Synchrotron tomography of a stem-lizard elucidates early squamate anatomy

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Squamates (lizards and snakes) include more than 10,000 living species, descended from an ancestor that diverged more than 240 million years ago from that of their closest living relative, *Sphenodon*. However, a deficiency of fossil evidence [1–7], combined with serious conflicts between molecular and morphological accounts of squamate phylogeny [8–13] (but see [14]), has caused uncertainty about the origins and evolutionary assembly of squamate anatomy. We report the near-complete skeleton of a stem-squamate *Bellairsia gracilis* from the Middle Jurassic of Scotland, documented using high-resolution, synchrotron, phase-contrast tomography. *Bellairsia* shares numerous features of the crown-group, including traits related to cranial kinesis, an important functional feature of many extant squamates, and those of the braincase and shoulder girdle. Alongside these derived traits, *Bellairsia* also retains inferred ancestral features including a pterygoid-vomer contact and the presence of both cervical and dorsal intercentra. Phylogenetic analyses return strong support for *Bellairsia* as a stem-squamate, suggesting that several features that it shares with extant gekkotans are plesiomorphies, consistent with the molecular phylogenetic hypothesis that gekkotans are early-diverging squamates. We also provide confident support of stem-squamate affinities for the enigmatic *Oculudentavis*. Our findings indicate that squamate-like functional features of the suspensorium, braincase and shoulder girdle, preceded the origin of their palatal and vertebral traits, and indicate the presence of advanced stem-squamates as persistent components of terrestrial assemblages up to at least the mid Cretaceous.

Squamates are among the most speciose of extant vertebrate radiations and are characterised by numerous derived features of both the skull and postcranium. They diversified from an ancestor possessing some or all of these traits, giving rise to taxa as morphologically disparate as snakes, amphisbaenians, chameleons, geckos, and the extinct marine mosasaurs. However, definite stem-squamate fossils representing the early history of the group have until now been rare or absent, spanning from their inferred time of origin in the early Middle Triassic (240 million years ago based on fossils, and older from molecular clock studies [3,15]), up to the late Early Cretaceous [11,16,17]. This lack of fossil data may explain deep uncertainties regarding the ancestral anatomical states of the squamate crown-group, as evident from conflicts between phylogenetic hypotheses of the relationships among major groups [1,2]. In particular, morphological hypotheses place iguanians as the sister to all other squamates, implying that traits such as presence of a choanal fossa on the palatine, lack of vomer-pterygoid contact, vertebral procoely, and loss of distal tarsal 2 are potentially plesiomorphic for squamates [11]. In contrast, molecular phylogenetic hypotheses have consistently resolved iguanians as being deeply-nested, with snakes (Serpentes) and anguimorphs, instead finding gekkotans and/or dibamids as the earliest-diverging crown squamates [10,12,13]. Morphological evidence for this has been scarce [8,11] (but see [14]).

We report a near-complete (~70%) skeleton (Fig. 1, Extended Data Fig. 1) of the tiny, Middle Jurassic squamate-like taxon *Bellairsia gracilis* from the Bathonian Kilmaluag Formation of the Elgol site of special scientific interest (Elgol SSSI), Isle of Skye, Scotland [18]: NMS G.2022.1.1 (see SI for taxonomy and locality data). *Bellairsia gracilis* was previously known only from more fragmentary, microvertebrate remains that, along with other microvertebrate remains from the Middle Jurassic (Bathonian) of the UK [18–22] share features with crown-squamates [21]. However, the disassociated nature of these specimens has limited their usefulness for understanding early squamate evolution. Here, we use high-resolution laboratory X-ray micro-CT and phase contrast synchrotron X-ray micro-CT of the new specimen to visualise the whole skeleton of *Bellairsia*, excluding the mid-distal tail and the anterior portion of the snout, which are not preserved. Phylogenetic analysis provides strong evidence that *Bellairsia* is a stem-squamate, shedding light on the origins of squamate crown-group anatomy. We also find evidence of stem-squamate affinities for some other fossil species, indicating that stem-squamates persisted in terrestrial ecosystems up to at least the mid Cretaceous (Albian-Cenomanian).

