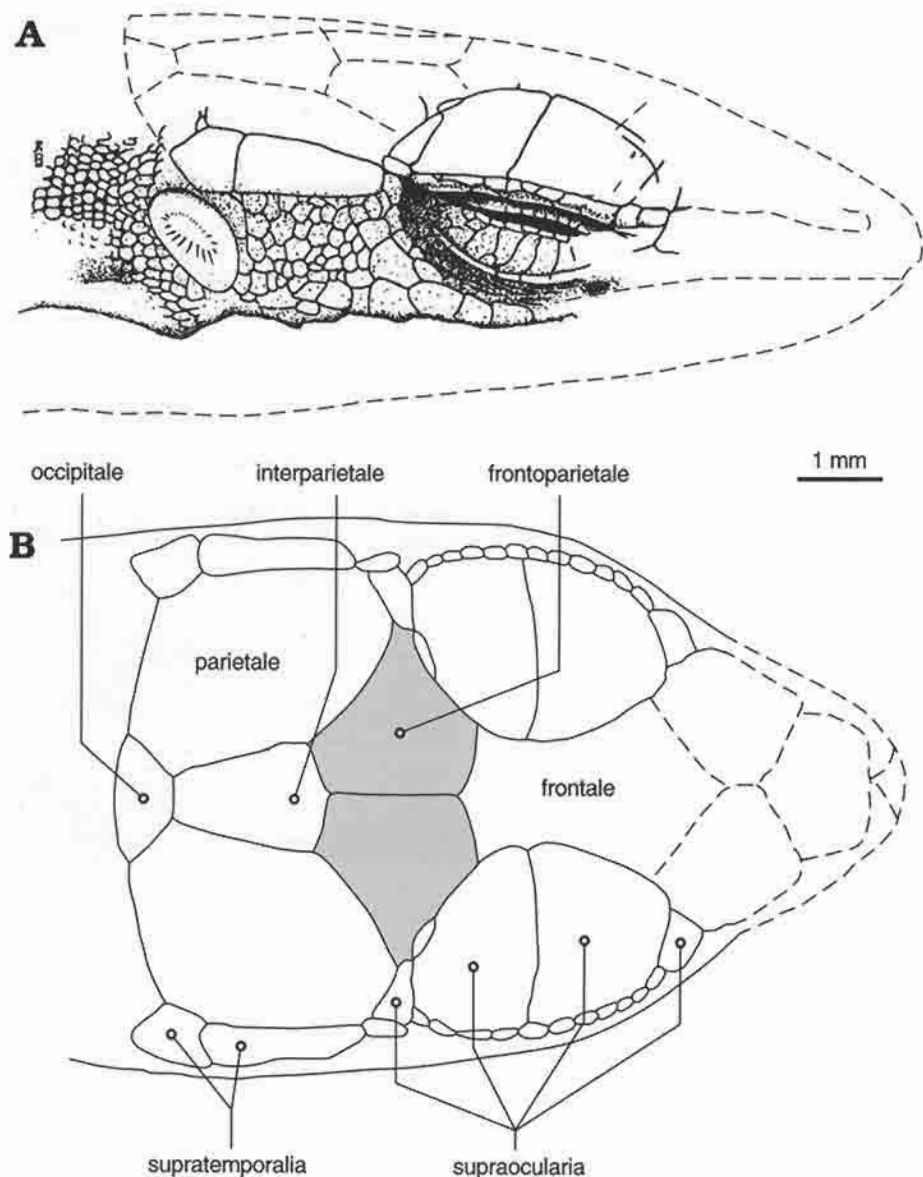


Fig. 3. *Succinilacerta succinea* (Boulenger, 1917), G.G.1. A. Orbit in lateral view. B. Pileus reconstruction in dorsal view. Frontoparietal scales are shaded.

single occipital separates the parietals from each other. Anterior to the frontoparietals, the frontal scute extends over the surface between the level of the posterior 1/4 of the orbits up to that of their anterior margins, but the very anterior extent of the frontal scute is unknown. The frontal scute is rather short and wide, constricted in the posterior half, while broadening slightly at the contact with the frontoparietals and more so anteriorly. Symmetrically at each side of the pileus, at the contact of the frontoparietal with the third supraocular, and touching the medial angle of the fourth, there is a tiny intercalary scute. The transition between the head and body scale covering is quite abrupt on the dorsal side of the fossil while being obscure ventrally. The contact line is straight and transverse.

Body: The body (Figs 1, 2) is subquadrangular in cross section. The squamation of the dorsum consists of tiny oval, or subhexagonal scales. In the anterior part of the body the scales are arranged in transverse rows, with their longer diameters perpendicular to the long axis of the body. Towards the rear the squamation changes into a longitudinal arrangement. The scales become slightly keeled, and subimbricate with the long axes parallel to that of the body. The transition between the dorsum and ventrum is abrupt. The latter is covered by six longitudinal rows of large, quadrangular, imbricate scales (the anterior scales overlapping the posterior ones in each row). The scales of the neighbouring rows do not alternate in position but are arranged in regular transverse zones. The gular region is preserved but obscured by a deep cover of amber. It is covered by numerous small scales and posteriorly limited by a gently serrated collar zone (Halsband). The overall structure resembles that of *Succinilacerta succinea* as figured by Böhme & Weitschat (1998: pl. III: 2), except for the size and number of scales contributing to the collar.

Tail: The preserved part of the tail (Figs 1, 2) is stout, subquadrangular in cross-section at the base and suboval at the end. A distinct furrow extends along the dorsum. The squamation of the anterior half of the preserved part is in continuation with that of the dorsal side of the body. Small subhexagonal, imbricate and keeled scales are arranged with their long axes parallel to that of the tail. They get gradually longer posteriad, but at about less than half the length of the preserved part of the tail (the distance equal to about 2/3 the length of the femur from the tail base) there is an abrupt increase in scale lengths. Posterior to this zone, the arrangement of the scales in verticils is quite distinct. The scales of the subsequent verticils do not form longitudinal rows, but alternate instead. The verticils of this part of the tail continue on the ventral side of the tail, but the cloacal region is obscured by the amber, and cannot be studied.

Extremities: The forelimbs (Fig. 4) are rather long and slim with the elbow joint very high and a long hand. The length of the forearm is about 1.5 that of the arm, and the length of the hand over the longest digit (IV) is almost the same as that of the forearm. The digits are long and cylindrical, the shortest of them, the first and the fifth one being subequal, the third one almost as long as the fourth one (which is almost the rule in lacertids), the second much shorter.

Large, imbricate crescent-shaped scutes cover the anterior and anterodorsal face of the limb down to the dorsal side of the carpus. Their sizes diminish at the level of the elbow joint and over the carpus. Posterior part of the forearm is covered by polygonal scales of an irregular pattern. Crescent-shaped scutes, similar but smaller than those of the proximal part of the limb, cover dorsal surfaces of the digits, extending over the lateral side of each digit, which is obscured by opaque amber.

The hind limbs (Figs 1, 5) are longer and stouter than the anterior ones, and the foot is much bigger than the hand. The extremities differ in proportions, the shin being obviously slightly shorter than the thigh. The length of the foot over the fourth digit seems to be much greater than that of the thigh. However, the exact measurements are difficult to take because of the inaccessibility of the measured parts and the flexed position of the digits. The fourth digit is much longer than the third one, the fifth one about the size of the second one, but opposed, the first one is the smallest. A position of the first digit in the left foot may show its great mobility or may be an artefact. Each digit bears a claw, which is embedded in a gas pocket interpreted herein as an artefact of preservation. As shown in transmitted light, the digit scale next to the ungual produces a bulb-shaped structure (Fig. 6A) that may be interpreted as a gutter-like ventral ungual scale on the basis of a comparison with *Takydromus* (Fig. 6E, F). Given that the amber specimen is not congeneric with *Takydromus*, this structure is considered convergent.

The anterior and dorsal faces of the hind limb bear crescent-shaped scutes of the same kind and of similar pattern to the forelimb. The sizes of the scutes decrease posteriad the change in size being quite abrupt on the lateral surface of the leg (Fig. 1A), and less so on its medial side (Fig. 5D). The small scutes of the posteriormost row of the medial surface of the thigh bear femoral pores, 14 (or 15) in number.

Individual age and body size. — The absolute size of G.G.1 does not help in determination of its ontogenetic age. With its s-v length of about 27 mm and a roughly estimated total length of no more than 60 mm, it matches the lower limit of variability range for many living lacertid species (e.g., *L. andreanszkyi*, some *Algyroides*, some *Psammodromus* according to Arnold 1973), and so it might be just an adult or semiadult of a small-sized lizard.

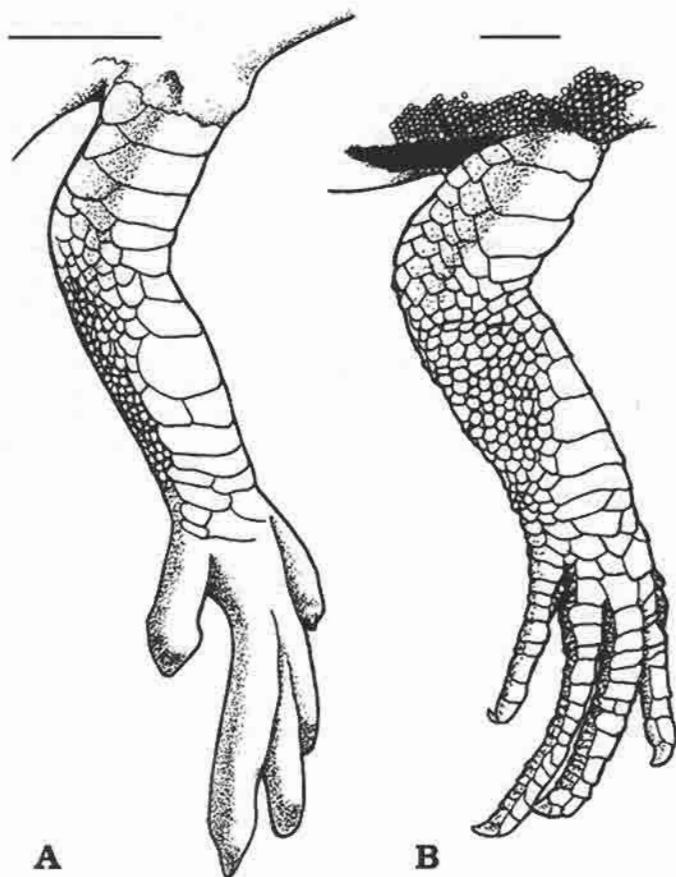


Fig. 4. A. *Succinilacerta succinea* (Boulenger, 1917), G.G.1. Right forelimb in lateral view. B. The same of *Podarcis pityusensis* (Bosca, 1883), ZPAL R-I/70. Recent. Scale bars 2 mm.

