

An Early Eocene gecko from Baltic amber and its implications for the evolution of gecko adhesion

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Abstract

A new genus and species of gecko from the Lower Eocene of north-western Russia is described from a superbly preserved specimen in Baltic amber. It is the oldest gekkonid lizard to be represented by more than fragmentary skeletal remains. The digits of the specimen are mostly intact and reveal a unique combination of characters not seen in any living form. Expanded sub-digital scansors on the toes, however, are essentially similar to those of modern climbing geckos and verify the existence of a complex adhesive system 20–30 million years earlier than supported by previously discovered fossil geckos.

Key words: *Yantarogekko*, Gekkonidae, Early Eocene, amber, sub-digital scansors

INTRODUCTION

The fossil record of autarchoglossan lizards extends back at least to the mid-Jurassic (Evans, 1993, 1998a) and autarchoglossans, particularly scincomorphs, are generally well represented throughout the Late Jurassic and into the Cretaceous (Estes, 1983a,b; Evans, 1995, 1998b). Recently an autarchoglossan of indeterminate affinities has been identified from a partial specimen in amber from the Lower Cretaceous (120 million years ago–Ma) of Lebanon (Arnold *et al.*, 2002), providing the first information about the external morphology of early members of this clade. In contrast, the Gekkota, widely accepted as the sister group of the Autarchoglossa (Estes, de Queiroz & Gauthier, 1988) or at least the Scincomorpha (Macey *et al.*, 1997; but see Lee, 1998; Harris, Marshall & Crandall, 2001), is poorly represented before the Tertiary. Although the Jurassic taxa *Ardeosaurus*, *Bavarisaurus*, *Eichstaettisaurus* and *Yabeinosaurus* have been hypothesized to have gekkotan affinities (Hoffstetter, 1964, 1967; Estes, 1983a,b), more recent interpretations have called this into question (Kluge, 1987; Evans, 1993, 1994, 1995, 1998b) and only *Eichstaettisaurus* remains as a putative Jurassic gekkotan.

The oldest undoubted gekkotans are *Hoburogecko* and *Gobekko* from the Upper Cretaceous of Mongolia (Alifanov, 1989; Borsuk-Białynicka, 1990; but see Conrad & Sereno, 2004), followed by an undescribed

species from the Paleocene of Brazil (Estes, 1983b). Thereafter a greater diversity of gekkotans is reflected in the fossil record, particularly that of Europe. Eocene material includes *Rhodanogekko vireti* Hoffstetter, 1946, *Cadurcogekko piveteaui* Hoffstetter, 1946, and unidentified material (Rage, 1978; Augé, 1990b), all from France. Miocene geckos are represented by the extinct genera *Gerandogekko* Hoffstetter, 1946 and *Palaeogekko* Schleich, 1987, the still extant *Euleptes* (Estes, 1969; Müller, 2001; Müller & Mödden, 2001), and limited material of uncertain taxonomic allocation (Rage, 1976; Augé & Rage, 2000), all from the Lower or Middle Miocene of Europe or North Africa. All of these Tertiary taxa are represented only by partial skeletal remains (crania, mandibles, isolated vertebrae). Because generic-level diagnostic characters are notoriously difficult to identify in isolated gecko elements (Hoffstetter, 1946; Augé & Rage, 2000) almost nothing is known about the identities or affinities of Early to mid-Tertiary geckos.

The oldest substantially intact geckos are those found as inclusions in amber from the Oligocene or Miocene of the Dominican Republic (Böhme, 1984; Kluge, 1995). These fossils, however, are referable to the extant genus *Sphaerodactylus*, which is believed to be nested well within the Gekkonidae (Kluge, 1987, 1995), and provide little insight into the morphology and evolution of the group. All other geckos reported from amber (e.g. Giebel, 1862; Vaillant, 1873a,b) have subsequently been regarded as deriving from Holocene copal (recently deposited resin) (Vaillant, 1874, 1875; Klebs, 1910; Bachofen-Echt, 1949; Estes, 1983a; Bauer & Branch, 1995). Here we describe

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a new genus and species of Lower Eocene gecko from Baltic amber that exhibits digital morphology not seen in living geckos and provides the oldest direct evidence of adhesive sub-digital scansors in lizards.