Description

The specimen is dorsoventrally compressed but preserves most of the skull and skeleton in partial articulation (Fig. 1). Based on the preserved portion of skeleton we estimate the snout-pelvis length (roughly equivalent to snout-vent length in living lizards) as roughly 60-70 mm. The specimen appears to be close to adult size, but was probably not fully mature, based on the co-ossification of the scapula and coracoid, the near fusion of the pelvic elements and of the astragalus and calcaneum in the ankle, and the ossification of the long-bone epiphyses, although slight displacements suggest these epiphyses were not yet completely fused to the diaphyses.

The skull roof is displaced ventrolaterally relative to the basicranium, due to compression, and most of the snout is missing (premaxillae, septomaxillae, vomers, anterior maxillae). The preserved part of the skull roof (complete parietal and frontal, posterior part of nasal) is about 10 mm long. The orbits are relatively large and, consequently, the frontal is only 2.2 mm wide at its narrowest point. The upper and lower temporal fenestrae were open.

The nasals are damaged but may be fused. The unpaired frontal is not sculptured, but the posterior portion bears a shallow Y-shaped groove that may mark the original positions of large head scales (scutes). The frontal is of similar width through the anterior two-thirds, with little orbital emargination, suggesting the eyes were not enlarged. Ventrally, the frontal bears shallow subolfactory ridges. Anterior to the orbit, the prefrontal facet occupies more than one third of the frontal length but, unusually, there is no posterolateral facet for the postfrontal. At the fronto-parietal suture, the straight mid-frontal margin bears a narrow shelf that underlaps the parietal, whereas the posterolateral frontal processes overlap the parietal. Together, these features create a firm, akinetic, articulation. The domed parietal is preserved in two parts but is broken rather than paired. There is no trace of a parietal foramen, and the posterior margin is extended into a median postparietal projection.

The prefrontals form the entire anterior margin of the orbit and each tapers posteroventrally to contact the jugal, lacrimal, maxilla, and ectopterygoid. The lacrimal duct lay between the lacrimal and prefrontal. The small postfrontals are dorsoventrally flattened and quadriradiate (Extended Data Fig. 2). Their medial surface is smooth, with no obvious facets for the frontal or parietal. This suggests the contact between the postfrontal and skull roof was ligamentous, an interpretation consistent with the lack of a postfrontal facet on the frontal. A shallow facet on the lateral margin may be for a postorbital, but this element has not been confidently identified. The jugal is a large, robust bone that bears a very short posterior process. The tapering postorbital process also appears short and may not have been in bony contact with the postorbital. It is therefore possible that the postorbital bar was incomplete. A flattened, rod-like element near the top of the quadrate may be part of a squamosal.

The quadrates were displaced during compaction. The left one is better-preserved. It bears a deep dorsal squamosal notch and a well-developed, but shallow, lateral conch. Ventromedially, there is a small anteromedially directed pterygoid lappet, but no medial wing (Extended Data Fig. 3).

The palate is represented by the palatines and pterygoids, with the latter completely separating the former in the midline. The palatine lacks both teeth and a choanal groove. The pterygoids met the vomers anteriorly but were not themselves in contact. A small oval group of denticles lies in the centre of each bone and the quadrate process bears an oval dorsal pit (fossa columellae) for the epipterygoid (Extended Data Figs 2, 3).

In the braincase the basisphenoid has long slender basipterygoid processes with expanded distal ends (Extended Data Fig. 3). These processes are pierced at their base by a short vidian canal. A foramen for cranial nerve VI (abducens) perforates a low crista sellaris. The basioccipital basal tubera are well developed. The lateral opening of the recessus scalae tympani is visible next to the right basal tuber. It forms an occipital recess, bordered posteroventrally by a crista tuberalis that separates it from the vagus foramen. The exoccipital is pierced by hypoglossal foramina and seems firmly fused to the basioccipital. Whether it was also fused to the opisthotic is unclear due to compression.

