Integumentary remains and abdominal contents in the Early Cretaceous Chinese lizard, *Yabeinosaurus* (Squamata), demonstrate colour banding and a diet including crayfish

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Highlights:

- A new specimen of *Yabeinosaurus robustus* is the largest complete example on record
- Abdominal contents show that this individual had fed on a large crayfish
- Integumentary traces indicate the lizard's body was strikingly banded in life

Abstract

The Early Cretaceous lizard *Yabeinosaurus* is well-represented in the Jehol Biota of northeast China, with specimens yielding information on ontogenetic development, reproductive strategy, and diet, as well as skeletal morphology. However, a large, well-preserved, new specimen of *Yabeinosaurus robustus* from the Lamadong locality, Liaoning, provides further insights into the morphology and biology of this species. Integumentary traces demonstrate that, in life, *Y. robustus* was coloured with well-defined light and dark banding through both the body and the tail. The integumentary traces also confirm that *Yabeinosaurus* was covered with thin, non-overlapping osteoderms, each of which seems to have underlain only part of a scale. Previous specimens have contained fish remains, suggesting that *Yabeinosaurus* foraged in, or close, to the water. The new specimen supports that hypothesis as it contains the remains of a large crayfish, identified as belonging to the species *Palaeocambarus licenti* Taylor et al. 1999. Body parts of the crayfish provide an estimated original total length of 120-140 mm.

Keywords

Early Cretaceous; gut contents; lizard; crayfish; skin colour; China

1. Introduction

Yabeinosaurus (Endo and Shikama 1942) was the first lizard to be described from the Chinese Early Cretaceous Jehol Biota. However, the original authors, and many that followed (e.g. Estes 1983; Hoffstetter 1964; Ji et al. 2001), failed to recognize that the type specimen was juvenile, leading to misdiagnosis (as small and weakly ossified) and misattribution (as a gekkotan). The recovery of mature specimens (Evans and Wang 2012; Evans et al. 2005) revealed that the adults of *Yabeinosaurus* were actually large, robust lizards. They are certainly not gekkotan, but their phylogenetic position currently remains unresolved. Phylogenetic analyses based on morphological characters have placed it either on the stem of Scleroglossa (essentially all non-iguanian squamates in a morphological tree; Conrad 2008; Evans et al. 2005), of Anguimorpha (Conrad 2008), or of Scincoidea (Tałanda 2018).

Yabeinosaurus robustus (sensu Dong et al. 2017) has been reported from both the Yixian Formation (~125 Ma, Wang and Zhou 2003; Zhou 2006) and the overlying Jiufotang Formation (~120 Ma, He et al. 2004), both part of the Jehol Group. It is unique among Early Cretaceous lizard specimens in being represented by several dozen specimens, representing a full ontogenetic range. As a result, its skeletal anatomy and ontogeny is relatively well known. Moreover, like other Jehol Biota fossils, many of the *Yabeinosaurus* specimens have been recovered from very fine silty mudstones and shale. This can result in the preservation of soft tissue structures and delicate body contents that provide rare insights into lifestyle and ecology. Notable examples include a gravid female *Yabeinosaurus* containing multiple near-term embryos, indicative of viviparity (Wang and Evans 2011), and several specimens with fish remains in the gut (Evans and Wang 2012; Wang and Evans 2011; Zhou and Wang 2010). Here we report on a new specimen of *Yabeinosaurus robustus* with parts of a crayfish in its gut, providing confirmation of aquatic or riparian foraging. Moreover, soft tissue preservation of the lizard's integument demonstrates that, in life, *Yabeinosaurus robustus* was distinctively coloured with a strong light/dark banding pattern along the body and tail.