More conclusive are the head-to-body proportions. As demonstrated by e.g. Peters (1964: fig. 10), the dimensions of the head allometrically diminish during the early ontogeny, as do those of the extremities and the length of the tail, which agrees with our observations. Such a proportionally large head compared to body length as demonstrated by G.G.1 specimen (Rh index is 32%) is seldom among the extant adult scincormorphans, except for the cordyliforms in which case it may attain 31% (see Appendix). Among lacertids, this high value (36%) has been matched only in a juvenile *Algyroides*. When decidedly big-headed cordyliforms and short-headed lacertids (*Nucras*) are removed from the samples, the ranges of Rh for the studied lizards (see Appendix) are 20–27% for the adults and 21–36% for the youngsters. So even as a juvenile, the amber specimen belongs to a big-headed lizard.

Apart from head to body proportions (Fig. 1), the shortness of the postorbital part of the pileus (Figs 3, 7), with the stocky proportions of the frontoparietals and parietals, as well as the huge supraorbitals II and III, all testify to the juvenile age of the amber lizard.

Assuming that the amber specimen is actually a juvenile, the problem of adult length appears. Its estimated total length of 60 mm is much less than the value of over 100 mm given by Bischoff *et al.* (1984) for the total length of hatchlings of large-sized (about 60 cm) lacertids. Thus, we are most probably dealing with small lizards comparable to South European *Algyroides* species (s-v adult

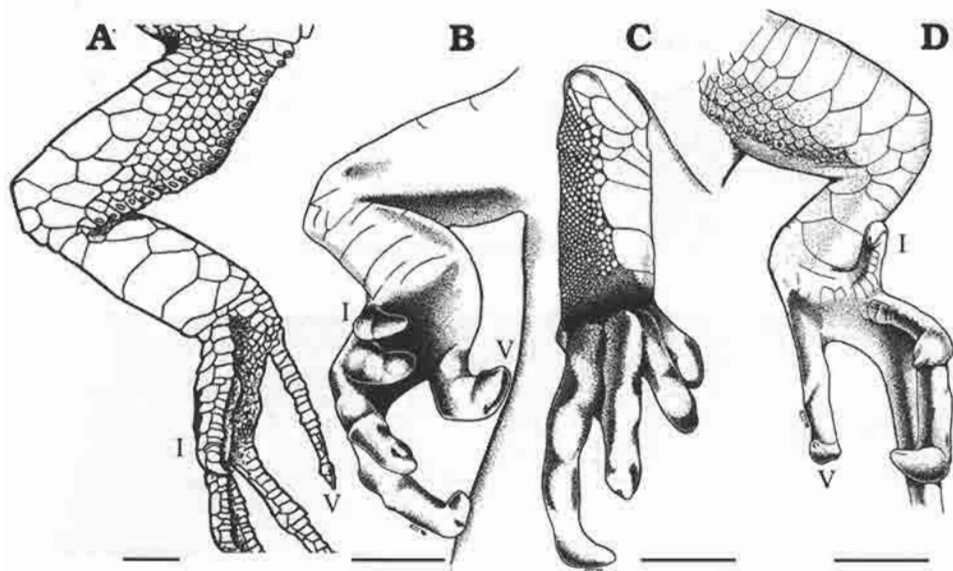


Fig. 5. A. *Podarcis pityusensis* (Bosca, 1883), ZPAL R-I/70. Recent. Right hind limb in ventral view. B–D. *Succinilacerta succinea* (Boulenger, 1917), G.G.1. B. Right hind limb in ventral view. C. Right foot and shin in dorsal view. D. Left hind limb in ventral view. Scale bars 2 mm.

length about 70 mm according to Arnold 1973) or with medium-sized lizards similar to European *Lacerta vivipara* and *Lacerta agilis* (at most 90 mm adult s-v length and about 170–180 mm total adult length according to Juszczyk's 1987 data).

Family level affiliation

All the preserved characters of the G.G.1 specimen remain within the variability range of the family Lacertidae. They are as follows: the pattern of the skull table scalation (pileus), the sharp transition of the latter into the body scalation as well as the pattern of scale covering of the extremities and tail. This indicates that the specimen is a crown-group lacertid or belongs to a clade including it. The first possibility is preferred here and will be discussed below.

Generic and specific affiliation

The non-amber Eocene lizards related to lacertids, the genera *Plesiolacerta* Hoffstetter, 1942 and *Eolacerta* Nöth, 1940, grew to large size. As estimated on the basis of Estes (1983: fig. 24B), the total length of the representatives of *P. lydekkeri* Hoffstetter, 1942 was about 360 mm (130 mm of s-v length). The complete skeleton of *Eolacerta robusta* Nöth, 1940 from the Middle Eocene of Geiseltal is about 650 mm in total length, 240 mm being the s-v length (Nöth 1940). Some other smaller forms have been collected but not yet described (Schaal & Ziegler 1988). The Oligocene durophagous

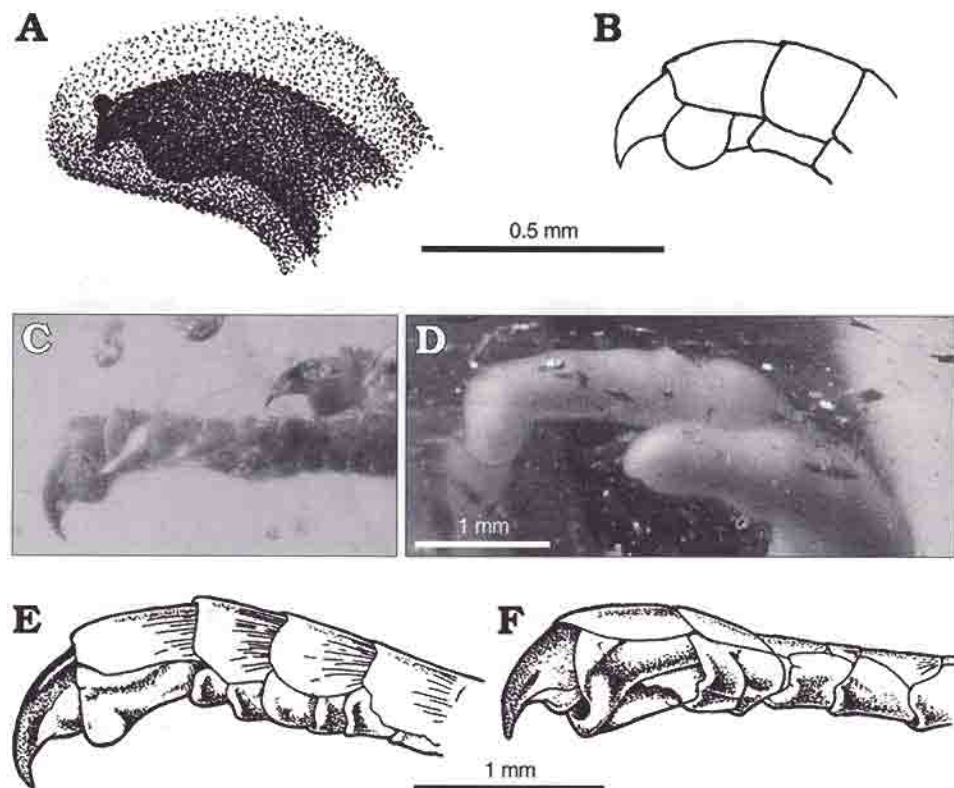


Fig. 6. Posterior limb claw structure. A–D. *Succinilacerta succinea* (Boulenger, 1917), G.G.1. A. Distal extremity of the digit IV of the right foot as seen in transmitted light. B. Reconstruction of the unguis scales of the digit IV from Böhme & Weitschat (1998: fig. 1a). C. Distal toe structure of the left foot of the specimen illustrated in Böhme & Weitschat (1998: pl. III: 1, 2 without scale). D. Digits III and IV of the right foot. E, F. *Takydromus sexlineatus* Daudin, 1802, ZPAL R-1/71. Recent. Claw and scale pattern of the digit IV in lateral (E) and anterolateral (F) view.

(amblyodont) forms with heavy jaws and probably correspondingly heavy skulls belonging to the genera *Dracaenosaurus* Pomel, 1846 and *Pseudeumeces* Hoffstetter, 1944 (Rage & Augé 1993) are estimated to have been about 120 mm and 180 mm in s-v length respectively. The congenerity of the present specimen with any of these Paleogene lizards is excluded.

Of greater value is a comparison between G.G.1 and *Succinilacerta succinea* (Boulenger, 1917) a lacertid already described from the Baltic amber. Three new specimens assigned recently to this specimen are fragmentary but to some extent complementary to the holotype (Böhme & Weitschat 1998).

The total length of the holotype first given by Andree (1937) amounts to 42 mm without the tail tip. It is of the same order of size as that of the present specimen (27 mm estimated s-v length + about 13 mm for the preserved tail fragment). The size differences between the specimens (Böhme & Weitschat 1998: Addendum p. 12) have

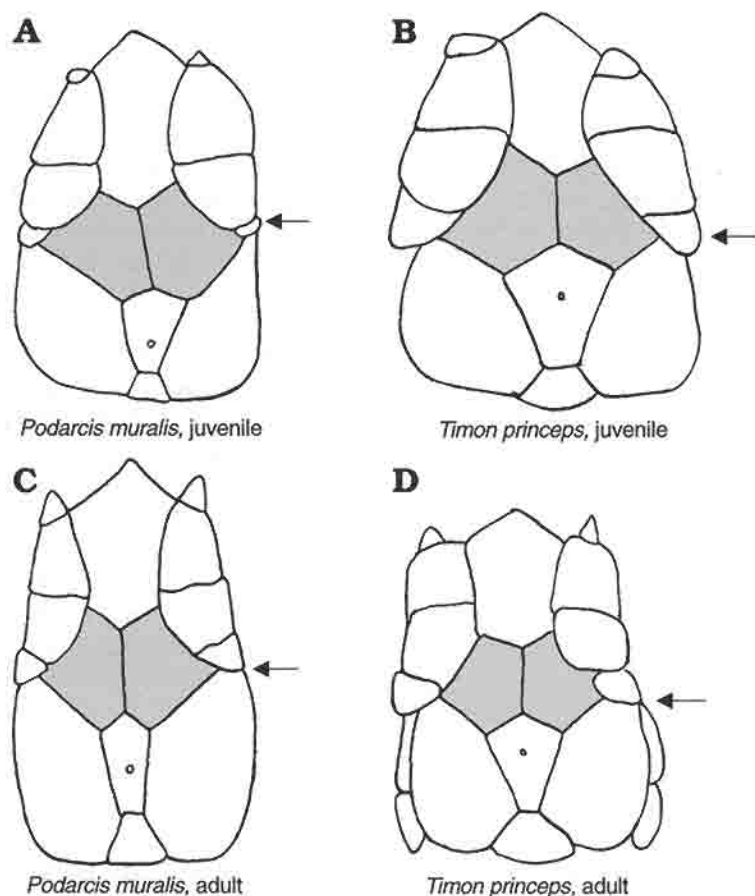


Fig. 7. Postembryonic development of the pileus of lacertids. **A, B.** Juveniles. **C, D.** Adults. **A** – ZFMK 4188, **B** – ZFMK 42723, **C** – ZFMK 584, **D** – ZFMK 4274. All Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture. Out of scale.

been overestimated. Also the difference described in the tail scaling is. All the specimens, those described by Böhme & Weitschat (1998: pl. III: 1–3; see also Weitschat & Wichard 1988) and the present one, display a slight alternation of longer and shorter whorls (inspection of the earlier specimens by W.B.). The unique scalation of the toe tips, present in the holotype of *Succinilacerta succinea*, is also present in the specimen G.G.1. Though each toe is covered by a gas-bulb, the structure may be studied by shining a light through the translucent bulb (Fig. 6A, D). Posteroventral to the claw the ventral border of the scale next to it protrudes ventrally, recalling the ventrally protruding scale, bulbous in lateral view, unique of *Succinilacerta* studied by Böhme & Weitschat (1998), and reminiscent of gutter-like scale of *Takydromus sexlineatus* Daudin, 1802 (Fig. 6E, F). On this basis, congenerity of the studied specimen (G.G.1) with those described earlier, is here proposed. The conspecificity also seems most probable, because of the same stratigraphic and biogeographic provenience of all the specimens.

