LETTER

Eocene lizard from Germany reveals amphisbaenian origins

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Amphisbaenia is a speciose clade of fossorial lizards characterized by a snake-like body and a strongly reinforced skull adapted for head-first burrowing[1,2]. The evolutionary origins of amphisbaenians are controversial, with molecular data uniting them with lacertids[3,4], a clade of Old World terrestrial lizards, whereas morphology supports a grouping with snakes and other limbless squamates[5–9]. Reports of fossil stem amphisbaenians[10] have been falsified[11], and no fossils have previously tested these competing phylogenetic hypotheses or shed light on ancestral amphisbaenian ecology. Here we report the discovery of a new lacertid-like lizard from the Eocene Messel locality of Germany that provides the first morphological evidence for lacertid–amphisbaenian monophyly on the basis of a reinforced, akinetic skull roof and braincase, supporting the view that body elongation and limblessness in amphisbaenians and snakes evolved independently. Morphometric analysis of body shape and ecology in squamates indicates that the postcranial anatomy of the new taxon is most consistent with opportunistically burrowing habits, which in combination with cranial reinforcement indicates that head-first burrowing evolved before body elongation and may have been a crucial first step in the evolution of amphisbaenian fossoriality.

Reptilia Laurenti, 1768
Squamata Oppel, 1811
Lacertibaenia Vidal and Hedges, 2005
Cryptolacerta hassiaca gen. et sp. nov.

Etymology. *Crypto-*, from the ancient Greek κρυπτς, meaning 'hidden' or 'secret', referring to the inferred ecology of the animal; *lacerta* (Latin), meaning lizard; *hassiaca* (Latin), female adjective for Hesse, the German province of the Messel locality.
Holotype. SMF ME 2604 (Fig. 1), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany.
Locality and horizon. West of Quarry 2, 50 cm above Level β[12]. Messel Pit World Heritage Site, Hesse, Germany; Eocene (Lutetian).
Diagnosis. Lacertibaenian squamate with a snout–vent length of approximately 7 cm; skull capsule-like, anteriorly downturned and heavily ossified; transverse nasofrontal suture; small narial openings facing strictly anteriorly owing to a unique dorsolateral covering by the maxilla; small posterodorsal coronoid process of the dentary; 14 dentary, 7 premaxillary and 12 maxillary teeth with the posterior-most maxillary tooth enlarged; 27 presacral vertebrae; manus and pes strongly reduced in size relative to the remaining limb. Shares with amphisbaenians a relatively elongated postorbital skull portion, blunt and rounded snout, sutural contact between prefrontal and postorbito-frontal, contact between prefrontal and jugal, absence of a lacrimal, small jugal with only little angulation, subequal width of the anterior and posterior borders of the frontal, absence of frontal constriction between the orbits, loss of the tympanic crest, neural spines reduced, seven or fewer cervical vertebrae, rod-like clavicles, absence of an

anterior coracoid emargination and interclavicle, fusion of cephalic scales, transversely widened frontal subolfactory processes, thickening of maxilla and frontal, small orbits, a vertical tongue-and-groove articulation between the frontals, and absence of an iliac anterodorsal projection.