Only the posterior parts of each dentary are preserved in NMS G.2022.1.1. However, other specimens (NHMUK PV R12678; NMS G.2019.34.1; NMS G1992.47.10 [Extended Data Fig. 4]) give a dentary tooth count of around 25. The teeth are supported by a well-developed subdental shelf that bears a splenial facet above an open Meckelian fossa. The preserved portion of the dentary has subparallel dorsal and ventral margins and forks posteriorly into two processes of similar length. Of the post-dentary elements, the right coronoid bears a well-developed dorsal (coronoid) process but no labial process. The surangular and angular form the dorsal and posteroventral parts of the mandible respectively, and there is a well-developed retroarticular process with a sharp lateral crest.

The tooth implantation is pleurodont. The teeth are unworn, and the crowns are labiolingually flattened with apicobasally-oriented anterior and posterior grooves on their lingual surfaces. The tooth rows show lingual replacement pits and gaps for unimplanted teeth.

There are 24 deeply amphicoelous and notochordal presacral vertebrae, with free intercentra persisting intervertebrally along the whole presacral column (Fig. 2). Post-axial cervical vertebrae are short and bear a mid-ventral sagittal ridge and well-developed neural spines. It is uncertain which cervical vertebra bore the first pair of ribs, but they were certainly present from the fourth cervical. All dorsal vertebrae bear ribs. Two short sacral vertebrae are crushed against the pelvis. Most of the tail was lost.

The scapulocoracoid has a shallow scapulocoracoid embayment, as well as deep scapula and primary coracoid emarginations (Extended Data Fig. 5). The ilium, pubis, and ischium are also conjoined, albeit with some of the suture lines still visible (Fig. 3). The hind limb is much longer than the forelimb (~ 32.2 mm vs 24.5 mm), and the pes forms the longest segment. Both femoral epiphyses are slightly dislocated suggesting that they were not fully attached. The tibial epiphysis bears a slight distal concavity suggesting the presence of a distal notch. The astragalus and calcaneum are fused. Distal to them are a large trapezoidal distal tarsal (DT) IV; a much smaller DT III; and a small irregular DT II (Fig. 3). Metatarsal (Mt) I-IV are elongated and slender, whereas the hooked Mt V is very short (~2 mm), with well-developed medial and lateral plantar tubercles (Fig. 3). The pedal phalangeal formula is 2-3-4-5-4.

Phylogenetic results

Phylogenetic analyses of a modified version of the matrix of [14,23,24] recovers strong support (posterior probability [pp] = 1.0) for *Bellairsia gracilis* as a stem-squamate, as part of a sister-clade to the squamate crown-group that also includes the mid-Cretaceous taxa *Huehuecuetzpalli mixtecus* (Albian, Mexico) and *Oculudentavis naga* (Cenomanian, Myanmar) (Fig. 4). Their position close to the crown of Squamata is supported by 23 synapomorphies, including the absence of quadratojugals and gastralia, fusion of parietals, and an anterolaterally directed transverse flange of the pterygoid (see SI for complete character optimisations). Stem-squamate affinities were previously recognised for *Huehuecuetzpalli* [11,14,16,25], but our expanded analysis resolves previous uncertainties regarding *Oculudentavis*. *Oculudentavis* was initially described as a bird[26] before recognition of squamate-like features of the braincase, suspensorium and pectoral girdle[27,28], with uncertain affinities as either a stem- or crown-squamate depending on analysis[27,28].

