

A gravid lizard from the Cretaceous of China and the early history of squamate viviparity

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Received: 22 April 2011 / Revised: 20 June 2011 / Accepted: 22 June 2011 / Published online: 16 July 2011
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Abstract Although viviparity is most often associated with mammals, roughly one fifth of extant squamate reptiles give birth to live young. Phylogenetic analyses indicate that the trait evolved more than 100 times within Squamata, a frequency greater than that of all other vertebrate clades combined. However, there is debate as to the antiquity of the trait and, until now, the only direct fossil evidence of squamate viviparity was in Late Cretaceous mosasauroids, specialised marine lizards without modern equivalents. Here, we document viviparity in a specimen of a more generalised lizard, *Yabeinosaurus*, from the Early Cretaceous of China. The gravid female contains more than 15 young at a level of skeletal development corresponding to that of late embryos of living viviparous lizards. This specimen documents the first occurrence of viviparity in a fossil reptile that was largely terrestrial in life, and extends the temporal distribution of the trait in squamates by at least 30 Ma. As *Yabeinosaurus* occupies a relatively basal

position within crown-group squamates, it suggests that the anatomical and physiological preconditions for viviparity arose early within Squamata.

Keywords Viviparity · Squamata · Reptilia · Cretaceous · China

Introduction

Among living amniotes, viviparity is a reproductive trait typically associated with therian mammals. However, although birds, crocodiles, turtles and tuatara are exclusively egg-laying, viviparity (sensu Shine 1985) does occur in around 20% of Squamata, the group that encompasses lizards, snakes and amphisbaenians (Shine 1985). In squamate viviparity, the eggs are retained within the uterus until the young are fully developed. The reduction of the eggshell brings the embryo in contact with the uterine walls, permitting the exchange of gases and, in the most derived cases, nutrients (Shine 1985; Blackburn 2000, 2006). Viviparity is estimated to have arisen more than 100 times within Squamata (Blackburn 2000, 2006; Lee and Shine 1998; Schulte and Moreno-Roark 2010; Shine 1985), more than in all other vertebrates combined (Blackburn 2006), and most major squamate clades have at least one taxon showing the trait (exceptions being Teiidae, Varanidae, Helodermatidae and non-diplodactylid geckos, Shine 1985; see [Electronic supplementary materials](#)). This suggests that the preconditions for squamate viviparity (e.g. loss of embryonic diapause permitting egg retention, enhanced vascularity of the uterine walls, Blackburn 2000, 2006; Shine 1985) are widespread, but there is disagreement as to the antiquity of the trait. Blackburn (2006) argued that unlike mammalian viviparity which arose in the Cretaceous, squamate viviparity evolved

Communicated by: Robert Reisz

Electronic supplementary material The online version of this article (doi:10.1007/s00114-011-0820-1) contains supplementary material, which is available to authorized users.

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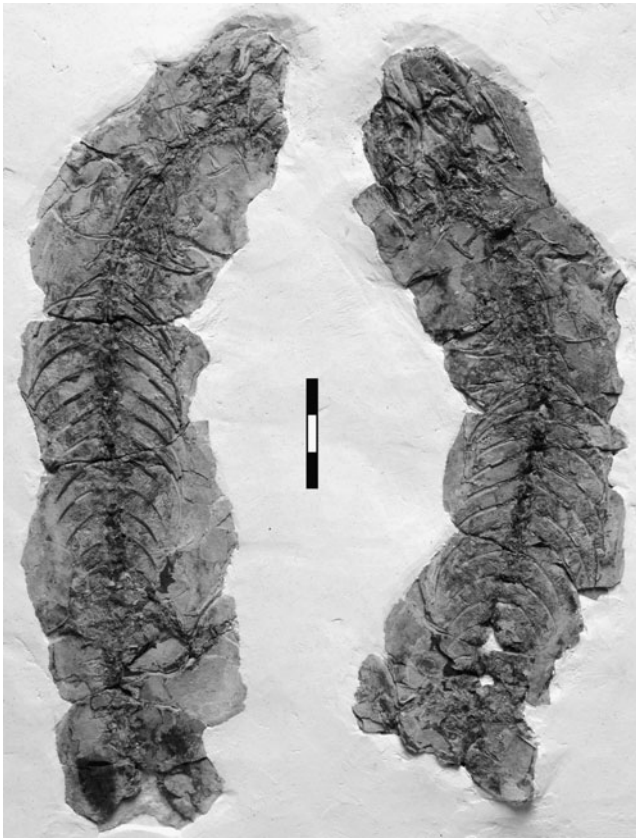