The type and only known specimen of *Cryptolacerta hassiaca* is nearly complete, missing only the distal tail (Fig. 1a). Computed tomography (CT) imaging and specimen examination (Figs 1b, c and 2) reveal a mosaic of lacertid and amphisbaenian anatomical characters. The skull is massive and heavily ossified, with an anteroventrally downturned anterior portion (Fig. 1d). Extensive dermal sculpturing covers the skull roof and well preserved scute sulci reflect the presence of large, transversely oriented scales. Both maxilla and frontals display a massive thickening in cross-section coupled with an increase in bone density, obscuring the vascularized internal structure seen in the more posterior cranial elements as well as in lacertids and most other lizards; the same condition in *Cryptolacerta* occurs in amphisbaenians. The external nares are small and anteriorly oriented and are bounded dorsally by a unique anteromedial flange of the maxilla. Small orbits indicate reduced eyes, and the prefrontal and postfrontal have a strong sutural contact similar to fossil amphisbaenians[13–15]. *Cryptolacerta* has a vertically tall tongue-and-groove interdigitation of the median contact of the paired frontals as in amphisbaenians (Fig. 2a), and the prominent frontal subolfactory processes, although lacking a median contact as in lacertids, are notably widened transversely and form the major part of the posterior wall of the nasal capsule, a feature shared with amphisbaenians (see Supplementary Information). The parietal table is prominent and shows the typical lacertid Y-shaped crest that articulates with the braincase on its ventral surface (Fig. 2b). The large size and ventral extension of the crest indicates close proximity or ossification with the prootic and supraoccipital, resulting in reduced cranial kinesis. The braincase is crushed, and only the parabasisphenoid and slender basipterygoid articulations are preserved. The middle ear is reduced as evidenced by the absence of a quadrate tympanic crest (Fig. 2c). The dentary has a posterolateral extension covering the anterolateral part of the coronoid (Fig. 1c), as in many amphisbaenians, despite retaining a typically lacertid shape.

Cryptolacerta possesses a distinctive heterodont dentition. The six preserved teeth on the premaxilla are conical and diminutive. The 11 maxillary teeth continuously increase in size posteriorly, with the last tooth being expanded and bulbous in shape and the remaining teeth having bicuspid crowns. The 14 teeth on the dentary also are similar to the maxillary teeth, but lack an enlarged posterior-most tooth.