Discussion

Lacertidae are a successful extant Old World lizard family widespread in Europe, Asia and Africa represented by 240 species (Arnold 1989). Whereas the criteria of species level (mainly minute scutellation characters including colour pattern, and adaptations to some narrow ecological niches + interbreeding possibilities) are more or less clear, the problem of interrelationships of species, i.e. of their grouping into the higher level taxa representing monophyletic groups is more difficult. We are dealing with the adaptative radiation of a group with a very consistent and successful morphotype. The small variability range of the latter facilitates the repeated evolution of novelties eventually resulting in a high frequency of parallelisms. This complicates the use of morphological criteria in phylogenetic analysis. The novelties that allow for further success of the evolutionary lines having them, are probably those of physiology and behaviour (e.g., sound communication in Gallotinae according to Mayer & Bischoff 1996) rather than morphology. Vicariance phenomena may also contribute. This is why the traditional grouping of lacertid species into genera by Boulenger (1920–1921), and more recently by Arnold (1989), does not quite correspond to phylogenetic relationships within the family given by immunological distance analysis (Mayer & Benyr 1994), the results of which are by itself just tentative (see Fig. 9).

The fossil record of the Lacertidae begins about the early Eocene with representatives of the genus *Plesiolacerta* Hoffstetter, 1942, from the locality of Dormaal, Belgium (Hecht & Hoffstetter 1962; Augé 1990). In the Eocene, the single species *P. lydekkeri* Hoffstetter, 1942 was widely distributed in Europe (the Upper Eocene of Lower Headon Beds, Hordle, England; the Upper Eocene Phosphorites du Quercy, France). According to Augé (1988), the genus did not survive the Eocene–Oligocene boundary. Some other possible lacertids from the Middle Eocene Messel locality (Germany) have been recognized but not yet described (Schaal & Ziegler 1988). *Eolacerta robusta* Nöth, 1940 from the Middle Eocene of Geiseltal (Germany), originally assigned to the Lacertidae (Nöth 1940; Haubold 1977), turned to be a representative of the stem non-teioid scincomorphans (?scincoid relative according to Müller 1998). Two genera of amblyodont lacertids *Dracaenosaurus* Pomel, 1846, and *Pseudeumeces* Hoffstetter, 1944 from France, have been recorded in the Middle and Upper Oligocene (Rage 1987; Rage & Augé 1993). The Eocene lacertid from the Baltic amber, *Succinilacerta succinea* (Boulenger, 1917), supplements the list. Remains attributable to the genus *Lacerta*, but not really determinable in terms of neoherpetological taxonomy, appear first in the Oligocene (*L. filholi*, see Augé 1988).

Plesiolacerta? paleocenica Kuhn, 1940 and *Pseudeumeces? wahlbeckensis* Kuhn, 1940 from the Upper Paleocene of Wahlbeck (Germany) have been questionably referred to the lacertids by Estes (1983, see also Rage & Augé 1993).

Two cladistic approaches to relationships amongst squamates by Estes *et al.* (1988) and by Evans & Chure (1998) suggest an early date of appearance of the Lacertidae. According to Estes' *et al.* (1988) phylogenetic hypothesis, as supplemented by a new affiliation of the early Cretaceous *Meyasaurus* Vidal, 1915, (quite recently shifted from the early autarchoglossan to the early teioid position, see Evans & Barbadillo 1997), this date may be the late Jurassic (see Fig. 8A). A still earlier middle Jurassic date seems to be suggested by the Evans & Chures' (1998) cladogram, the earliest

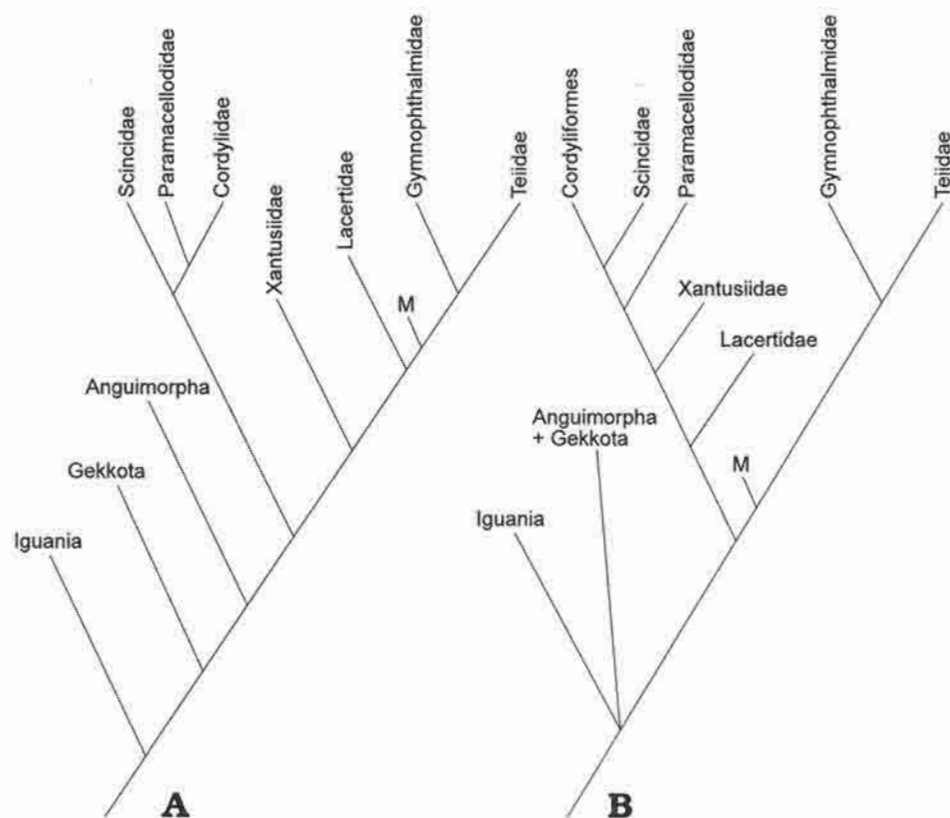


Fig. 8. Cladograms of squamate relationships. **A.** According to Estes *et al.* (1988: fig. 6) with Paramacellodidae and *Meyasaurus* Vidal, 1915 (M) added. **B.** According to Evans & Chure (1998: fig. 4).

paramacellodid record being late Jurassic in age (Fig 8B). In a possible contrast is a conclusion from the studies on immunological distances among extant lacertid genera (Mayer & Benyr 1994) combined with the molecular clock methodology (Kimura 1982). A chronologically scaled dendrogram (Mayer & Bischoff 1996, Fig. 9) indicates the date of appearance of the common lacertid ancestor not earlier than the Oligocene. A direct implication of this hypothesis is that the Paleogene, and possible earlier lacertids (to be discovered) do not belong to this very clade, but instead are its immediate out-groups contributing to a more inclusive clade. The phylogenetic picture that appears suggests we are dealing with an early radiation that produced several lines of a primitive lacertid grade. A purely taxonomic conclusion is a discrimination between two hierarchical groups: the Lacertidae *sensu stricto* or the crown lacertids, and the more inclusive Lacertidae *sensu lato* (regarded herein as a synonym of the family Lacertidae Bonaparte, 1931), including the pre-Oligocene stem lacertids in addition (the term lacertoids has been preoccupied by Camp 1923, and then by Estes *et al.* 1988, this time for a group including lacertids, teioids and xantusiids). If this is true, no pre-Oligocene lacertid should be considered congeneric with those belonging to the crown-group, although one of them may be a strict crown-group ancestor.