Fig. 1 The gravid female *Yabeinosaurus* (IVPP V 18005) (part and counterpart). Scale bar=3 cm

relatively recently in many lineages in conjunction with Pleistocene climatic cooling and glaciation. However, based on divergence data analysis, Schulte and Moreno-Roark (2010) concluded that in 13 of the 14 iguanian lineages examined, viviparity evolved at least 32 million years ago (mya).

Direct evidence from the fossil record is, for obvious preservational reasons, exceptionally rare (Delfino and Sánchez-Villagra 2010). Among fossil reptiles generally, viviparity has been recorded only in aquatic clades: marine ichthyosaurs (e.g. Maxwell and Caldwell 2003) and sauropterygians (e.g. Cheng et al. 2004; Renesto et al. 2003); freshwater choristoderes (Ji et al. 2010; Wang et al. 2005 [although the latter was reported as cannibalism]); and marine mosasauroids (Bell et al. 1996; Caldwell and Lee 2001). The latter, a specialised group of Late Cretaceous lizard predators with no modern ecological equivalents, currently provide the only examples of viviparity in the squamate fossil record: the aigialosaur *Carsosaurus* (c. 95 mya, Caldwell and Lee 2001) and the more derived mosasaur *Plioplatecarpus* (c. 72 mya, Bell et al. 1996). Here, we describe an example of viviparity in a more generalised, largely terrestrial lizard, *Yabeinosaurus tenuis*, from the Lower Cretaceous deposits of northeastern China (c. 125–120 mya).

Description

Yabeinosaurus was the first lizard to be described from the Chinese Jehol Biota (Endo and Shikama 1942), and it is now relatively well known (Evans et al. 2005) from both the Yixian Formation (~125 mya, Wang and Zhou 2003; Zhou 2006) and the overlying Jiufotang Formation (~120 mya, He et al. 2004). Phylogenetic analyses based on morphological characters place it either on the stem of Scleroglossa (essentially all non-iguanian squamates in a morphological tree; Conrad 2008; Evans et al. 2005) or of Anguimorpha (Conrad 2008). The new specimen, IVPP V 18005, was recovered from the Jiufotang Formation in Jianchang County, Liaoning Province. The vertebrate assemblage at this locality also includes *Lycoptera* fish,