Postcranially, *Cryptolacerta* possesses 29 procoelous precaudal vertebrae with very low neural spines, including seven cervicals and two sacrals. The pectoral girdle consists of recurved clavicles, slender scapulacoracoids and the sternum, whereas the interclavicle is absent (Fig. 2d). The pelvic girdle possesses a well-developed ilium that lacks an anterodorsal process (Fig. 2e). Although not all autopodia are fully
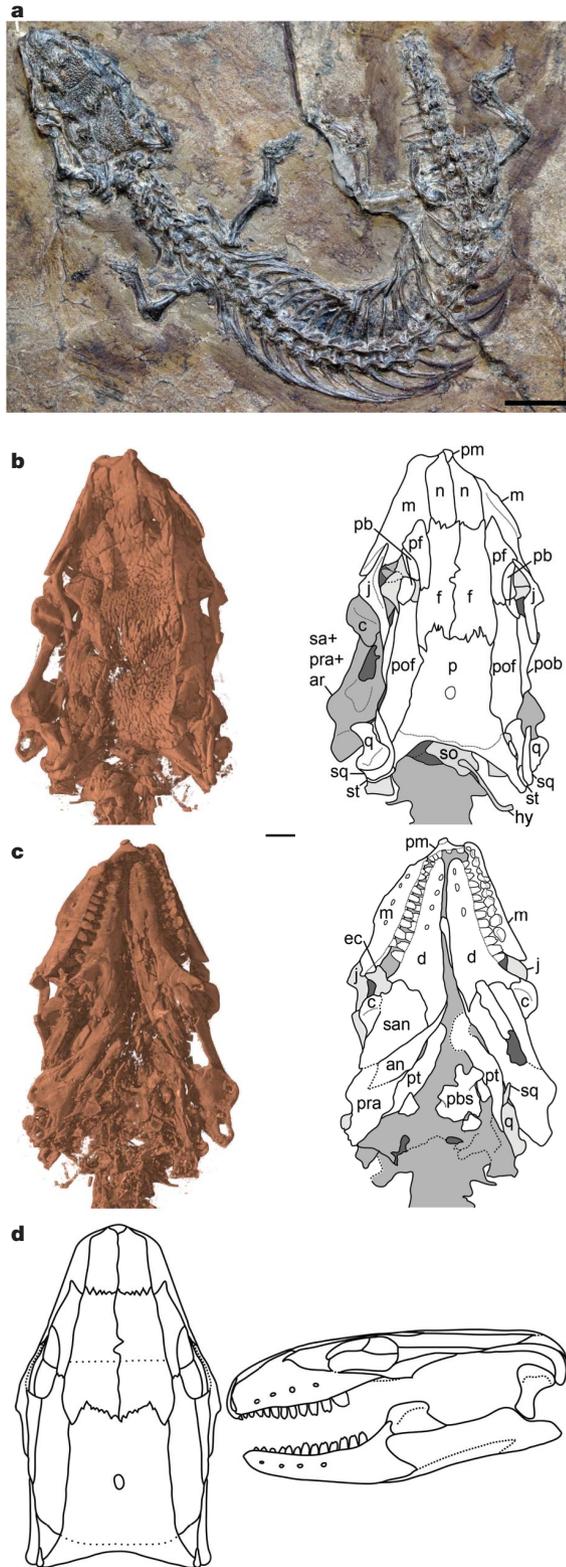
Figure 1 | *Cryptolacerta hassiaca* gen. et sp. nov., holotype (SMF ME 2604). **a**, Nearly complete specimen. **b**, Micro-CT scan of skull and outline of bones in dorsal view. **c**, Micro-CT scan of skull and outline of bones in ventral view. **d**, Reconstruction of skull in dorsal and lateral view. Scale bars, 5 mm (**a**), 2 mm (**b**, **c**). Abbreviations: an, angular; ar, articular; c, coronoid; d, dentary; ec, ectopterygoid; f, frontal; hy, hyoid; j, jugal; m, maxilla; n, nasal; p, parietal; pb, palpebral; pbs, parabasisphenoid; pf, prefrontal; pob, postorbital; pof, postfrontal; pm, premaxilla; pra, prearticular; pt, pterygoid; q, quadrate; sa, surangular; so, supraoccipital; sq, squamosal; st, supratemporal.
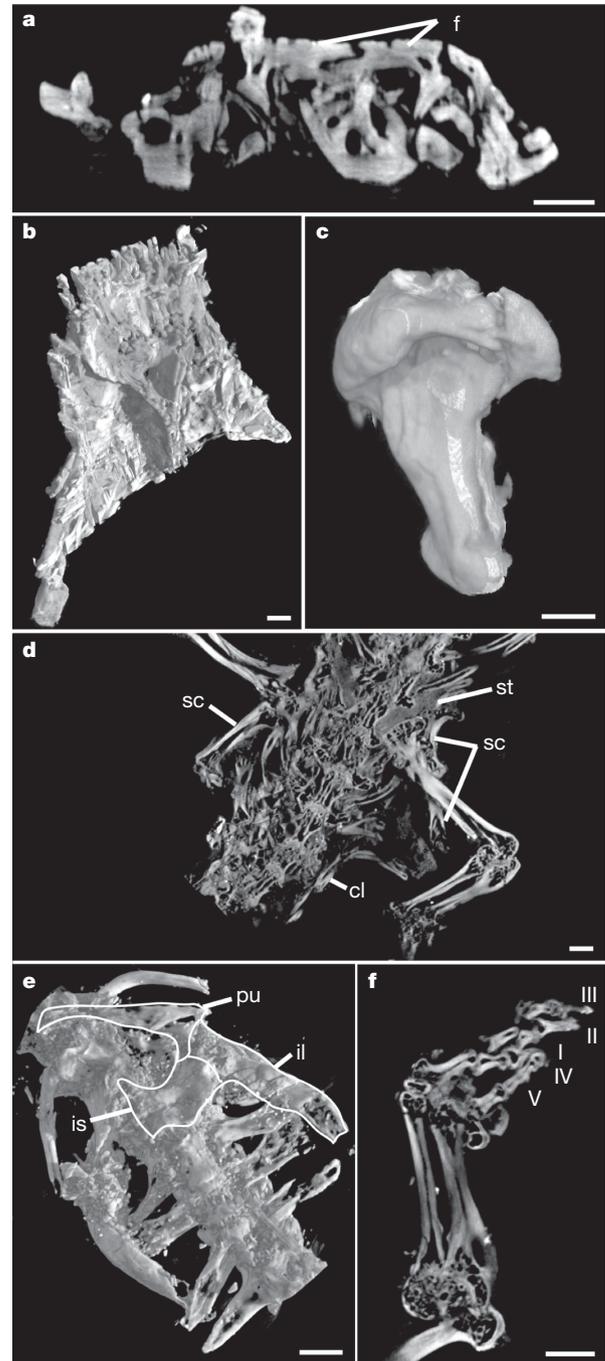