2. Material and methods

The specimen, YLSNHM00798, was recovered from the Lamadong locality, Jianchang County, Liaoning, China (Fig. 1) and is accessioned in the collections of the Yingliang Stone Nature History Museum (YLSNHM), Nan'an, China. The deposits from which it was excavated are those of the Jiufotang Formation that have been dated as Aptian, approximately 120 Ma (He et al. 2004). The Jiufotang Formation comprises primarily lacustrine sandstones, shales, mudstones, and interbedded tuffs (Chang et al. 2003). Other vertebrates from the locality include confuciusornithid, enantiornithine, and ornithurine birds, lizards, pterosaurs, and mammals (Wang et al. 2011; Zhou et al. 2010).

The specimen was imaged at high resolution using a Canon digital camera (SD Mark III EF 100mm f/2.8 IS USM) fitted to a macro rail (Cognisys); the images of the part and counterpart blocks were then processed using helicon Focus 5.1 and Adobe Photoshop software to increase the depth of field in the images. Adobe Photoshop was also used to digitally dissect the abdominal contents from the background.

3. Results

3.1 Yabeinosaurus morphology

YLSNHM00798 consists of the part and counterpart of a relatively large lizard (estimated 220 mm snout–pelvis length [SPL], 580 mm total length) with well-preserved skull, axial skeleton and the fore- and hind limbs (Fig. 2).

All features of the skull (e.g. coarse cranial sculpture, strongly interdigitated fronto-parietal suture, distinctive parietal; sharp conical teeth, large postfrontal partially closing the upper temporal fenestra, reduced postorbital closely fitted against the postfrontal) match the diagnosis of *Yabeinosaurus robustus* (Dong et al. 2017) (Fig. 3A). As such, this is the largest complete skeleton of the species on record; the holotype, IVPP V 16361, has an SPL of ~190 mm (Evans and Wang 2012). Moreover, YLSNHM00798 is the first adult specimen with a complete, non-autotomised tail that is almost twice the length of the body. However, even with a skull length of ~56 mm, YLSNHM00798 is still substantially smaller than IVPP V

13285 (Evans et al. 2005), a skull of ~79 mm in length, giving an estimated SPL of at least 300 mm (total length ~800 mm). Although the skeleton of YLSNHM00798 is well ossified, there is some evidence of immaturity: the scapula and coracoid, the components of the pelvis, and the astragalus and calcaneum are sutured but not co-ossified; and the articular ends of the long bones have ossified, but detached, epiphyses.

Yabeinosaurus robustus is relatively well known from several well-preserved skeletons. The new specimen, YLSNHM00798, confirms previous descriptions (e.g. in the form of the postorbitofrontal complex and skull roof morphology, Fig. 3A), but the braincase and palate of this taxon remain poorly known. In the postcranial skeleton, YLSNHM00798 preserves a complete tail with autotomy septa in all but the proximal four caudal vertebrae (Fig. 2) and shows the scapulocoracoid (Fig. 3C), and parts of the pelvis (Fig. 3D) clearly for the first time. The scapula is relatively tall, narrow element without dorsal expansion, and the hemicircular coracoid plate has a small primary emargination. The ankle and pes are well preserved, demonstrating the presence of a third and fourth distal tarsal (Fig. 3E).

Although some other specimens of *Yabeinosaurus robustus* preserve skin traces (Evans et al. 2005, Evans and Wang 2012), YLSNHM00798 is remarkable in showing a very clear pattern of light and dark bands that cover both the body and the tail. From the shoulder girdle to the pelvis, there are 15–17 dark bands with an average width of around 50 mm, separated by narrower light bands of about 20 mm in width. The tail bears about 33 dark bands that are wider than those on the body (60-70 mm), again separated by light bands of ~20 mm in width.

YLSNHM00798 also confirms the presence of small rounded osteoderms across the body (Evans and Wang 2012). The osteoderms are thin mineralized plates, roughly circular, and coarsely woven (Fig. 2, 3B). They are spaced across the skin, in both the light and dark regions, and do not form an imbricated sheet. There are no obvious osteoderms associated with the skull, but we cannot be certain they were not originally present, for example in the gular region, prior to preparation.