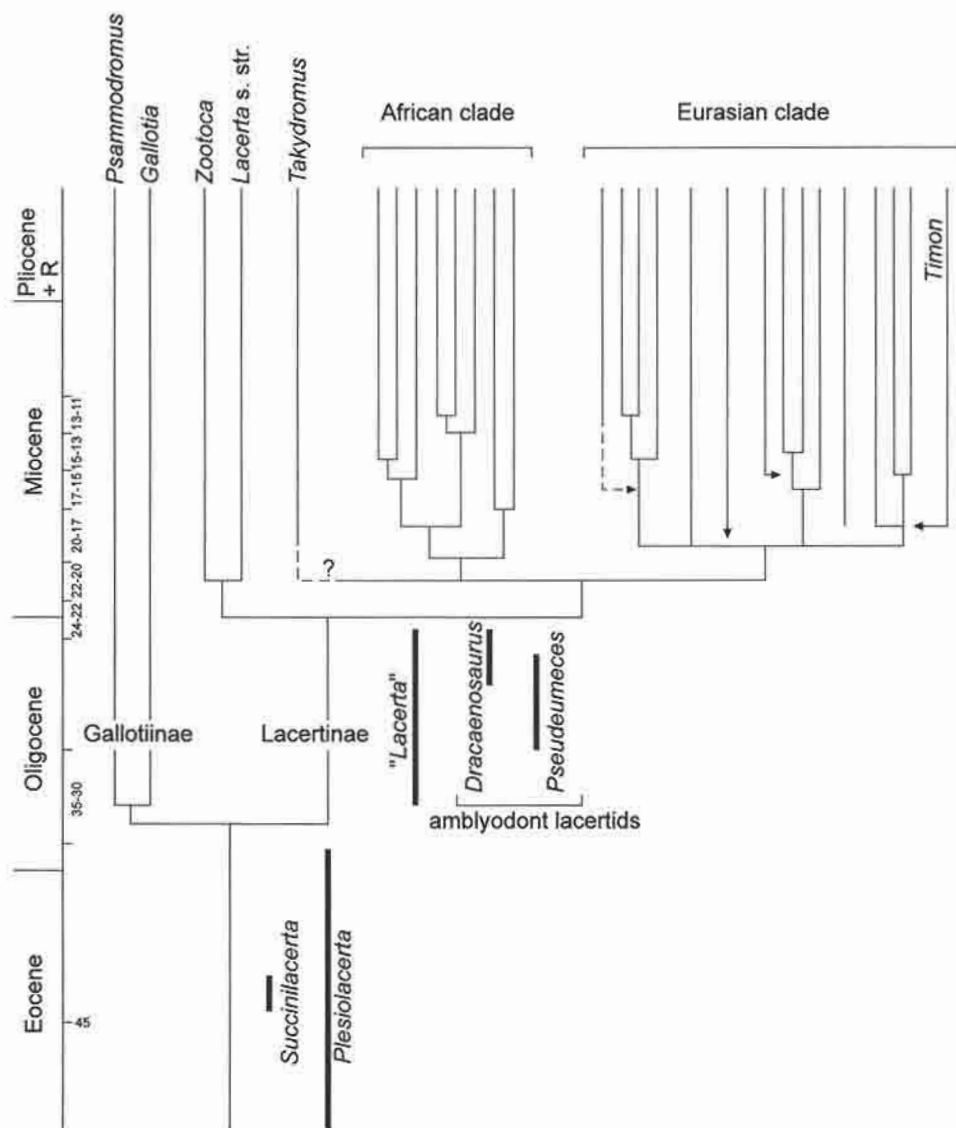


Fig. 9. Dendrogram of the lacertid relationships based on Mayer & Bischoff (1996: fig. 2), modified.

With the Eocene fossils at hand, it is clear that the so called lacertid morphotype is older than the possible Oligocene ancestor of the crown lacertids itself hypothesised by Mayer & Benyr (1994). These fossils included into the out-group analysis of lacertid morphology as immediate out-groups, may shed some light on the order of appearance of the remaining characters of the lacertid morphotype. However, more conclusive is a combination of the immediate out-group analysis with a large scale analysis (including all the important squamate branches). As stated in the Introduction, the analysis is reduced to the characters preservable in the amber inclusions, and mainly to those of the pileus.

Analysis of some characters (1–6) of pileus and body scaling (7) pattern characteristic of modern Lacertidae

(1) Frontoparietal scales having long sagittal contact extending forward at the expense of the unpaired frontal scale up to at least a posterior one third of the orbit length. (Figs 3B, 10A, B). This character is probably more ancient than the family itself.

(2) Four supraoculars, the second and the third one much larger than the two terminal ones (I and IV) (Figs 3B, 10A).

(3) Central position of both the parietal foramen and interparietal scale on the parietal table, posterior to the anterior reach of parietal scales; a complementary large posterior extent of the frontoparietals, over the fronto-parietal suture, is equally typical of the lacertid pattern (Figs 3B, 11A).

(4) Large subquadrangular to roughly ovoid parietal scales extending from the level of the frontoparietal suture to the posterior margin of the pileus (Figs 3B, 11A) – the lateral extent is subjected to variability as shown by Arnold (1973, 1989)

(5) Consistent pattern of the pileus beginning at an early stage of ontogeny.

(6) Occipital scale separating the parietal scales at the posterior margin of the pileus (Figs 3B, 11A).

(7) An abrupt transition from the large pileus scaling to small body scales, usually and primarily arranged in tessellated pattern.

(1) This character state is shared by most teiids, cordyliforms (*sensu* Lang 1991) and scincids (see Figs 10, 11), and absent from the out-groups of the Scincomorpha. It might thus be considered a scincomorphan synapomorphy under the assumption that it has secondarily changed in some specialized scincids and some gymnophthalmids (scale fusion in hard ground burrowers, possibly in connection with subterranean life, Friederich 1978: p. 22) and in xantusiids (in various directions and without clear functional significance, Friederich 1978: pp. 10–11).

A typical interfrontoparietal suture is present in the Late Cretaceous possible xantusiid sister-group the genus *Eoxanta* Borsuk-Białynicka, 1988, and in the earliest representative of lacertoid stem (*sensu* Estes *et al.* 1988) *Globaura venusta* Borsuk-Białynicka, 1988 (Borsuk-Białynicka 1988).

The presence of the long interfrontoparietal suture is associated with a posterior position of both the parietal foramen and interparietal scale in extant lacertids. However, it should be kept in mind that the shape of the interparietal is more variable than the position of the foramen itself. In some lizards, the scale may increase in length anteriorly to touch the suture, or even further forward than that (as e.g. in *Cordylus cataphractus* SMF 73659, or *Diploglossus costatus*, fig. 29 in Friederich 1978), a feature which obscures the main evolutionary trend.

(2) The four pair pattern of the supraoculars is very consistent within the lacertids but not so in the other Scincomorpha. Within the last named group, it is shared by most cordyliforms, some scincids (e.g. *Chalcides ocellatus* SMF. 68808, but not in *Eumeces* Fig. 10E), some teioids (e.g. *Proctoporus striatus* SFM.333, but not in *Calloplites*

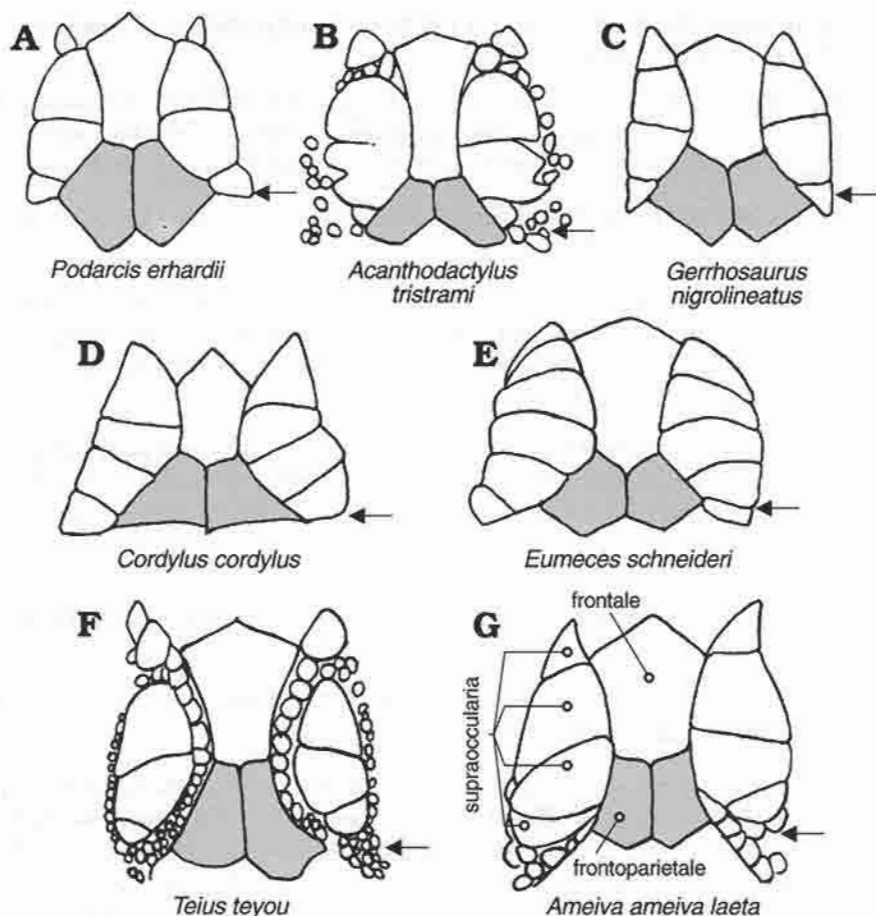


Fig. 10. Interorbital part of the pileus in lacertids: **A** – ZFMK 25093, **B** – ZFMK 44347; gerrhosaurids: **C** – ZFMK 6122a; cordylids: **D** – SMF 82540; scincids: **E** – SMF 56840; teiids: **F** – SMF 26642, **G** – ZFMK 29995. All Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the frontoparietal suture. Out of scale.

Fig. 12A), and by some xantusiids (*Cricosaura* see Friederich 1978: fig. 7) while being absent from the out-groups of the Scincomorpha (the regular pattern of five supraoculars in the anguids is here considered homoplastic). In teiids the fourth supraocular seems to develop from the postero-lateral corner of the third one (Fig. 10G but not in 10F). Posterior to it a narrow space is filled up by a mosaic of small scales. The small scales continue along the external margin of the supraoculars and supratemporals (Fig. 10F). The first supraocular is, too, often represented by several units. A fragmentation of the second and the third supraocular is rare, and homology of these scales within the scincomorphan group is most probable.

A possibility that the four pair pattern of supraoculars is synapomorphic for a group more inclusive than the lacertids, requires numerous reversals. Rather the teiid pattern (two supraoculars + anterior and posterior mosaic) is a point of issue for the Scincomorpha. This is consistent with a position of teioids in the Evans & Chure's

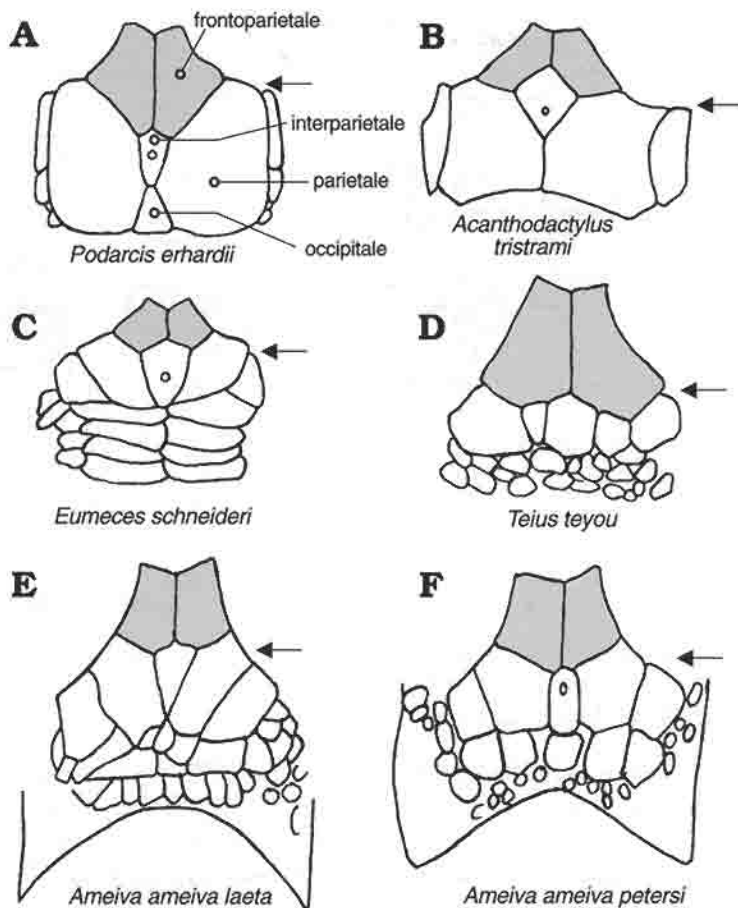


Fig. 11. Parietal part of pileus in lacertids: A – ZFMK 25093, B – ZFMK 44347; scincids: C – SMF 56840; teiids: D – SMF 26642, E – ZFMK 29995, F – ZFMK 38297. All Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture. Out of scale.