Figure 2 | *Cryptolacerta hassiaca* gen. et sp. nov., holotype (SMF ME 2604), anatomical features as revealed by CT. a, Transverse section through the anterior part of the frontals (f). **b**, Parietal in ventral view showing the Y-shaped crest. **c**, Left quadrate in posterolateral view. **d**, Section showing shoulder girdle with sternum (st), scapulocoracoid (sc) and clavicle (cl). **e**, Pelvic girdle with outlines to emphasize the morphology of ischium (is), ilium (il) and pubis (pu). **f**, Manus with digits I–V; note that digit IV lies on top of digit V, as revealed by different CT sections. Scale bars, 1 mm.

preserved, the phalangeal formula of 2–3–4–4/5?–3 suggests that no digits are lost, but the phalangeal elements are miniaturized relative to the remaining limb bones (Fig. 2f).

The systematic position of amphisbaenians within Squamata is poorly constrained. Molecular data support a sister-taxon relationship with lacertids[3,4,16,17], but there is no morphological character support among living taxa uniting the highly derived amphisbaenians with lacertids. Most morphological analyses support a common ancestry of amphisbaenians and snakes[6–9], but character support for this

hypothesis has been considered homoplastic[18]. To determine the significance of *Cryptolacerta* for resolving systematic relationships of amphisbaenians, we performed a phylogenetic analysis on a combined data set of morphological characters and nuclear gene sequences (*rag-1*, *c-mos*) for extant and fossil squamates using parsimony and Bayesian methods (Fig. 3a). Analyses of combined data recover a monophyletic lacertid–amphisbaenian ('lacertibaenian'[4]) clade, with *Cryptolacerta* clustering as sister taxon to Amphisbaenia in both the parsimony and Bayesian analyses (Fig. 3a). The sister relationship with Amphisbaenia is supported by 19 characters distributed across the entire skeleton (see Supplementary Information). Although homoplasy is common in many squamate osteological characters[9,18], the tongue-and-groove articulation of the frontals is unique to *Cryptolacerta* and Amphisbaenia, the transver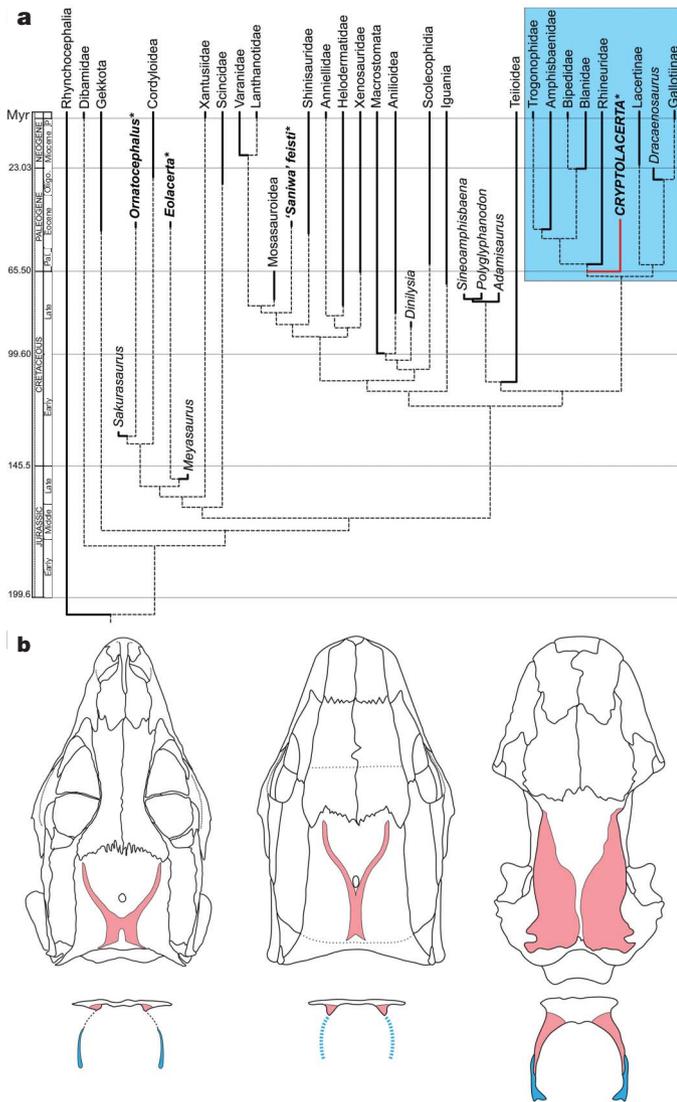sely widened frontal downgrowths occur otherwise only in some scolecophidian snakes, the thickened frontal and maxilla can be found to a variable extent only in dibamids, snakes and varanids, the absence of a tympanic crest and the very low neural spines otherwise occur only within fossorial snakes, dibamids and some anguimorphs, and a sutural prefrontal–postorbitofrontal contact is shared only by some anguimorphs and *Sineoamphisbaena*. This last taxon, a Mesozoic squamate previously considered a stem-amphisbaenian[10], falls within Polyglyphanodontidae as in other recent analyses[11] (Fig. 3a).