Although we are confident that *Bellairsia*, *Huehuecuetzpalli* and *Oculudentavis* are stem-squamates, the hypothesis that they form a clade is less well-supported. Seven synapomorphies are inferred (see SI). However, four of these are not known due to missing data in *Huehuecuetzpalli* and only one step is required to remove this taxon from the grouping in parsimony analysis. Support for the position of *Bellairsia* and *Oculudentavis naga* in this clade is stronger than for *Huehuecuetzpalli* as the two require at least five more steps to move them into a different place in the tree (and see SI for shared character states of *Bellairsia* and *Oculudentavis*). *Bellairsia* and *Oculudentavis* could potentially represent an unrecognized clade of stem-squamates. However, they are separated by a long period of geological time, and future finds and analyses will test their phylogenetic relationships.

Crown squamates are supported by 13 synapomorphies that are absent in *Bellairsia*, including closure of the notochordal canal in adults[29] (except in gekkotans) and the presence of a styloid process on the radius (for details of the characters supporting these nodes, see SI). In our main analysis (Extended Data Figure 7B), *Hongshanxi* from the Middle/Late Jurassic (late Callovian or early Oxfordian) of China[30] is found in a polytomy at the base of the squamate crown-group and therefore is also a possible stem-squamate, but could alternatively be a member of the crown more advanced than Gekkota, given its procoelous vertebrae and temporal osteoderms[30].

Discussion

Near-complete skeletal preservation of the stem-squamate *Bellairsia gracilis* provides new insights into the evolutionary assembly of squamate anatomy. The anatomy of *Bellairsia* may have particular relevance to inferring character state transitions preceding squamate origins, given its early stratigraphic occurrence (~167 Ma), pre-dating the occurrence of *Huehuecuetzpalli*[17], from the Early Cretaceous (Albian) of Mexico [16,17], by more than 60 million years, and therefore with less time for the independent evolution of derived states. Previously, *Huehuecuetzpalli mixtecus* was the only taxon to be confidently identified as a stem-squamate [11,14,24,28] (but see [31] who placed it as a stem-iguanian), but has not been subject to high-resolution CT, and occurred 105 million years ago, approximately 100 million years after the inferred origin of the squamate crown-group in the Late Triassic or Early Jurassic [1,3,14]. Moreover, it possessed various specialisations, including posteriorly extended narial openings, an anteriorly placed parietal foramen, and hypothesised bipedal locomotion[17,25].

Bellairsia was original attributed to Scincomorpha[21], a grouping of scincoid and lacertoid lizards[8,11] that is not supported by molecular phylogenies[9,10,12,13]. However, this was based mainly on jaw and dental characters now known to be more widely distributed. The new specimen is considerably more complete and shows that *Bellairsia* possesses a mosaic of primitive (ancestral) and derived traits, indicating that squamate-like functional features of the suspensorium, braincase and shoulder girdle preceded the origin of their palatal and vertebral traits. *Bellairsia* (like *Oculudentavis*) shares numerous derived features with crown-squamates, including the divided metotic fissure, enclosed vidian canal, fully pleurodont teeth, absence of gastralia, and emarginated scapulocoracoid. The quadrate was streptostylic, possibly enabling anteroposterior translational movements during feeding [32], and there was a synovial joint between the epipterygoid and palate, as indicated by the fossa columellae on the pterygoid of *Bellairsia*. These observations suggest that key aspects of squamate skull function first appeared on their stem-lineage. Nevertheless, *Bellairsia* also lacks some of the derived cranial traits that are present in most squamates. For example, *Bellairsia* lacks the choanal groove found on the palatine of most crown-taxa. It also has a contact between the pterygoid and vomer, which is absent in most crown squamates due to expansion of the palatines, possibly to reduce the strain between the muzzle unit and the rest of the skull [33]. The retention of a pterygoid-vomer contact, in combination with the firm frontal-parietal suture, suggests that mesokinesis, an important functional feature of many crown-squamates, was not yet developed in *Bellairsia*.