3.2 Abdominal contents

As noted above, several specimens of *Yabeinosaurus robustus* contain fish remains within the abdominal cavity. However, YLSNHM00798 is unique in preserving the remains of a large crustacean within the body cavity (Fig. 4). The gut contents include: 1, large pereiopods, in which the entire dorsal surface of the cuticle is covered with fine granulations; 2, an elongate fragment of one of the pereiopods, possibly a propodus (proximal part with claw); 3, rostrum area; and 4, broken antennule(s) and antenna(e).

Two large decapods of the Infraorder Astacidea, commonly known as crayfish, have been recorded from the Jehol Biota. They are *Cricoidoscelosus aethus* and *Palaeocambarus licenti* (Taylor et al. 1999). There is also a small crustacean, *Liaoningogriphus quadripartitus* (Shen et al. 1998) that has been referred to the Spelaeogriphacea.

In both *Palaeocambarus licenti* and *Cricoidoscelosus aethus* the propodus and dactylus of pereiopod 1 (see Fig. 5 for terminology) were modified to form a robust claw that was heavily decorated with spines and pitting. Although the crayfish limb seen here is incomplete, the largest visible unit (most likely the propodus) is elongate and slender. This suggests it came from a specimen of *Palaeocambarus licenti* (Fig. 5A) and not *Cricoidoscelosus aethus*, which possessed broader chelae (pereiopod 1). Another identifiable crayfish element is a triangular rostrum. Although incomplete, it possesses smooth sides and gradually increases in width towards its proximal end, more closely resembling the rostrum of *P. licenti* than *C. aethus* (which possessed a more rounded base). The rostrum seen here is slightly less than 1 cm long, suggesting that the crayfish was 12-14 cm in total length. This would have been a substantial meal for the lizard (Fig. 5B), although it is likely that only parts of the crayfish were eaten.

Although the Jehol Biota has been studied extensively in recent years, the environmental setting(s) of the region at the time of deposition has not yet been fully established (Hethke et al. 2013). *Palaeocambarus licenti* probably lived in the shallow marginal regions of a freshwater lake, surrounded by large amounts of living plant and animal material as well as decaying organic matter.

3.3 Taphonomy

It is notable that, despite the exceptional preservation of the skin and the relatively well-preserved skull and hind limbs, the ribs are disrupted and disarticulated. This is likely to be due to decomposition of the gut, perhaps within a partly mummified exposed carcase.

4. Discussion

4.1 New morphological information

4.1.1 Osteoderms

Osteoderms are small, mineralized structures that lie within the dermis of many reptiles and almost certainly represent a primitive trait (Vickaryous and Sire, 2009). However, lizards show by far the greatest range of variation in osteoderm size, shape, pattern and distribution. Within this variation, there are three main patterns: a complete body covering of imbricate flattened plates that may be single or compound (as in many scincoids and anguids); nodular osteoderms that are juxtaposed but do not overlap, and may be separated by soft tissues (e.g. *Heloderma* and *Gekko*); and thin vermiform osteoderms that form a chain-mail-like covering (many *Varanus*, *Lanthanotus*). In YLSNHM00798, the osteoderms are most similar to those of *Heloderma* in being non-imbricate, but they are thinner and flatter, and seem to be limited to the distal part of each scale. They appear to be constructed of rather loosely woven bone, without the capping of denser tissue that characterizes the osteoderms of *Heloderma* and many other lizards (Vickaryous & Sire, 2009; SE and collaborators, work in progress). Given the apparent difference in distribution density of the osteoderms between specimen IVPP V 16362 (Evans and Wang 2012, SPL ~135 mm) and the larger YLSNHM00798 (SPL ~220 mm), it seems likely that these structures became larger and denser with age, as in the living *Heloderma* (Vickaryous and Sire 2009). Nonetheless, it is unlikely that they ever formed an overlapping sheet like that of many scincoids and anguids.