The age of Baltic amber deposits of the ‘blue earth’ of the Samland Peninsula of north-western Russia has recently been determined as *c.* 54 million years (Lower Eocene) on the basis of absolute dating of glauconites (Ritzkowski, 1997; Weitschat & Wichard, 2002). Arthropod inclusions in Baltic amber are relatively common but vertebrate remains are exceedingly rare, especially in comparison with younger (Oligocene–Miocene) Dominican amber, which has yielded substantially complete fossils of frogs (Poinar & Cannatella, 1987; Poinar, 1992), as well as lizards (Rieppel, 1980; Böhme, 1984; Kluge, 1995; de Queiroz, Chu & Losos, 1998).

To date the only authentic lizards in Baltic amber have been lacertids. The earliest known specimen was first regarded as a member of the teiid genus *Cnemidophorus* (Klebs, 1889), then of the lacertid *Nucras* (Klebs, 1910; Boulenger, 1917, 1920). It was subsequently regarded as being a relatively recent specimen embedded in Holocene copal (Loveridge, 1942, 1957; Estes, 1983*a*; Böhme, 1984; Poinar, 1988, 1992), but more recently, it has been validated as a Baltic amber specimen and assigned to a new genus, *Succinilacerta* (Böhme & Weitschat, 1998). Additional lacertid material representing at least three different species has been reported by Katinas (1983), Kosmowska-Ceranowicz, Kulicka & Gierlowska (1997*a*, 1997*b*), Krumbiegel (1998), Böhme & Weitschat (1998, 2002) and Borsuk-Bialynicka, Lubka & Böhme (1999). Lacertids remain the dominant reptile group in Europe today. Northern Europe in the Eocene, however, supported a diverse sub-tropical to tropical herpetofauna that was more phyletically diverse than at present and included representatives of squamate groups that no longer survive in the region, including cordylids and pleurodont iguanians (Augé, 1987*a,b*, 1990*a,b*; Augé & Smith, 1997). These taxa are known from conventional fossils, but have not previously been found in amber deposits (Larsson, 1978).

An exceptionally well-preserved lizard from the Baltic coast of western Russia confirms that geckos, which have been recorded from both the Upper and Lower Eocene of France (Hoffstetter, 1946; Rage, 1978; Augé, 1990*b*), were also present in the amber forests of north-eastern Europe. It also represents the oldest gekkotan in amber and the only substantially intact gekkonid specimen before the Miocene.

MATERIAL

Family Gekkonidae

Yantarogekko balticus gen. et sp. nov. (Figs 1–3)

Etymology

Yantarogekko: from the Russian ‘янтарь’ (yantar) meaning amber and the onomatopoeic, Malay-derived ‘gekko’; *balticus*: in reference to the origin of the specimen from Baltic amber.



Fig. 1. *Yantarogekko balticus* sp. nov. from Baltic amber of the Lower Eocene of north-western Russia. Lateral view of holotype illustrating general habitus and scalation features. Darker area in centre of eye is an artefact and does not represent the pupil. Oak bud trichomes in the amber matrix beneath the head of the specimen are indicator fossils for Baltic amber. Scale = 5 mm.

Holotype

Specimen in the Deutsches Bernstein-Museum in Ribnitz-Damgarten, Germany; registration number GAM 1400.

Type locality and horizon

Lower Eocene of the Samland Peninsula, Kaliningrad District, Russian Federation. The pattern of concentric resin layers around the specimen is indicative of natural resin embedded inclusions. Further, both the authenticity of the specimen and its provenance are confirmed by the inclusion in the resin of numerous stellate oak bud trichomes (Fig. 1), which are indicator fossils characteristic of Baltic amber, and of an undetermined specimen of dolichopodid fly, one of the most common of arthropod fossils from Baltic amber (Poinar, 1992; Poinar & Poinar, 1994; Weitschat & Wichard, 2002).