The postcranial skeleton of *Bellairsia* also shows some apparently primitive features. The ankle retains three distal tarsals and MTV is hooked, as seen in all crown-lepidosaurs, but is not inflected, unlike that of most crown squamates. Moreover, *Bellairsia* has amphicoelous, notochordal vertebrae with intercentra present along the presacral series, whereas most extant lizards have procoelous vertebrae with intercentra restricted to the neck. Only geckos (procoelous and amphicoelous) and xantusiids have intercentra on the dorsal vertebrae [29].

The anatomy of *Bellairsia* may also help resolve questions regarding the primitive morphology of squamates and provide morphological support for gekkotans as early-diverging squamates. Classic morphological hypotheses of squamate evolution proposed Iguania as the sister to ‘Scleroglossa’, comprising all other extant squamate lineages, including gekkotans [8,11,31]. This hypothesis has been repeatedly challenged by molecular phylogenetics, which return a deeply-nested position of Iguania, and find support for Gekkota and/or Dibamidae as the sister to all other extant squamate lineages[9,10,34,35]. However, morphological evidence for this has been limited, or strongly contradictory (e.g. [11]; but see[14]), and represents one of the most contentious uncertainties of vertebrate phylogenetics (e.g. [12]).

Bellairsia shares several features with gekkotans, including the lack of a parietal foramen (also in dibamids, teiids, gymnophthalmids, *Heloderma*, *Lanthanotus*, variable in scincoids[32]), intercentra present between all presacral vertebrae (also in xantusiids [29]), and amphicoelous vertebrae. We find strong evidence that these traits are plesiomorphic for the squamate crown-group rather than being derived traits of a *Bellairsia*+Gekkota clade: the phylogenetic hypothesis that *Bellairsia* is the sister to Gekkota requires 15 additional steps and the hypothesis that *Bellairsia* is sister to Gekkota+*Dibamus* or to *Eichstaettisaurus*+(*Dibamus*+Gekkota) requires 10 additional steps. Therefore, key aspects that differentiate gekkotans from most other extant squamates may result from the retention of primitive features in Gekkota, and not from independent specialisation.

Identification of *Bellairsia* as a stem-squamate provides support for the transitional nature of the Middle Jurassic tetrapod assemblages, which retained components of archaic lineages alongside early members of the living crown groups, not only among squamates and other lepidosaurs, but also in mammals and amphibians. For example, *Bellairsia* co-occurs at both Kirtlington and the Elgol SSSI alongside the stem-lepidosaur *Marmoretta*, stem-mammals such as docodonts, and stem-salamanders such as *Marmorerpeton* [18,23,36–39]. Our phylogenetic analysis indicates that some of these stem-squamate elements persisted longer still, and with greater diversity than previously recognised. If our placement of *Huehuecuetzpalli* and *Oculudentavis* is confirmed, then stem-squamate lineages persisted on different continents alongside crown-squamates at least until the mid-Cretaceous (Albian-Cenomanian).

Taken together, our results provide evidence of the anatomical transformations involved in the origins of squamate anatomy. This early diversification phase gave rise not only to important living groups within the crown, but also to other lineages, including crownward stem-squamates, that are now extinct. The transition to more modern-like assemblages took place gradually over more than 100 million years across a global arena. The acquisition of the derived traits that characterise crown-squamates and led to the evolution of groups as diverse as snakes, geckos, chameleons and mosasaurs occurred in a mosaic fashion which we are only now beginning to understand.