There is also no evidence of cranial osteoderms but it remains possible that some of these were lost during preparation. The skull roofing bones are heavily sculptured but this is the result of direct metaplastic ossification of the dermis adjacent to the skull bones, not separate osteodermal ossifications that have fused to skull bones (as, for example, occurs in mature specimens of *Heloderma*). This is evident from an examination of growth series of *Yabeinosaurus* in which the sculpture gradually develops with age.

4.1.2 Colour pattern

One of the most conspicuous features of the new specimen is the clear evidence of original transverse colour banding. Linear stripes that run parallel to the body axis are common among extant lizards, particularly in small active foragers like scincids, small teiids, lacertids, and gymnophthalmids. Banding that runs perpendicular to the body axis is less common and although examples can be found in most major lizard clades (most strikingly in Banded geckos of the genus *Coleonyx*), it tends to be limited to a few taxa in each. Numerous recent studies have suggested that linear stripes on a fast-moving lizard make it difficult for a predator to gauge speed, so that it is more likely to grab the expendable tail than the anterior body (e.g. Hughes et al. 2015; Murali and Kodandaramaiah 2016; Stevens et al. 2008). Studies that have attempted to assess the advantages of transverse bands versus longitudinal stripes (e.g. Allen et al. 2013; Hughes et al. 2015; Jackson et al. 1976; Stevens et al. 2008; Von Helversen et al. 2013) have failed to reach a consensus. Nonetheless, several authors suggest that transverse banding might have a 'dazzle effect' that also affects perception of speed. Jackson et al. (1976) concluded that regular transverse banding might be an intermediate between the antipredator strategies of defense (where cryptic coloration is best) and rapid flight (with longitudinal stripes). Hughes et al. (2015) made a similar suggestion, associating transverse banding with erratic movements rather than rapid escape behavior. This would certainly be consistent with the large size, solid build, and relatively short limbs of *Yabeinosaurus*.

4.2 Diet and lifestyle

As noted above (1. Introduction), fish remains have been found in the gular region and abdominal cavity of several specimens of *Yabeinosaurus robustus* (Evans and Wang 2012; Wang and Evans 2011; Zhou and Wang 2010). These remains suggest that *Yabeinosaurus* foraged on the shoreline of the Jehol lake, or that it actively hunted in the water, despite a lack of obvious morphological specializations for swimming (e.g. no deep compressed tail or webbing between the toes). The recovery of a new specimen of *Yabeinosaurus* with parts of a crayfish in its body cavity provides confirmation of aquatic or riparian foraging, although the apparent absence of the crayfish carapace within the body cavity may indicate scavenging of a moulted crayfish remains at the shoreline rather than active predation.

5. Conclusions

The new specimen of *Yabeinosaurus robustus* described herein adds to our knowledge of this Cretaceous species in relation to its outward appearance and dietary preferences. With respect to the latter, the presence of crayfish remains in the abdomen confirms the conclusions drawn from previous specimens, with fish bones in their guts, that this lizard is likely to have lived and fed in close proximity to the water body central to the Jehol ecosystem. This may also explain the relative abundance of *Yabeinosaurus* specimens in the deposits. A similar lifestyle has been proposed for the Iberian Cretaceous taxon *Meyasaurus* (Evans and Barbadillo 1997) which is the most commonly recovered lizard from the wetland environment of Las Hoyas (Evans and Bolet 2016). *Y. robustus* was much larger than other Jurassic and Early Cretaceous lizards recovered to date. As a heavy-bodied, short-limbed, shoreline forager, *Yabeinosaurus* could have been an attractive and vulnerable prey species for contemporaneous dinosaurs and predatory birds. The striking transverse colour banding may have been part of its defense strategy.