(1998) cladogram rather than with that in Estes *et al.* (1988) (Fig. 8A, B). Two pairs of supraocular (II and III) are most probably synapomorphic for the Scincomorpha. The supraocular I and IV may have evolved in parallel within different scincomorphan lines including the lacertids. They may be synapomorphic for the latter group.

Fragmentation of supraocular I and IV, which occurs in *Acanthodactylus* (Fig. 10B), is considered a reversal, one of the elements of a 'new look' of pileus of this derived (Mayer & Benyr 1994) genus.

(3) The position of the interparietal scale is roughly associated with that of the parietal foramen around which this scale develops. It is also associated with the position of the frontoparietal scales adjoining the interparietal scale anteriorly. The larger the posterior overlap of the frontoparietal scales on the parietal table, the more posterior the position of the interparietal scale with the parietal foramen on it.

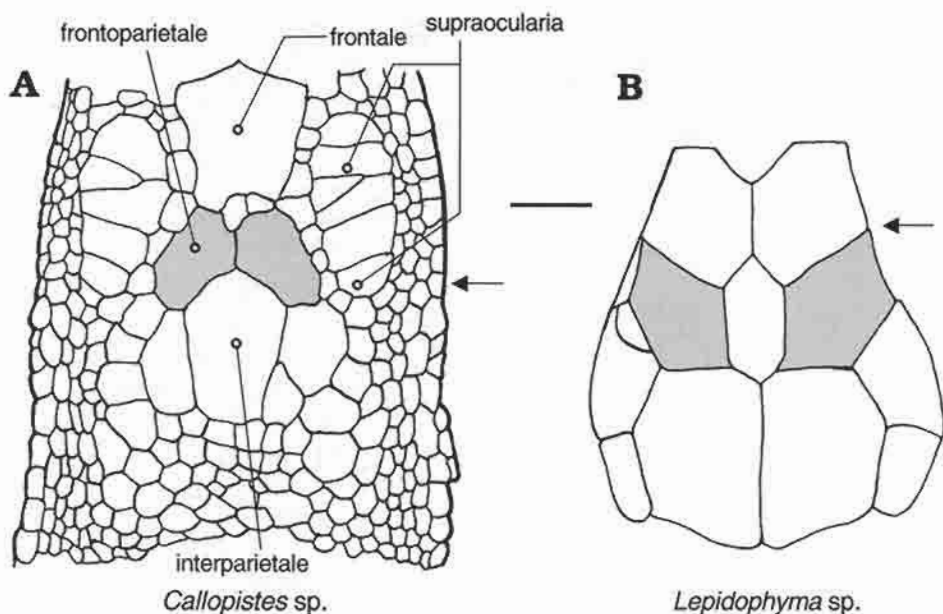


Fig. 12. Parietal part of pileus. A. *Callopiastes* (a teiid). B. *Lepidophyma* (a xantusiid); both after Friederich 1978: figs 15 and 6 respectively. Both Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture. Scale bar 3 mm.

Typical of the lacertids is the large posterior extent of the frontoparietal (Figs 3A, 7, 10A, 11A). It is approached by some gerrhosaurids (e.g., Fig. 13D) and some scincids (Fig. 10E), but unknown outside the Scincomorpha, and is thus a possible novelty of the Lacertidae or of a more inclusive scincomorphan group. In the origin of this group, we must envisage an evolutionary process causing a posterior shift of the parietal foramen + interparietal scale, associated with a complementary posterior growth of the frontoparietal scales. However, according to Estes *et al.* (1988), the position of the foramen within the middle part of the parietal, clear of the fronto-parietal suture, is primitive in squamates. Consequently, the central position of the interparietal scale on the parietal table consistent in the lacertids and common in the non-teioid scincomorphans is plesiomorphic rather than derived according to these authors (Estes *et al.* 1988).

A morphocline polarity of this character implicit in the cladogram of Evans & Chure (1998: fig. 4) may be interpreted in a different sense. According to this cladogram (Fig. 8B) the teioids make up an early scincomorphan offshoot (instead of the most derived group of lacertoids), and their character states may thus be primitive for the Scincomorpha. The teiid position of the parietal foramen and interparietal scale, close to the fronto-parietal suture and subjected to variability (Figs 11D–F, 12A, 14) may be thus an ancestral scincomorphan state. This hypothesis is consistent with the anterior position of the parietal foramen in the primitive autarchoglossans: the anguimorphans (e.g., upper Jurassic *Dorsetisaurus* Hoffstetter, 1967, middle Jurassic to lower Cretaceous *Parviraptor* Evans, 1994, and late Cretaceous *Gobiderma* Borsuk-Bialynicka, 1984), and the primitive, middle Eocene non-teioid scincomorphan

(*Eolacerta* Nöth, 1940), as well as in a stem-teiidoid, the early Cretaceous *Meyasaurus* Vidal, 1915).

Estes *et al.* (1988: p. 148) assumed the short parietal table and long supratemporal processes to be primitive in squamates. According to these authors, the long parietals and short supratemporal processes found in lacertids, xantusiids and cordylids, as well as in xenosaurids 'appear to have been separately derived by the deposit of secondary bone'. According to a scenario proposed herein, we are dealing with allometric growth of the parietals in phylogeny, mainly posteriad, to roof the angle between the supratemporal processes, and not affecting the underlying brain. This growth was associated with a relative anterior shift of the parietal foramen on the parietal table. The typical central position of the foramen in the lacertids is here considered a compensatory reversal. The posterior shift of the foramen that must have occurred in the evolution of this lizard group was obviously followed by the frontoparietal scales. Hence, the large overlap of these scales on the frontoparietal suture (Figs 3, 10A) which is quite consistent within the lacertids and unique for them is here considered synapomorphic for the family, along with the central position of the parietal foramen.

(4) Large, roughly subquadrangular parietal scales occur in the lacertids, cordyliforms and xantusiids, each of these groups displaying a pattern of its own. The large scales of this type evolve if directly underlain by flat dermal bones. If the roofing bones are deep under the skin surface or they are missing at all (the case of the unroofed supratemporal fenestra and an unroofed angle between supratemporal processes), the small scale pattern develops rather than large scales. This mechanical dependence on craniological characters suggests the possibility of parallel development of scaling pattern.

The association of scale pattern with craniological characters is best shown in the Cordyliformes. The Gerrhosauridae, one of the constituent families of the latter group (Fig. 13B, D), have short parietals and short anterior parietal scales on them, whereas the second family, the Cordylidae (Fig. 13A, C) have the angle between supratemporal processes wholly roofed and the posterior parietal scales developed on this roof.

The short pileus of the scincids resembles the medial parietal part of that of the teiids in its oblique posterolateral margins. It corresponds to a flat central surface of the parietal bone (Fig. 11C), and may be the oldest part of the posterior pileus whereas the postero-lateral parts are more recent additions. This postero-lateral zone of the pileus is extremely variable in teiids, in both taxonomic (Figs 11D-F, 12A) and ontogenetic terms (Fig. 14). Most common is a presence of an outer parietal scale contacting the main parietal along the oblique line (compare Figs 11E and 14E with Fig. 11C) as well as transverse division of parietal region scales (Figs 11E, 14D, F). A mosaic of scales, variable in size, covers as a rule the posterior, posterolateral and lateral regions of the head. The size of the parietal scales variates from quite small (Fig. 14D) through middle-sized (Fig. 14E) to rather big (Fig. 14F). The interparietal relatively decreases in size in ontogeny (Fig. 14).

(5) The posterior pileus pattern is quite consistent within the Lacertidae, including the juveniles (Fig. 7), and unique among the lizards. It demonstrates that a strict genetic control operating from an early stage of ontogeny has been developed in this family.

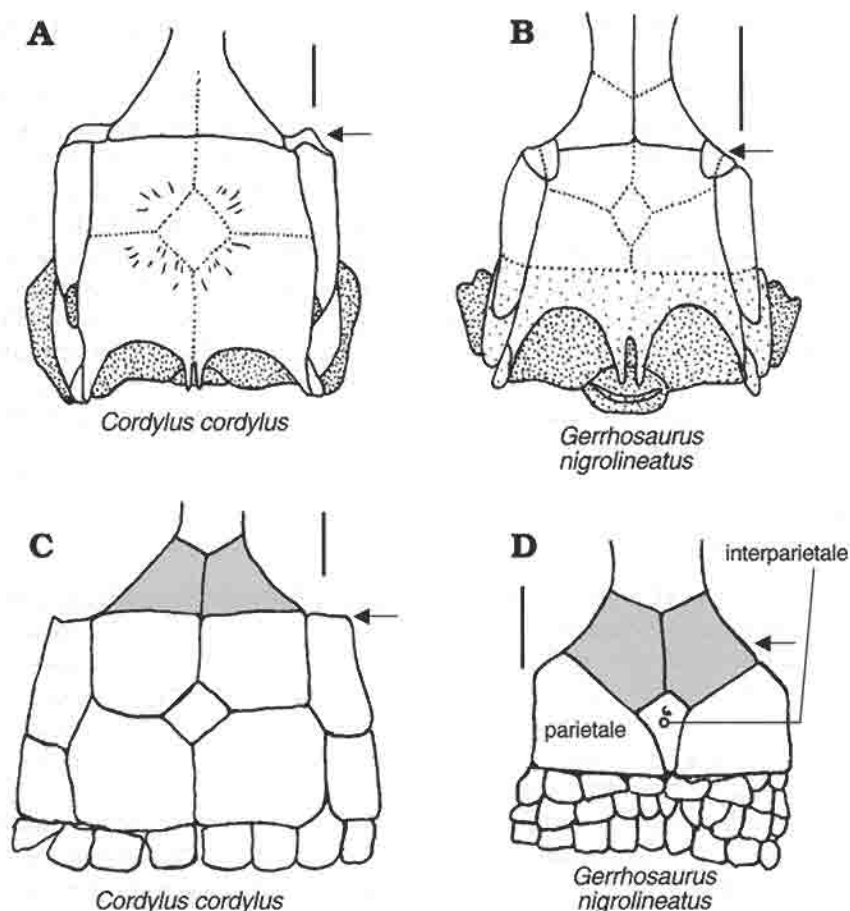


Fig. 13. A, B. Parietal part of skull in Cordyliformes. After Lang (1991: figs 21A and 30 respectively). C, D. Parietal part of the pileus in Cordyliformes: C – SMF 8251, D – ZFMK 6122a. A, C. Cordylidae. B, D. Gerrhosauridae. All Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture. Scale bars 3 mm.