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Methods

Phylogenetic analysis. We evaluated the affinities *of Bellairsia gracilis* by Bayesian phylogenetic analysis of two datasets: (Dataset 1) An amended version of the morphological character matrix of [23,24], which was originally modified from [14] and is our preferred dataset due to extensive sampling of relevant outgroups, and (Dataset 2) the matrix of [28], which was originally modified from [11]. Our main analyses use a molecular backbone to constrain the relationships of extant squamates (Extended Data Fig. 6), but we also ran minimally-constrained analyses, in which we only specified the monophyly of extant squamates relative to *Sphenodon*. Scoring of *Bellairsia* in both datasets was based on the new Skye specimen, two additional attributed dentaries from Skye (NMS G.1992.47.10 and G.2019.34.1), and the original attributed specimens from Kirtlington in Oxfordshire[21]. Modifications of Dataset 1 (from ref. [24]) include correction of some scorings of *Fraxinisaura* and *Megachirella* based on first hand observations as well as updates to scores for the Late Jurassic *Ardeosaurus*[40], and the stem-lepidosaurs *Paliguana* (Early Triassic[24]) and *Marmoretta* (Middle Jurassic[23]). We added three Mesozoic lizards, including the recently described taxa *Hongshanxi xiei* from the Middle/Upper Jurassic of China [30] and *Oculudentavis* spp. from the mid-Cretaceous of Myanmar [28], as well as *Scandensia ciervensis* from the Early Cretaceous of Spain[41]. We also added two recently-described Triassic diapsids, *Vellbergia bartholomaei*[42] and *Taytalura* *alcoberi*[43], and one new character numbered 382: metotic fissure undivided (0) or subdivided (1).

All trees from the modified matrix of [23,24] (Dataset 1) placed *Bellairsia* in a small stem-squamate clade, as the sister taxon to the Mexican Cretaceous *Huehuecuetzpalli* [16] + *Oculudentavis* [28] (Extended Data Figs 7–8), including using the full molecular backbone constraint (Extended Data Figs 7 and 8A) and when minimally constrained (Extended Data Fig. 8B), and when omitting taxa with less certain phylogenetic affinities that limit resolution of the consensus tree when included in analyses (Extended Data Fig. 7): the Early Cretaceous (Barremian) *Scandensia ciervensis*[41] from Spain and the Triassic diapsid *Vellbergia bartholomaei*[42]. *Scandensia*, for which the skull is incompletely known, grouped with *Bellairsia*, *Huehuecuetzpalli* and *Oculudentavis* on the squamate stem when included, and *Vellbergia* groups among stem-lepidosaurs, but with low posterior support as to its precise affinities (Extended Data Fig. 8). Neither taxon causes topological differences to the tree shown in Fig. 4 (based on Extended Data Fig. 7).

Analysis of the matrix of [28] (itself modified from [11]) also finds strong support for *Bellairsia* as a stem-squamate, though in a group with only *Oculudentavis*, more crownward than *Huehuecuetzpalli* (Extended Data Figs 9 and 10). This result was returned whether extant squamates were constrained to a molecular backbone (Extended Data Fig. 9), or unconstrained (other than to specify *Sphenodon* and other rhynchocephalians as an outgroup; Extended Data Fig. 10). It therefore does not conflict with the results of Dataset 1, or with our broad conclusions.

Phylogenetic inference was carried out using Bayesian inference in MrBayes 3.2.7a[44], using a FBD tree prior [45,46] and relaxed clock transition model. The ages of all OTUs were specified using a uniform distribution between their minimum and maximum possible stratigraphic ages, modified from ref [14] to reflect updated or corrected knowledge of the ages of various taxa. Analysis of Dataset 1 was run for 100 million generations, sampled every 10,000th generation, with a burn-in of 50%. The effective sample size was greater than 200 for all tested parameters and an average potential scale reduction factor was 1.01 or less on all parameters, indicating convergence. Analyses of Dataset 2 took longer before convergence and were run for 200 million generations. In addition to topology and branch lengths, our analysis return estimates of variation in rate of evolution (transition frequencies among character states). These are shown for completeness in Extended Data Figs 7–10.

Computed tomography (CT). We imaged the specimen in 3D using lab-based and synchrotron computed tomography (CT) and segmented these to produce 3D digital models of the skeleton in Avizo Lite software.

Lab-based CT scans were conducted using a Zeiss Xradia 520 Versa in the Department of Materials, University of Oxford. The whole skeleton was scanned at a voxel size of 20.10 µm, and the anterior part of the skeleton was also scanned again, at a voxel size of 11.10 µm. The left forelimb was segmented from the scan of the whole specimen. Furthermore, portions of this image volume were merged to our synchrotron data prior to segmentation of the pes. This was done to restore pedal phalanges that were lost during physical preparation of the specimen prior to synchrotron scanning.