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Author Contributions

LX and SE planned the research; KN collected the fossil, supervised technical preparation and conservation; LX, RT, KN, and SE carried out the research; LX, RT and SE wrote the paper.

Declarations of Interest: none.

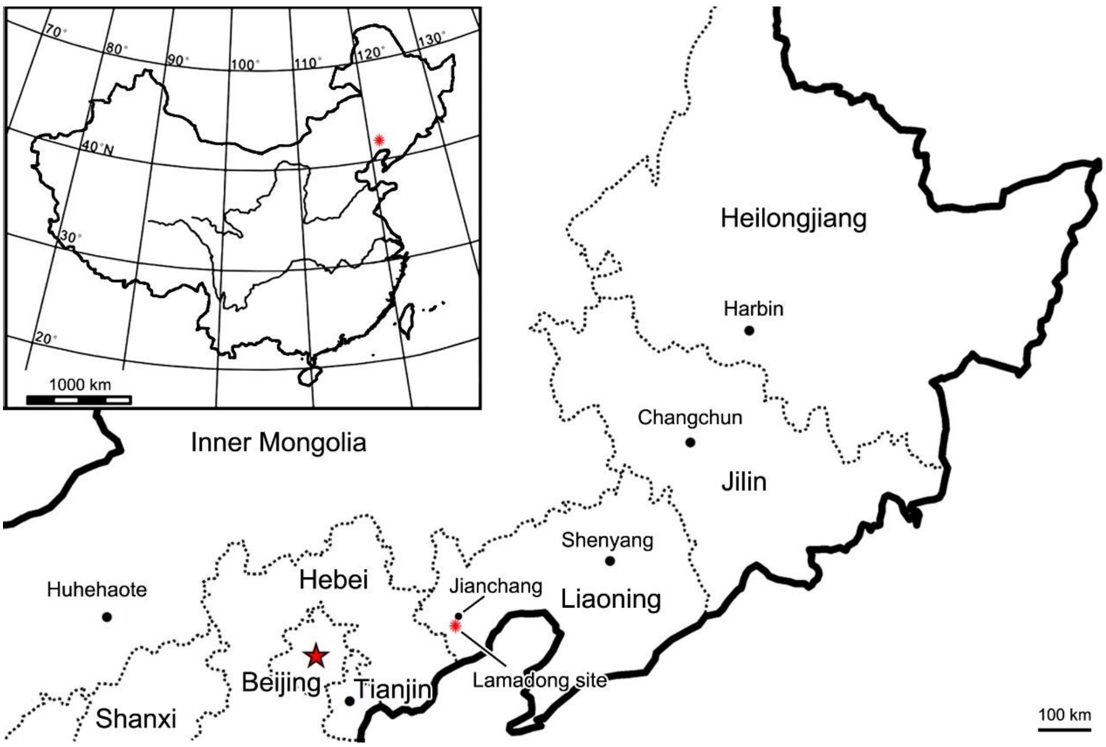

Figure 1. Map of Liaoning Province, China, showing the locality near Lamadong Village in Jianchang County, Liaoning, where specimen YLSNHM00798, referred to *Yabeinosaurus robustus*, was recovered.

Figure 2. The complete specimen of *Yabeinosaurus robustus* (YLSNHM00798), showing distinct colour banding along the body. Scale bar = 50 mm.