Cranial osteology of *Cryptolacerta* provides the first evidence of the origin of the derived amphisbaenian skull (Fig. 3b). In both *Cryptolacerta* and amphisbaenians the skull is reinforced by a strong vertical interdigitation of the frontals, thick, dense maxillae and frontals, and ventral downgrowth of the parietal. In lacertids the anterolateral portions of the ventroparietal crest closely approach the membranous alar processes of the prootic, and in amphisbaenians a membranous extension of the prootic is sutured to the ventrally extending parietal (Fig. 3b). Although the crest in *Cryptolacerta* is similar to lacertids, it is much more strongly developed and we infer extensive contact between the parietal and prootic. Additionally in basal amphisbaenians, the dorsal outline of the parietal table strongly reflects the shape of the ventroparietal crest of *Cryptolacerta*[13–15], suggesting that the lateral parts of a lacertid-like parietal became reduced during amphisbaenian evolution.

Body shape in squamates corresponds to locomotory habits[19,20], and the nearly complete skeleton of *Cryptolacerta* provides an opportunity to infer ecology near the origin of Amphisbaenia. To determine the habits of the taxon, we morphometrically analysed body shape in *Cryptolacerta* and extant squamates occupying habitats represented in the Messel depositional system (Fig. 4). Principal component analysis of cranial, axial and appendicular measurements[19] produced morphospaces within which ecological habits were defined for extant taxa, and inferred for *Cryptolacerta*. For all coordinated principal component axes, *Cryptolacerta* falls outside the morphospace defined by fully fossorial squamates (Fig. 4). Although the reinforced skull and superficially small limbs are suggestive of fossorial habits, *Cryptolacerta* occupies a position within morphospace defined by taxa that are cryptic, leaf litter specialists and opportunistic burrowers (Fig. 4), based on relative body size, limb lengths and head size.