This control is considered synapomorphic for the crown-group lacertids along with the posterior pileus pattern that results.

The lack of any strict genetic control of the posterior pileus pattern characteristic of teiids is probably plesiomorphic, which is consistent with their position in the cladogram shown in Fig. 8B rather than 8A.

(6) The absence of an occipital scale is almost the rule in non-lacertid scinciforms. According to Lang (1991), the occipital is rarely and randomly present in cordyliforms and in teioids as a derived character state of a lower taxonomic level. In contrast, the presence of the occipital, wedged in between the parietals, is the rule in lacertids, and it is considered synapomorphic for this clade. Its absence (*Acanthodactylus*, Fig. 11B, *Eremias*, and occasionally in *Psammodromus*) is consequently considered secondary.

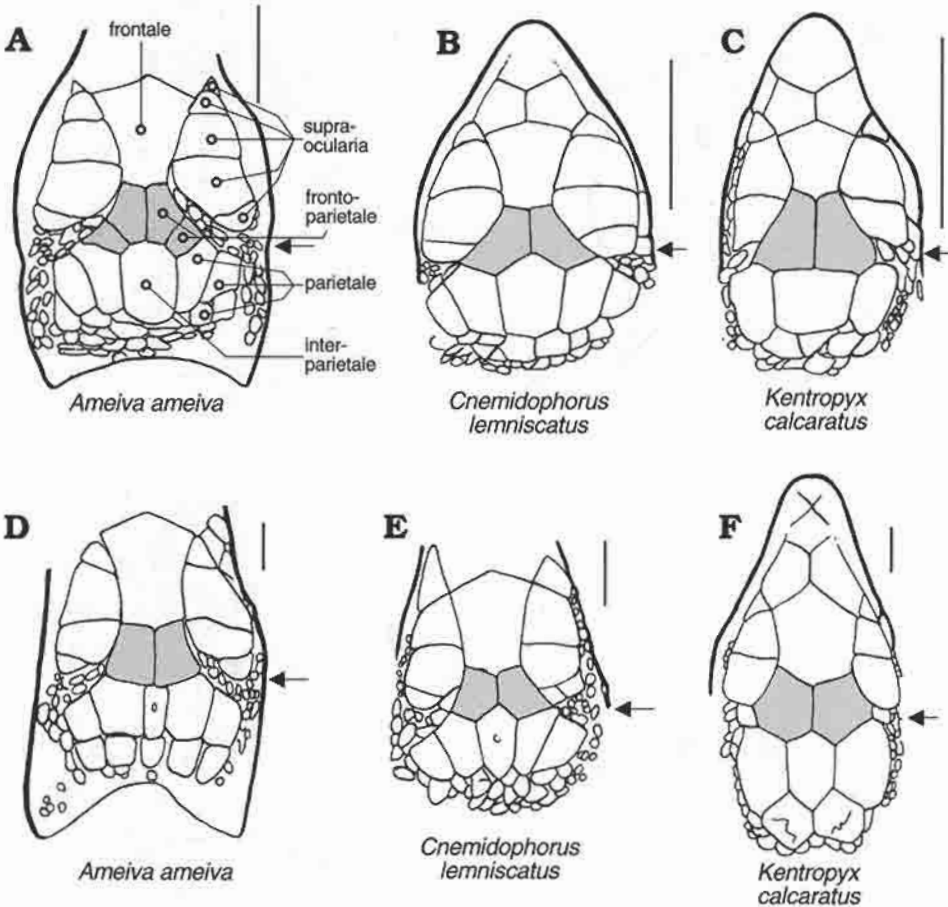


Fig. 14. Postembryonic development of the pileus in teiids. A – SMF 66826, B – SMF 11731, C – ZFMK 33339, D – SMF 38297, E – ZFMK 59577, F – ZFMK 5341. A–C. Juveniles. D–F. Adults. All Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture. Scale bars 3 mm.

The size and shape of this scale and its relations with respect to the interparietal vary to a certain extent at a generic level. Still, a similarity between *Plesiolacerta* and the stem-teioid *Meyasaurus* (Richter 1994: fig. 11) in the huge size and high triangular (or trapezoidal) shape of the occipital scale (Fig. 15B, C) suggests that this shape is a plesiomorphic state in lacertids. It may result from the simplest way of filling up a triangular space between the primitively long supratemporal processes (see p. 369).

(7) An abrupt transition from the large pileus scaling to small body scales, usually and primarily arranged in tessellated pattern is characteristic of lacertids. It is probably plesiomorphic rather than derived, according to out-group analysis. Outside the scincomorphan clade, the small element pattern of the body scaling prevails.

Fig. 17 illustrates the position of *Succinilacerta* and of other lizards discussed above in the squamate cladogram based on Evans & Chure (1998), as well as the implicit morphocline polarity.

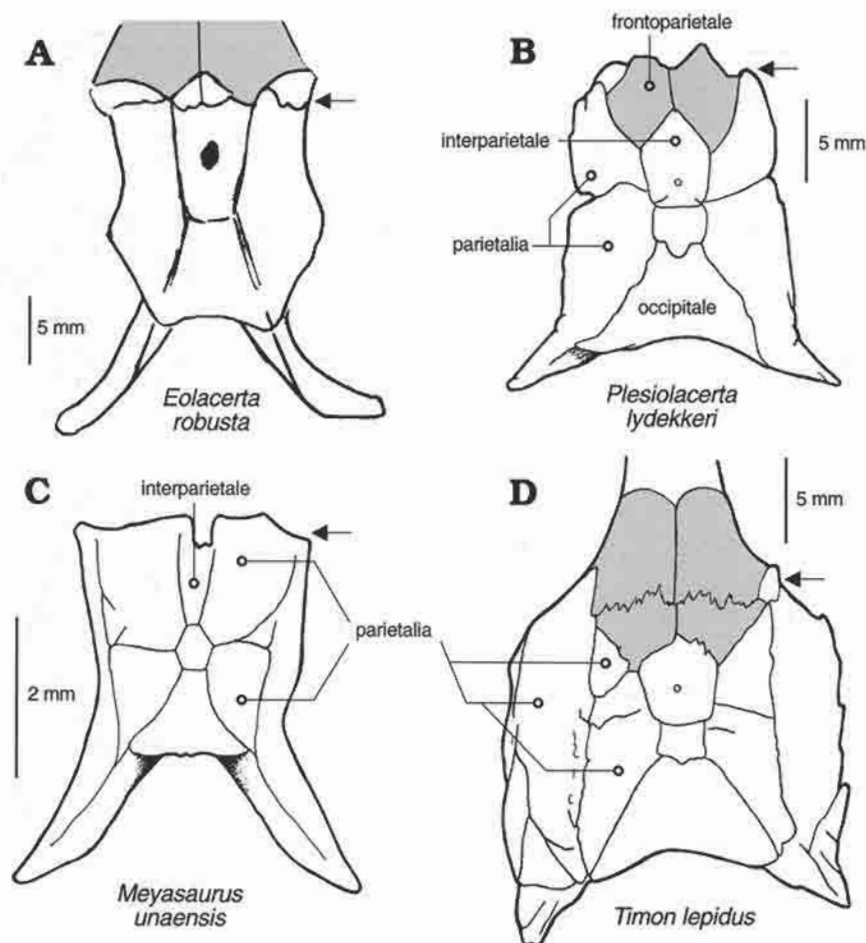


Fig. 15. Parietal part of skull bearing pileus traces of **A.** *Eolacerta robusta* Nöth, 1940, Middle Eocene, after Müller 1998: fig. 2. **B.** *Plesiolacerta lydekkeri* Hoffstetter, 1942, Eocene, after Estes 1983: fig. 24B. **C.** *Meyasaurus unaensis* Richter, 1994, Early Cretaceous, after Richter 1994: fig. 11. **D.** *Timon lepidus* (Daudin, 1802), ZFMK 31433. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture.

Succinilacerta (Figs 3, 17) shares all five (2–6) synapomorphies of the crown group lacertids discussed above, the early ontogenetic control of the pileus pattern included.

Plesiolacerta lydekkeri (Figs 15B, 17) is known to share synapomorphies 3 and 6, but displays some fragmentation of parietal scales, while being polymorphic in this regard (Augé 1988: fig. 6A and personal observation by MBB, 1999 in MNHN). Its frontoparietals overlap the frontoparietal suture, but the amount of overlap is less than usual in lacertids. The very long triangular occipital scale of this genus may be separated from the interparietal by a short transitional plate, and is either unpaired or divided into two parts. It recalls the occipital of both *Eolacerta robusta* (Fig. 15A), a stem non-teioid scincomorphan (Müller 1998), and the most plesiomorphic teioid

Meyasaurus unaensis (Figs 15C, 17), but we consider this similarity as parallelism. The pileus state of *Plesiolacerta* is admittedly plesiomorphic in lacertids, and suggests a lack of precise pileus control synapomorphic for crown-group lacertids.

Eolacerta robusta (Figs 15A, 17) displays a pileus pattern consistent with the hypothesised morphocline polarity (Fig. 17). The frontoparietal scales are short (they do not even reach the frontoparietal suture laterally) which corresponds with the anterior position of the parietal foramen (within the anterior one fourth of the parietal table). The occipital scale obviously develops within the triangular space (Müller 1998: fig. 2) produced by the long supratemporal processes. The scale would be extremely long if it reached as far posterior as these processes. What is the parietal scale in the lacertids, should have been represented in *Eolacerta* (Müller 1998) by the medial parietal scale, overlapping the frontoparietal suture anteriorly (Fig. 15A), and an unknown number of scales on the postero-lateral pileus corner.

The parietal of *M. unaensis* figured by Richter (1994: fig. 11) bears a sculpture that may be interpreted as a teiid-like scale pattern provided with a very long triangular occipital of a seemingly lacertid (but probably primitive) type, similar to that of *Plesiolacerta*.

Notes on the secondary fragmentation of the pileus

A cursory inspection of the skull integument in lizards shows that the developing pileus units follow the configuration of the skull surface as a whole rather than fitting the outlines of particular dermal bone units. Situated between the epidermal units and the skull bones, the osteodermal bone cover (called *crusta calcarea* by neoherpetologists; see e.g. Arnold 1989) displays an intermediate pattern. The osteodermal units do correspond to the epidermal scales, but are often cut into pieces by sutures between the underlying dermal bones (see e.g. Lang 1991: fig. 8). In some lizards (e.g. in anguids, see Borsuk-Białynicka 1984), the pieces fuse, and the integration of the osteodermal cover tends to increase in the ontogeny, but this is not the case in lacertids. In the latter lizard group, the pattern of the skull integument has been fixed at the early ontogenetic stage, and the juveniles, as a rule, display the same pattern as the adults. This may not be the case in big lizards.