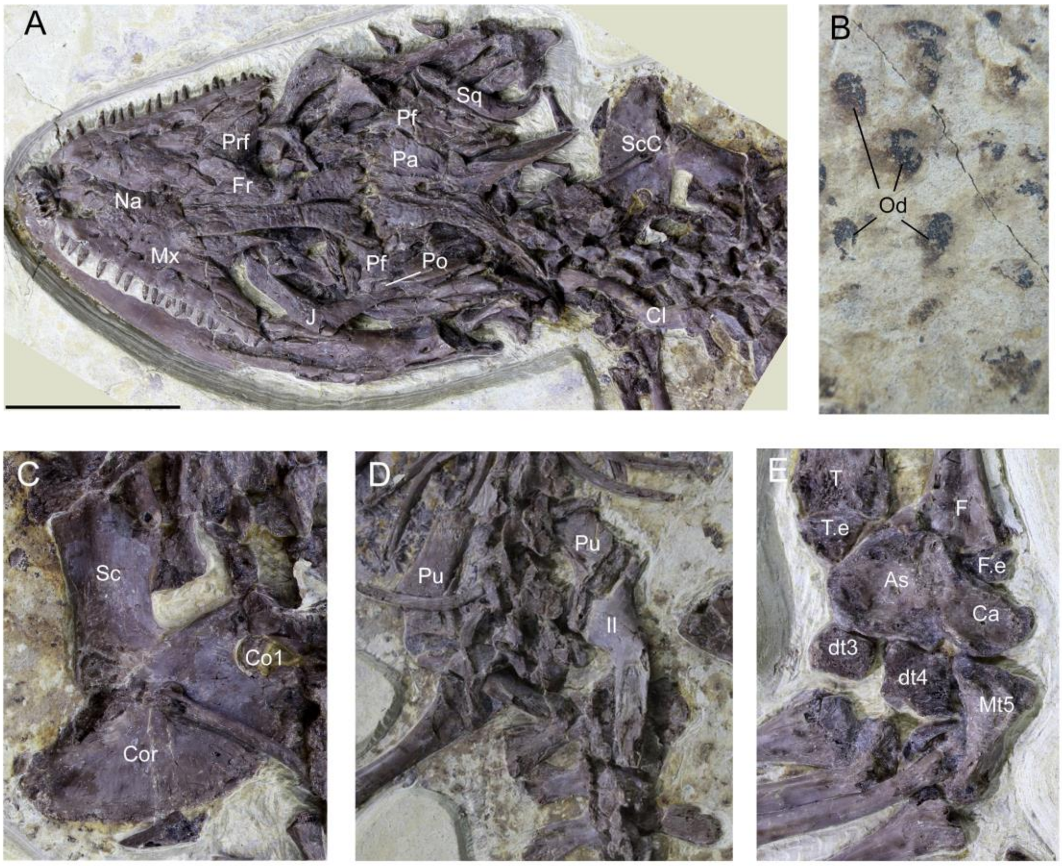

Figure 3. Morphology of *Yabeinosaurus robustus* (YLSNH00798), with A) dorsal view of skull; B) osteoderms; C) right scapulocoracoid; D) pelvis; and E, left ankle. Scale bar in (A) = 20 mm. Abbreviations: As, astragalus; Ca, calcaneum; Cl, clavicle; Cor, coracoid; Co.1, primary coracoid emargination; dt3,4, distal tarsals 3 and 4; F, fibula; F.e, fibular epiphysis; Il, ilium; Mt5, Metatarsal 5; Mx, maxilla; Na, nasal; Od, osteoderms Pa, parietal; Pf, postfrontal; Prf, prefrontal; Pu, pubis; Sc, scapula; ScC, scapulocoracoid; Sq, squamosal; T, tibia; T.e, tibial epiphysis.