Ecomorphometry of *Cryptolacerta* and adaptations for a reinforced skull indicate that the early ecology of amphisbaenians and their relatives consisted of cryptic behavioural habits combined with head-first substrate locomotion, possibly as a defensive or predation strategy.
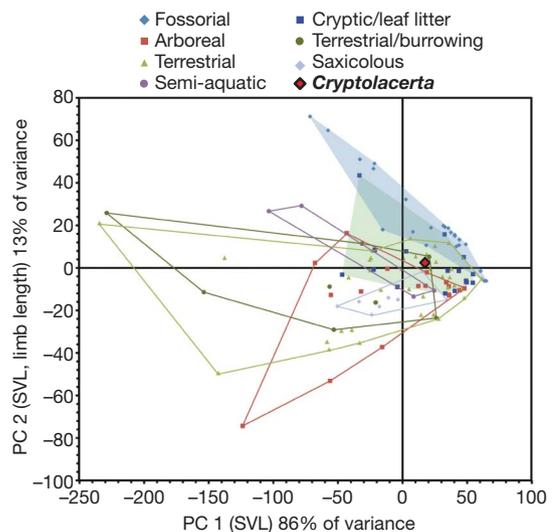

Figure 3 | Phylogeny of *Cryptolacerta* and the evolution of cranial akinesis in the origin of the amphisbaenian skull. a, Time-calibrated phylogeny of Squamata based on Bayesian analysis of morphological and molecular characters. Bold taxa with asterisks are from the Messel locality; the blue box denotes Lacertibaenia. **b**, Evolution of the amphisbaenian skull. Dorsal skull roofs and transverse sections through the dorsal braincase of (from left to right) *Podarcis pityusensis* (Lacertidae), *Cryptolacerta hassiaca* gen. et sp. nov. and *Rhineura floridana* (Amphisbaenia)[30]. The ventroparietal crest of lacertids is ventrally connected with the prootic (blue) through a membranous sheet. In *Cryptolacerta* the crest is more prominent and must have had an extensive contact with the prootic. In amphisbaenians the crest is in full contact with the prootic and forms a secondary temporal region.

Figure 4 | Ecomorphology of *Cryptolacerta*. Principal component analysis of squamate morphology with ecological habits projected into shape space. Fossorial and cryptic morphospaces are shaded. *Cryptolacerta* occupies a position within the cryptic and terrestrial habit spaces.

Body elongation and limb reduction or loss are often considered prerequisites of fossoriality in squamates[21–23]; however, *Cryptolacerta* demonstrates that modifications to cranial architecture preceded postcranial specializations in amphisbaenians, showing that hypotheses of ecological character correlation may mask radically different histories of character evolution in ecological specialization[18,23].

Recent molecular divergence estimates[24] and the fossil record[25] indicate that lacertids and amphisbaenians diverged in the Late Cretaceous, at least 20 Myr before the occurrence of *Cryptolacerta*. The late occurrence of *Cryptolacerta* is consistent with hypotheses that intermediate body forms in the evolution of body elongation and limblessness can persist for tens of millions of years[20]. It also suggests that the Palaeogene of Europe was a refugium for archaic Mesozoic squamate lineages, as indicated by co-occurring *Eolacerta*, '*Saniwa*', and *Ornatocephalus*[9,26–28] (Fig. 3a), probably resulting from the island geography of Europe during the Late Cretaceous and early Cenozoic[29].

METHODS SUMMARY

The specimen was scanned by CT at the Helmholtz Centre Berlin for Materials and Energy using a micro-focus X-ray tube. Cranial reconstructions were performed using a wax model based on the CT data. Phylogenetic analyses were run using a partitioned data set of 364 morphological and 3,216 molecular (*rag-1*, *c-mos*) characters as well as 65 terminal taxa, using both parsimony and Bayesian methodology. Morphometric analysis used principal component analysis of a published data set of linear measurements of squamate body forms for taxa inhabiting environments represented in the Grube Messel depositional system[19] to which *Cryptolacerta* was added based on measurements obtained from a digital calliper.

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