Diagnosis

A small, homogeneously scaled gecko, lacking moveable eyelids, with strongly clawed digits, well-developed, undivided sub-digital scansors, and highly asymmetrical digits of the manus (digits I and II much smaller than digits III–V). The lack of moveable eyelids (Fig. 1) and presence of enlarged, scansorial pads (Fig. 2) confirm the species as a member of the Gekkonidae (although these characters are also consistent with the related Diplodactylidae, the latter clade seems to have undergone its entire evolutionary history in eastern Gondwanaland (Kluge, 1987; Donnellan, Hutchinson & Saint, 1999; Han, Zhou & Bauer, 2004). The combination of straight, undivided scansorial plates along the length of the digits and a greatly reduced, but strongly clawed digit I is unique among the Gekkonidae (Russell & Bauer, 1990). Other geckos with reduced first digits possess slender, stylet-like

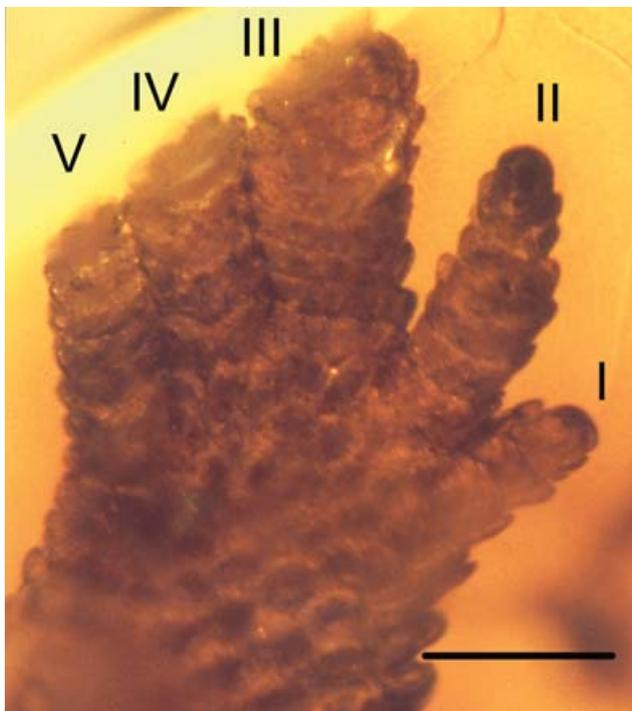


Fig. 2. Palmar view of right manus of holotype of *Y. balticus* illustrating broad sub-digital scansors, unmodified palmar scales, and short but robustly clawed digits I and II. Digits are numbered from preaxial (I) to postaxial (V). Scale = 0.5 mm.

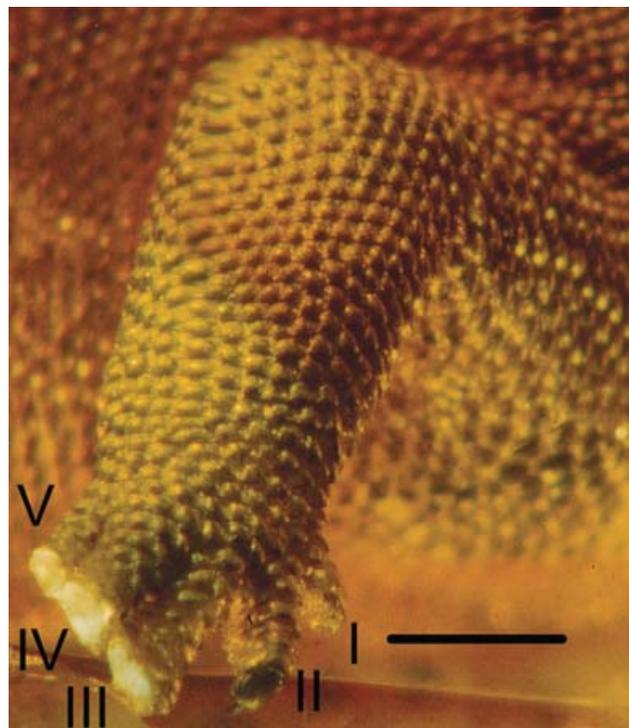


Fig. 3. Dorsal view of right arm of holotype of *Y. balticus* illustrating the damage to digits III–IV of the manus and the unique short but robustly clawed digits I and II. Digits are numbered from preaxial (I) to postaxial (V). Scale = 1 mm.