Propagation phase contrast synchrotron X-ray micro-Computed Tomography. NMS G.2022.1.1 was characterised at the ID19 beamline of the European Synchrotron Radiation Facility (ESRF, Grenoble France) using propagation phase contrast synchrotron X-ray micro-computed tomography. Imaging of the specimens was not done on the whole block but rather on specific regions of interest determined from prior investigation using laboratory X-ray micro-computed tomography. In total, 11 regions of interest were imaged on ID19, focussing on the skull, hind limbs and the pelvis area. All datasets were acquired with identical parameters: white beam from a wiggler 150B (gap 38 mm) filtered with 12 mm of copper; sample detector distance of 3 m; indirect detector comprising a 100 µm Ce doped Gadolinium-Gallium-Garnet scintillator, 1.5x magnification from a set of photographic lenses (Victor Hasselblad AB, Gothenburg, Sweden), a PCO.edge 4.2 USB 3 (PCO, Kelheim, Germany); the combination of the beam and indirect detector resulted in a total integrated detected energy of 134 keV and an isotropic reconstructed voxel size of 4.24 µm. Each acquisition consisted of 6000 projections of 0.1 second each (4 frames of 0.025 seconds accumulated) over a 360° rotation of the specimens. The centre of rotation of the sample manipulator was shifted laterally by a distance corresponding to 800 pixels on the detector (i.e., so-called half acquisition protocol [47], allowing to reconstruct tomograms with a diameter of 3648 pixels. The tomographic reconstruction was performed with PyHST2 [48] using the single distance phase retrieval approach [49]. Post-processing of the data included: change of the dynamic range from 32 to 16-bit, ring correction [50], cropping of the data.

Data availability

All CT data and 3D models reported in this paper are available at Morphosource for open download at www.morphosource.org/projects/00000C672. Our phylogenetic scripts, including full analytical settings, are available at http://doi.org/10.17605/OSF.IO/WHJT7.

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Figures

Figure 1. Skeleton of *Bellairsia gracilis* with bones digitally segmented. **a**, Preserved skeleton in dorsal view. **b**, Preserved skeleton in ventral view (see Extended Data Figs 2-4 for labelling of skull parts).

Figure 2. Cervical part of the vertebral column of *Bellairsia*. **a**, Atlas and axis in dorsal view. **b**, Atlas and axis in ventral view. **c-g**, Third, fourth, and fifth vertebrae with intercentra from various views. **h**, Intercentrum of the 22nd vertebra. **i-j**, Anterior and posterior cervical ribs.

Figure 3. Right pes and pelvis of *Bellairsia*. **a**, Preserved elements of the pes in ventral and dorsal views. **b**, Fifth metatarsal in plantar, medial, dorsal, and lateral view. **c**, Pelvis in medial and lateral view.

Figure 4. Linear reconstruction of the skull of *Bellairsia* and its phylogenetic position. **a**, Cranium, dorsal view. **b**, Cranium, left lateral view. **c**, Mandible, lingual view. **d**, Mandible, buccal view. **e**, Phylogenetic tree showing position of *Bellairsia* after a Bayesian analysis of the diapsid dataset (see Methods; the summary tree shown here is based on majority rule consensus of the posterior tree distribution from analysis of our modified version of the data matrix from refs [14,23,24] with molecular backbone constraint; for full tree see Extended Data Fig. 7). Numbers at nodes indicate posterior probabilities and nodes with posterior probabilities less than 0.5 are shown as unresolved. The lighter grey lines forming the snout region in A-D are speculative as these regions are not preserved, but overall snout length is based on jaw length.

Extended data figures

Extended Data Fig. 1. Preserved skeleton

A slab with visualized preserved skeleton of *Bellairsia gracilis* Evans, 1998 from the Middle Jurassic, Kilmaluag Formation, Skye. **a**, Dorsal. **b**, Ventral. **c**, Close-up of the visualized skeleton in the rock from anteroventral view.