The increasing production of osteodermal bone, associated with an increase in animal size, makes all the division lines occurring on the osteodermal units (traces of bone sutures) more distinct, and the units themselves more convex, which eventually results in corresponding disintegration of the epidermal scales on their surface. Moreover, the thicker skin of large sized animals tends to produce small, rather than large, dermal ossifications. Large units tend to develop when the skin is sandwiched in a narrow space between dermal bones and epidermis. Size increase may be, thus, a factor of fragmentation of the integument and of the pileus. However, a disintegrated pileus in a juvenile of *Timon lepidus* (Fig. 16A) demonstrates that the small individuals may also be affected. It is worth noting a similarity of the division lines in this pileus to those of the teiids. Given a derived position of *Timon* in the phylogeny of the Lacertinae (Mayer & Bischoff 1996), the fragmentation of the posterior pileus in this genus is tentatively regarded as a reversal. In this case a selective pressure for the increase in body size might have caused a withdrawal of regulatory mechanisms beginning with the early ontogeny.

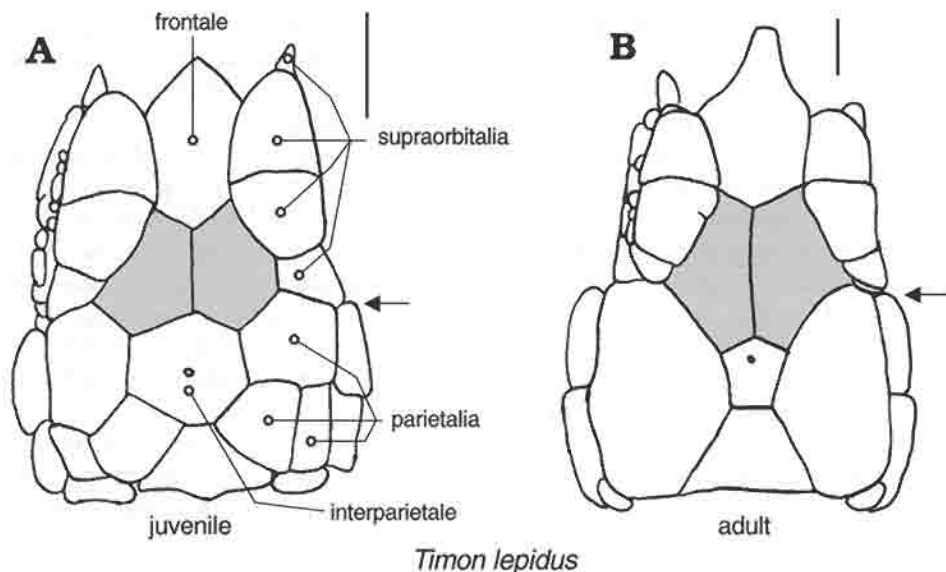


Fig. 16. Postembryonic development of the pileus in *Timon lepidus* (Daudin, 1802). A. Juvenile ZFMK 38165. B. Adult ZFMK 39616. Both Recent. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture. Scale bars 3 mm.

Another case of reversal is that of a member of the derived African clade ('Afrikanische Linie' of Mayer & Benyr 1994), the genus *Acanthodactylus* (ZFMK 443477). This genus displays a derived pattern with well integrated subquadrangular parietal scales, no occipital (Fig. 11B), an anterior position of the interparietal, and corresponding reduction of the posterior extent of the frontoparietals. Instead, the anterior and posterior supraoculars have been disintegrated resulting in a pattern similar to that of teiids (see Fig. 10B and F). Most probably, a reversal of the strict pileus control of the lacertid type is here associated with the anterior shift of the parietal foramen (see also *Pedioplanis* skull in Arnold 1989: fig. 3) to the frontoparietal suture causing some problems in the pileus character display.

Conclusions

A fossil lacertid lizard from the middle Eocene Baltic amber, described herein, is assigned to *Succinilacerta succinea* (Boulenger, 1917), a species to which all previous Baltic amber specimens probably belong (Böhme & Weitschat 1998). *Succinilacerta succinea* shares all the synapomorphies of the pileus of the crown group lacertids proposed herein, and is, thus, considered a member of this group.

The synapomorphies are as follows: The long posterior extension of the frontoparietal scales on the parietal table associated with the central position of both the parietal foramen and the interparietal scale on this table (3); the large subquadrangular parietal scales (4); an early ontogenetic control of the pileus pattern (5); the occipital

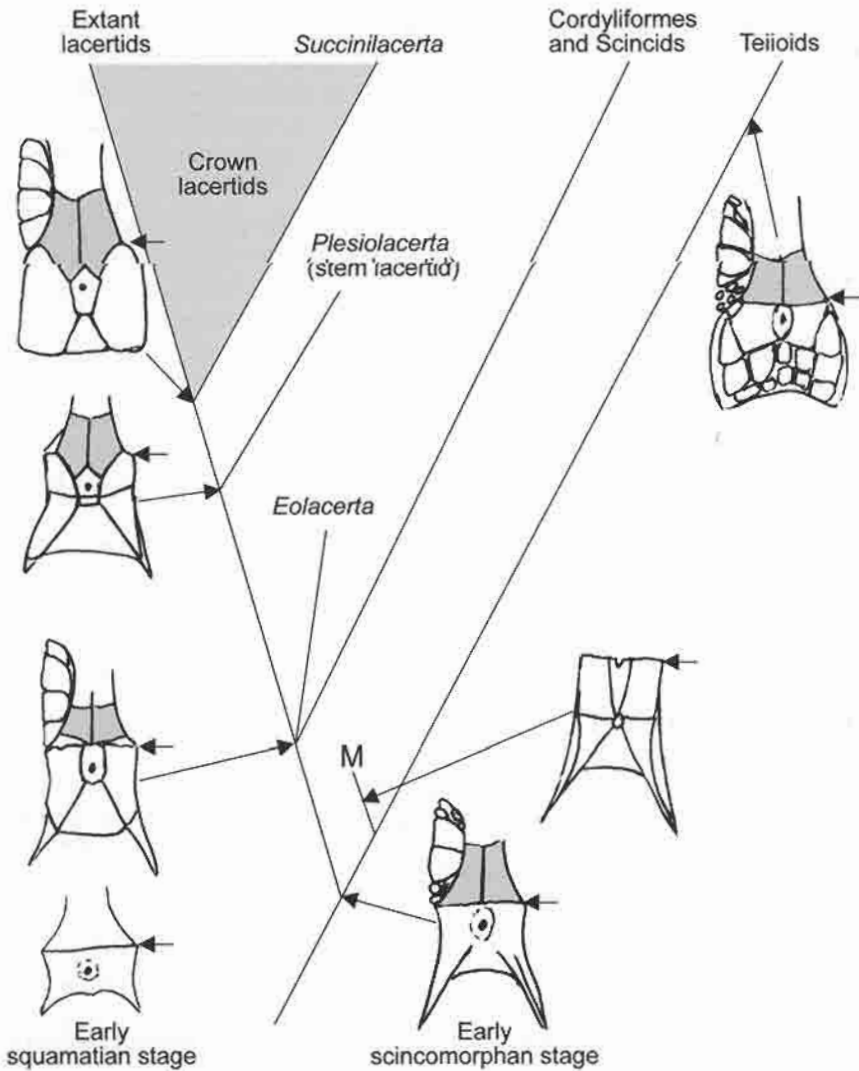


Fig. 17. Hypothesized sequence of the stages of posterior pileus evolution in squamatan phylogeny. Cladogram of scincomorphan relationships roughly according Evans & Chure (1998) with the Paleogene lacertids and *Meyasaurus* Vidal, 1915 included. Frontoparietal scales are shaded. Horizontal arrows indicate the level of the fronto-parietal suture.

scale (6) separating the parietal scales posteriorly; and possibly, two pairs of supra-oculars (I and IV) (2).

The long sagittal contact of the frontoparietal scales (1) is considered synapomorphic for the Scincomorpha, and thus antedates the character states (2–6).

The Eocene genus *Plesiolacerta* shares most, but not all, of the above synapomorphies of the crown group lacertids. It displays a certain amount of intrageneric variability of the posterior pileus pattern (lack of strict genetic control of the pattern), a primitive fragmentation of parietal scales and a very long occipital. Some features

(2 among others) are unknown. The genus represents a less advanced stage of lacertid phylogeny than *Succinilacerta*, and does not belong to the crown group lacertids. In view of scarcity of the pre-Oligocene lacertid fossil material, we do not discriminate between these stages in terms of formal taxonomy. The family Lacertidae Bonaparte, 1831 is here considered as a clade including both crown group and stem group lacertids.

According to our results, the lacertid morphotype of the pileus is more ancient than the Oligocene which is to read that the crown group lacertids is to be rooted earlier than the Oligocene, in contrast to Mayer & Benyur's (1994) opinion based on molecular data.

Although we cannot discriminate between a primitive and a secondary (see p. 373) fragmentation of the pileus in *Plesirolacerta* and *Eolacerta*, the early stratigraphic age of these genera suggests a primitive stage of development of the pileus ontogenetic control. In contrast, some fragmentation phenomena met with in extant genera (*Timon*, *Acanthodactylus*) may be secondary.

Though the present analysis of the epidermal integument patterns is not conclusive for the relationships within the scincomorphan clade, it better matches the cladogram by Evans & Chure (1998), according to which the teioids make up the most plesiomorphic branch of the scincomorphan clade, than the earlier hypothesis of Estes *et al.* (1988) in which they are the most derived group.

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Eoceńska jaszczurka z bursztynu bałtyckiego i pochodzenie grupy koronowej lacertidów

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Streszczenie

Opisany w pracy, drugi z kolei, prawie całkowity okaz jaszczurki zachowanej w środkowo-eoceńskim bursztynie bałtyckim został znaleziony na wtórnym złożu w osadach czwartorzędowych koło Gdańska (Kosmowska-Ceranowicz *et al.* 1996). Jest to przedstawiciel Lacertidae, konespicyficzny z okazem pierwszym, odkrytym w tych samych utworach na Sambii (Klebs 1909, oraz dwoma fragmentami z Sambii), zaliczonymi do *Succinilacerta succinea* (Boulenger, 1917) (Böhme & Weitschat 1998). Oznaczenie opisanego tu okazu oparte jest na diagnostycznej dla *S. succinea* specyficznej budowie łusek w okolicy pazurowej palców (Fig. 6). Okaz jest osobnikiem młodocianym.