claws (e.g. *Phelsuma*, *Hemiphyllodactylus*) or are totally clawless (e.g. *Perochirus*). In *Lygodactylus*, to which all copal-embedded geckos have been referred (Peters, 1865, 1866; Vaillant, 1875; Loveridge, 1942; Pasteur, 1995; we disagree with Wermuth's (1966) identification of Giebel's (1862) copal specimen as *Hemiphyllodactylus typus*), digit I is reduced and may be strongly clawed, but the remaining digits are substantially narrowed basally and digit IV is typically much longer than digit III. In no other gekkonid with basally expanded pads is digit II so narrowed with respect to digits III–V (Figs. 2, 3) and in no other taxa are the palmar scales unreduced in size with respect to those of the forearm (Fig. 2).

Among named fossil geckos, the geographically and temporally most proximate forms to *Yantarogekko* are *Rhodanogekko vireti* and *Cadurcogekko piveteaui*, both from the Upper Eocene of France. The former is known only from a narrow frontal bone bearing osteoderms (Hoffstetter, 1946), whereas *Yantarogekko* has a broad snout, implying an expanded frontal, and lacks the rugosity invariably accompanying underlying osteoderms. *Cadurcogekko* is doubtfully diagnosable within the Gekkonidae, but like *Rhodanogekko* and several other undetermined Eocene geckos known only from cranial fragments (Estes, 1983a; Augé, 1990b), it is much larger than *Yantarogekko balticus*. Although it is not possible to confirm that the holotype of *Y. balticus* is an adult, its moderate eye diameter relative to estimated body size (c. 5.5–6.0% snout–vent length) is comparable to that of

adults of typical extant gekkonids and smaller than might be expected for hatchlings or young juveniles (Werner, 1969).

Description

Head, forebody and right forelimb, embedded in 42 mm long piece of Lower Eocene amber from the Samland Peninsula, Russia. A hole (visible to the right of the gecko's head) was bored into the specimen by a previous owner and has subsequently been filled with resin to stabilize the piece. The right side of the specimen is intact, whereas the left side is largely macerated.

Length of specimen 15.0 mm. Head 6.4 mm long, 4.1 mm deep, distinct from neck. Lores and interorbital region inflated, snout short (40% of head length, eye diameter 1.2 mm). Scales on snout and forehead rounded, granular to slightly conical, scales on snout larger than those on occipital region. No eyelids, pupil shape not discernable; supraciliaries short. Ear opening oval, horizontally oriented, small (0.4 mm), eye to ear distance 1.6 times eye diameter. Nostril oval, laterally oriented, surrounded by rostral, first supralabial, supranasal, and a crescentic nasal scale itself bordered by two postnasal scales. Several rows of scales separate orbit from supralabials. Infralabials larger than supralabial, bordered medially by c. three rows of enlarged rounded scales. Supralabials (to mid-orbital position) 10; enlarged

supralabials to angle of jaws 12; infralabials 10? (partially obscured).

Body relatively robust. Dorsal, head and limb scales homogeneous, rounded to weakly conical granules, no tubercles present (Fig. 1). Ventral scales somewhat larger than dorsal. Estimated mid-body scale rows behind axilla 90–100 (based on those visible). Scales on palm smooth, flattened, subimbricate, not reduced in size relative to those of rest of limb (Fig. 2).

Forelimbs relatively stout, digits III–V obliquely severed, digits short, broad, without inflections, digits I–II much smaller than others, digit I especially reduced; digit II much shorter than digit III and only *c.* 60% its width; slightly recurved claws present on digits I–II (assumed present on other digits), claws sheathed dorsally by a large scale (Fig. 3); sub-digital lamellae broad and undivided, extending entire width of toes; lamellar counts: 2:5:8:5:5 (truncated in digits IV–V); the penultimate phalanx of digits II–III (and presumably IV–V) is distally free of the pad and is subtended by narrower, non-scansorial scales. Details of sub-digital setal morphology and arrangement could not be seen on the specimen.