Extended Data Fig. 2. Orbital bones

Bones surrounding the orbit of *Bellairsia*. **a**, Right orbit in dorsal view. **b**, Right orbit in ventral view. **c**, Left orbit in dorsal view. **d**, Left orbit in ventral view.

Extended Data Fig. 3. Posterior skull

Posterior part of the skull of *Bellairsia*. **a**, Dorsal view. **b**, Ventral view.

Extended Data Fig. 4. Mandible

Right mandible (ELGOL2016 021), dentary and premaxilla (NMS G1992.47.10) from Kilmaluag Formation, Skye; frontal, left premaxilla, left dentary, maxilla from Kirtlington. **a**, ELGOL2016 021 mandible in medial view. **b**, ELGOL2016 021 in lateral view. **c**, ELGOL2016 021 in dorsal view. **d-h**, NMS G1992.47.10 preserving right dentary and premaxilla, with dentary in (d) occlusal, (f) lingual, and (h) buccal views, and premaxilla in (e) lingual and (g) buccal views. **i**, NHMUK PV R16331 frontal from Kirtlington in dorsal and ventral views. **j**, NHMUK PV R12680 left premaxilla from Kirtlington, in dorsal, lingual, and buccal views. **k**, NHMUK PV R12678 left dentary from Kirtlington, in posterior, lingual, and buccal views. **l**, NHMUK PV R12679 anterior tip of right maxilla from Kirtlington in buccal and lingual views.

Extended Data Fig. 5. Forelimb

Left forelimb of *Bellairsia*. **a**, Whole preserved limb. **b-g**, Humerus in various views. **h-j**, Bones of the manus.

Extended Data Fig. 6. Molecular backbone constraint trees.
a, Constraint tree for Dataset 1 (dataset modified from ref. 24). **b**, Constraint tree for Dataset 2 (dataset modified from from ref. 28).

Extended Data Fig. 7. Bayesian analysis of Dataset 1 with taxa omissions
Majority rule consensus tree from Bayesian analysis of Dataset 1 (modified from ref. [24]) including molecular backbone constraint and omitting taxa with unstable phylogenetic positions that limit resolution of the consensus tree (*Scandensia ciervensis* and *Vellbergia bartholomaei*). **a**, Majority rule consensus including nodes with posterior probability <0.5; **b**, Majority rule consensus excluding nodes with posterior probability <0.5.

Extended Data Figure 8. Bayesian analysis of Dataset 1 without taxa omissions
Majority rule consensus tree from Bayesian analysis of Dataset 1 (modified from ref. [24]), not omitting any taxa. **a**, Tree from analysis including molecular backbone constraint; **b**, tree from analysis with minimal backbone constraint (constraining monophyly of extant squamates relative to *Sphenodon*).

Extended Data Figure 9. Bayesian analysis of Dataset 2 with molecular constraint
Majority rule consensus tree from Bayesian analysis of Dataset 2 (modified from ref. [28]) including molecular backbone constraint.

Extended Data Figure 10. Bayesian analysis of Dataset 2 without molecular constraint
Majority rule consensus tree from Bayesian analysis of Dataset 2 (modified from ref. [28]) without molecular backbone constraint.

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Author contributions

MT, RBJB and SEE planned the research. RBJB and EP collected new specimens. RBJB and VF scanned the specimens. MT segmented the CT data, wrote the description and drafted the manuscript with RBJB and SEE. MT and EP constructed the figures. MT, RBJB and SEE conducted the phylogenetic analysis. All authors provided feedback on the manuscript.

Declaration of interests

The authors declare no competing interests.

Extended Data and Supplementary Information is available for this paper.

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Supplementary Information

Systematic Palaeontology; extended osteological description; comments on phylogeny and results; supplementary references; list of synapomorphies of particular clades.