Okaz zachowuje cechy pokrycia łuskowego skóry, które jest podstawą taksonomii dzisiejszych jaszczurek. W przypadku materiału kopalnego istnieje z zasady jedynie możliwość rekonstrukcji pokrycia łuskowego sklepienia czaszki (zwanego pileusem) na podstawie odcisków tego pokrycia na kościach. W pracy przypomniano znane relacje pomiędzy łuskami epidermalnymi a kośćmi skórnymi i pokryciem osteodermalnym, przy wyeksponowaniu pewnych aspektów tych relacji, np. wpływu odległości między epidermą a kośćmi skórnymi na styl pokrycia łuskowego i osteodermalnego, a także przypuszczalny wpływ rozmiarów ciała na ten styl.

Głównym celem pracy jest odtworzenie kolejności pojawiania się w filogenezie cech pileusa przy użyciu kladystycznej metody analizy grup zewnętrznych, oraz określenie pozycji rodzaju *Succinilacerta* w stosunku do grupy koronowej (w sensie Jefferies 1979) lacertidów.

Wśród siedmiu cech pokrycia łuskowego charakterystycznych dla lacertidów, z których wszystkie posiada *Succinilacerta*, dwie: znaczną rozciągłość szwu łączącego łuski frontoparietalne (1) i ostrą zmianę typu pokrycia łuskowego na granicy tułowia i głowy (7), uznano za cechy plezjomorficzne. Parzyste, zbliżone w zarysie do owalu, nierozczłonkowane łuski parietalne (3) oraz utrwalenie stylu tylnej części pileusa na wczesnym etapie ontogenezy (5) to cechy synapomorficzne grupy koronowej z włączeniem do niej rodzaju *Succinilacerta*. Trzy pozostałe cechy: (3) głębokie nakładanie się łusek frontoparietalnych na kość ciemieniową poprzez szew fronto-parietalny i, związane z nim, centralne położenie łuski interparietalnej i otworu ciemieniowego (wbrew sugestiom Estesa *et al.* 1988), obecność (6) trójkątnej łuski potylicznej i, ewentualnie, supraokularii I i IV (2), uznano za synapomorficzne dla całej rodziny Lacertidae Bonaparte, 1831, którą traktuje się tu jako takson obejmujący zarówno grupę koronową, jak i grupy pniowe, z włączeniem rodzaju *Plesiolacerta*.

Stwierdzenie Estesa *et al.* (1988), jakoby centralne położenie otworu ciemieniowego było plezjomorfią u Squamata nie zostało tu podważone, choć pozornie stoi w sprzeczności z proponowanym tu kierunkiem morfokliny. Według proponowanego tu scenariusza allometryczny wzrost kości ciemieniowych ku tyłowi na wczesnym etapie filogenezy Squamata (zgodny z sugestią Estesa *et al.* 1988) powodował relatywne przesunięcie otworu ciemieniowego w kierunku szwu, a następnie, na etapie przodków Lacertidae, jego wyrównawczą wędrówkę do tyłu, wraz z towarzyszącymi łuskami interparietalną i frontoparietalnymi. Stąd ułożenie tych łusek jest synapomorficzne dla Lacertidae.

Włączenie *Succinilacerta* do grupy koronowej wskazuje na conajmniej środkowo-eoceński wiek tej grupy, co stoi w sprzeczności z proponowanym na podstawie metody zegara molekularnego wiekiem tej grupy nie starszym niż oligoceński (Mayer & Benyr 1994).

Appendix

Extant lizard material examined

Lacertidae

- Acanthodactylus tristrami* (Günther, 1864)
Algyroides nigropunctatus (Duméril & Bibron, 1839)
Eremias arguta deserti (Gmelin, 1789)
Gallotia galloti (Oudart, 1839)
Lacerta agilis Linnaeus, 1758
Lacerta trilineata Bedriaga, 1886
Lacerta viridis (Laurenti, 1768)
Nucras boulengeri Neumann, 1900
Nucras lalandii (Milne-Edwards, 1829)
Nucras tessellata (A. Smith, 1838)
Podarcis erhardii (Bedriaga, 1876)
Podarcis muralis (Laurenti, 1768)
Podarcis pityusensis (Bosca, 1888)
Psammodromus sp.
Succinilacerta succinea (Boulenger, 1917)
Takydromus sexlineatus (Daudin, 1802)
Teira d. dugesii (Milne-Edwards, 1829)
Timon lepidus (Daudin, 1802)
Timon princeps (Blanford, 1872)
Zootoca vivipara (Jacquin, 1787)

Scincidae

- Chalcides ocellatus* (Forsk., 1758)
Eumeces schneideri (Daudin, 1802)

Xantusiidae

- Lepidophyma gaigeae* Mosauer, 1936
Lepidophyma flavimaculatum Dumeril, 1851

Teiidae

- Ameiva ameiva* (Linnaeus, 1758)
Ameiva ameiva laeta Cope, 1862
Ameiva ameiva petersi Cope, 1886
Ameiva undulata (Wiegmann, 1834)
Callopistes maculatus Gravenhorst, 1838
Cnemidophorus lemniscatus lemniscatus (Linnaeus, 1758)
Cnemidophorus lemniscatus nigricolor (Peters, 1873)
Kentropyx calcaratus Spix, 1825
Teius teyou (Daudin, 1802)

Gymnophthalmidae

- Proctoporus striatus* (Peters, 1862)

Cordylidae

- Cordylus cordylus* (Linnaeus, 1758)
Cordylus jonesi (Boulenger, 1891)
Pseudocordylus microlepidotus (Cuvier, 1829)

Gerrhosauridae

- Gerrhosaurus nigrolineatus* Hallowell, 1857
Zonurus madagascarensis (Gray, 1831)

Measurements of extant lizards

| | Cat. Nos | s-v length | pileus length | Rh index |
|----------------------------------|-------------|------------|---------------|----------|
| Lacertidae | ZFMK | | | |
| <i>Acanthodactylus tristrami</i> | 44347 | 93 | 20 | 21% |
| <i>A. tristrami</i> | 44346 | 52 | 12.5 | 24% |
| <i>Algyroides nigropunctatus</i> | 39608 | 78 | 18.5 | 24% |
| <i>A. nigropunctatus</i> | 22434 | 47 | 17 | 36% |
| <i>Eremias arguta deserti</i> | | 53.2 | 12.3 | 23% |
| <i>E. arguta deserti</i> | 7121 | 40 | 9.5 | 24% |
| <i>Gallotia galloti</i> | 177 | 118.5 | | |
| <i>G. galloti</i> | 34877 | 46.8 | | |
| <i>Lacerta agilis</i> | | | | 24% |
| <i>L. agilis</i> | 6253 | 82.5 | 17 | 21% |
| <i>L. agilis</i> | 6263 | 39 | 10.5 | 29% |
| <i>L. viridis</i> | 50471 | 124 | 29 | 23% |
| <i>L. viridis</i> | 40623 | 43 | 10.5 | 24% |
| <i>L. trilineata</i> | 21238 | 50 | 12 | 24% |
| <i>Nucras lalandii</i> | 16311 | 78.5 | 13.2 | 17% |
| <i>N. lalandii</i> | 18578 | 101 | 18.5 | 19% |
| <i>N. tessellata</i> | 40445 | 70 | 14.5 | 20% |
| <i>N. tessellata</i> | 7072 | 33 | 7 | 21% |
| <i>Podarcis muralis</i> | 584 | | | 22% |
| <i>P. muralis</i> | 4188 | 29 | 7 | 27% |
| <i>P. muralis</i> | 7028 | 60 | 14.8 | 25% |
| <i>P. muralis</i> | 44190 | 39.2 | 9.5 | 24% |
| <i>Succinilacerta succinea</i> | | 27 app. | 10 app. | 32% |
| <i>Takydromus sexlineatus</i> | 68574 | 55.5 | 12.8 | 23% |
| <i>Timon lepidus</i> | 31433 | 175 | 38.6 | 22% |
| <i>T. lepidus</i> | 25889 | 60 | 15 | 25% |
| <i>T. lepidus</i> | 39616 | 210 | | |
| <i>T. lepidus</i> | 38265 | 40 | | |
| <i>T. princeps</i> | 42723 | 31.5 | 8 | 25% |
| <i>T. princeps</i> | 42724 | 60 | 15 | 25% |
| <i>T. princeps</i> | no no | 127 | 29 | 23% |
| Scincidae | | | | |
| <i>Chalcides ocellatus</i> | 68808 | 111 | 12 | 11% |
| <i>Ch. ocellatus</i> | | 57 | 9 | 16% |
| <i>Eumeces schneideri</i> | | 118 | | |
| <i>E. schneideri</i> | | 68 | 14 | 21% |
| Teiidae | | | | |
| <i>Ameiva ameiva</i> | 34029 | 150 | | 26% |
| <i>A. ameiva</i> | 36183 | 61.5 | | 26% |
| <i>A. ameiva laeta</i> | 29995 | 130 | 30 | 23% |
| <i>A. ameiva laeta</i> | 26489 | 59.5 | 16 | 25% |
| <i>A. ameiva petersi</i> | 38297 | 128 | 12.3 | 9.6% |
| <i>A. ameiva petersi</i> | 66826 | 46.2 | 6.5 | 14% |
| <i>A. undulata</i> | no no | 116 | | 27% |
| <i>A. undulata</i> | 78068 | 44.5 | | 31% |

| | | | | |
|--------------------------------------|------------|------|------|-------|
| <i>Cnemidophorus lemniscatus</i> | 59577 | 85 | | 22% |
| <i>C. lemniscatus</i> | 11731 | 30 | 7.1 | 24% |
| <i>Kentropyx calcaratus</i> | 47677 | 85.5 | 20.3 | 24% |
| <i>K. calcaratus</i> | 33339 | 31.3 | 5.4 | 33% |
| | ZMF | | | |
| <i>Cnemidophorus l. nigricolor</i> | 26546 | 64 | 14.9 | 23.3% |
| <i>Kentropyx calcaratus</i> | 5341 | 93 | 24 | 25% |
| <i>K. calcaratus</i> | 11675 | 42 | 12 | 29% |
| Cordyliformes | | | | |
| <i>Cordylus cordylus</i> | no no | 81 | | |
| <i>C. cordylus</i> | no no | 52.5 | | 32% |
| <i>Zonurus madagascarensis</i> | 58459 | 140 | 25 | 18% |
| <i>Z. madagascarensis</i> | 13976 | 48 | 18 | 37% |
| <i>Pseudocordylus microlepidotus</i> | 32706 | 140 | | 25% |
| <i>P. microlepidotus</i> | 18512 | 50 | | 32% |
| <i>Cordylus jonesi</i> | 73659 | 67 | | 30% |
| <i>C. jonesi</i> | 73405h | 32.5 | | 32.5% |
| <i>Gerrhosaurus nigrolineatus</i> | 61 | 22a | 78 | 24% |