No discernable colour pattern has been retained by the specimen.

DISCUSSION

Many living geckos are noteworthy for their complex pedal structure (Dellit, 1934; Maderson, 1970; Russell, 1975) and their ability to cling to surfaces using an adhesive system based on van der Waals forces (Autumn, Liang *et al.*, 2000; Autumn & Peattie, 2002; Autumn, Sitti *et al.*, 2002). The digital structure of *Yantarogekko balticus* is typical of geckos with adhesive abilities. The broad toe pads and expanded sub-digital scansors are indicative of the presence of a suite of anatomical features that universally accompany this morphology in geckos including the presence of a muscular and tendinous scansor control mechanism (Russell, 1975, 1976, 1979) and the elaboration of the Oberhäutchen of the sub-digital epidermis into fine setae (Maderson, 1964, 1970; Autumn & Peattie, 2002) that form micromolecular bonds with the substrate (Autumn *et al.*, 2000, 2002). Expanded scansors subtend the digits from their base to the inflection of the penultimate phalanx, illustrating a variant of the basally derived undivided multi-scansorial design that is typical of many extant gekkonid genera and which has been interpreted as plesiomorphic with respect to the divided scansors of certain other geckos (Russell, 1976). Based on the natural history of living forms sharing similar scansors, it is probable that *Yantarogekko* was arboreal. Its tiny size (estimated 20–22 mm snout–vent length) is comparable to that of some smaller extant gekkonids, among which members of the Afro-Malagasy climbing genus *Lygodactylus* are perhaps the most likely ecological analogues.

Evidence of sub-digital scansors has been found in other amber-preserved lizards, including several polychrotids of the genus *Anolis* (Lazell, 1965; Rieppel, 1980; de Queiroz

et al., 1998) and at least two species of gekkonids referable to the extant genus *Sphaerodactylus* (Böhme, 1984; Kluge, 1995). These specimens, however, are as much as 20–30 million years (my) younger than *Yantarogekko* (Grimaldi, 1995; Iturralde-Vinent & MacPhee, 1996) and are all assignable to extant species groups within their respective genera (Kluge, 1995; de Queiroz *et al.*, 1998).

Yantarogekko demonstrates that the gekkonid scansorial system was already established in the Lower Eocene, but it is probable that it evolved much earlier. Primitively padless (non-scansorial) geckos occur in both the Gekkonidae and its sister group, a clade including the Diplodactylidae and Pygopodidae (Kluge, 1987; Donnellan *et al.*, 1999; Han *et al.*, 2004), implying that the scansorial system has evolved independently on several occasions (Russell, 1976, 1979) and that its origin post-dates the split of these lineages, which has been hypothesized to have occurred 85 Ma (Kluge, 1987). The age of deep intrafamilial divergences in the Gekkonidae has not been reliably estimated, but based on data from mitochondrial and nuclear gene sequences the split of closely related genera of pad-bearing geckos is in the 14–24 my range (Chambers *et al.*, 2001; Carranza *et al.*, 2002) and it is probable that basal cladogenetic events in the family date from the early Tertiary or Upper Cretaceous (Borsuk-Bialynicka, 1990), with the initial divisions within the Gekkota having occurred as early as 180 Ma (Kluge, 1987).

Unfortunately, the characters preserved in the holotype of *Y. balticus* do not suggest specific affinities to extant genera within the Gekkonidae. *Yantarogekko*, therefore, may be part of a lineage that diverged before the common ancestor of all living gekkonids, or it may represent an extinct member of the modern gekkonid radiation. The recent discovery of numerous specimens of lacertid lizards in Baltic amber (Böhme & Weitschat, 1998, 2002) holds promise that additional gekkonids may also be found and that these may provide further insight into the evolution and early diversification of adhesive mechanisms in geckos.

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