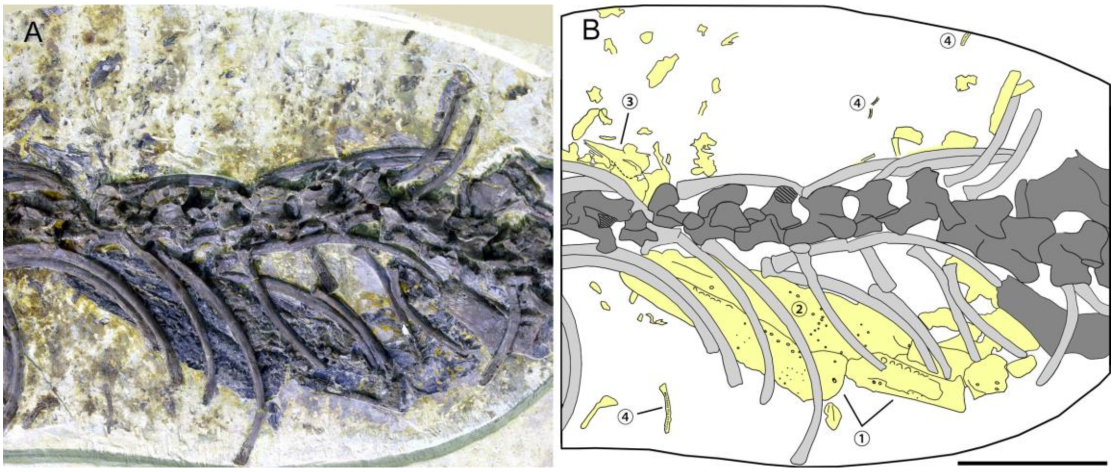

Figure 4. *Yabeinosaurus robustus* (YLSNH00798) with parts of the crayfish *Palaeocambarus licenti* in the gut. A) abdominal region of the specimen; B) line drawing of (A) showing the component parts of the crayfish described in the text, 1, pereiopods with granulations on surface, 2, elongate fragment of one of the pereiopods, possibly a propodus, 3, rostrum area, and 4, broken antennule and antenna. Scale bar = 20 mm

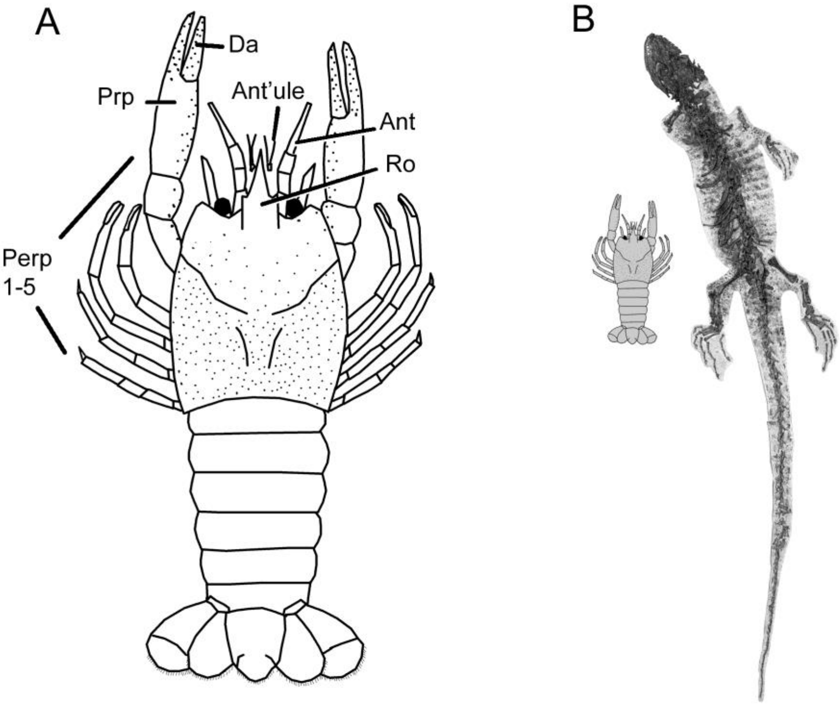

Figure 5. *Palaeocambarus licenti*. A) Drawing of the crayfish modified from Taylor et al. (1999) to show parts discussed in the text; B) outline of *Palaeocambarus* scaled to match the size of the individual within *Yabeinosaurus* as preserved in YLSNHM00798. Abbreviations: Ant, antenna; Ant'ule, antennule; Da, dactylus; Perp 1-5, first to fifth pereiopods; Prp, propodus; Ro, rostrum.