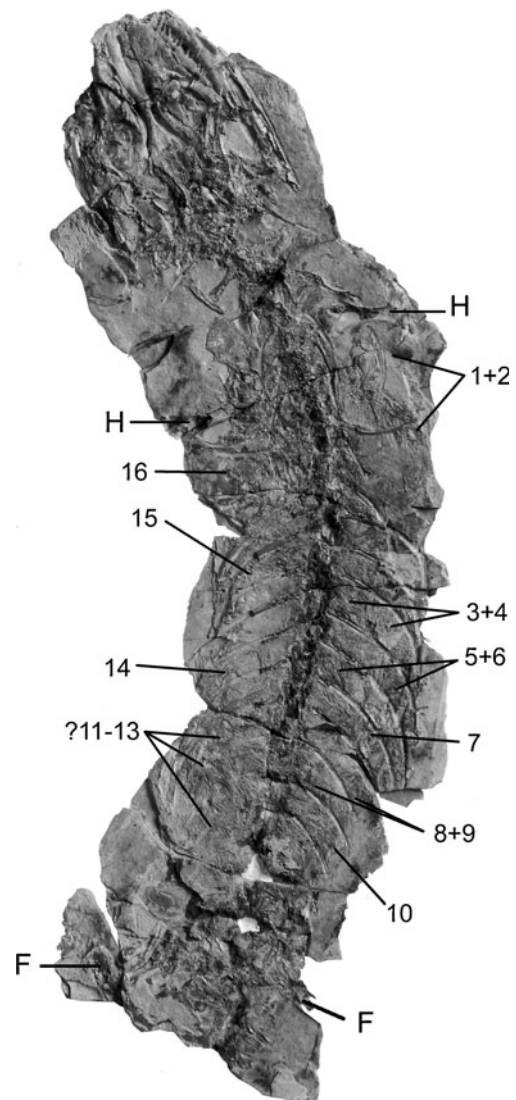
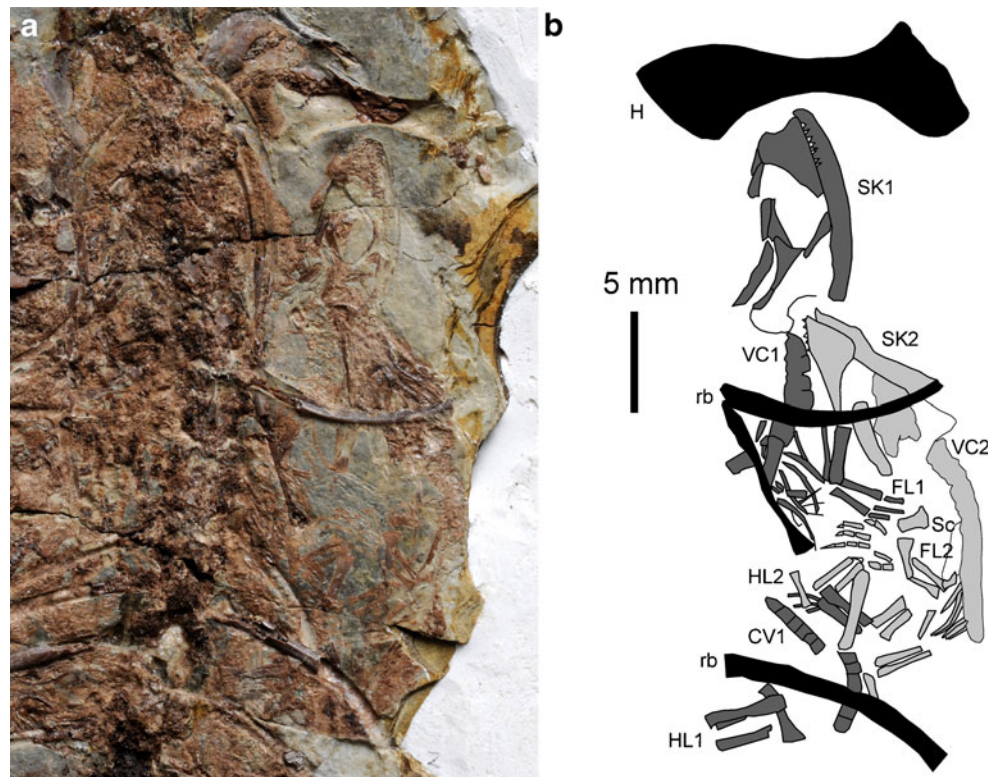


Fig. 2 The gravid female *Yabeinosaurus* (IVPP V 18005, counterpart), showing the positions of the embryos (numbered) and the humeri (*H*) and femora (*F*) of the adult

Fig. 3 Close-up of the anterior pectoral region of IVPP V 18005. **a** Photograph, **b** line drawing showing humerus and ribs of the mother in black and two embryos (1, 2) in different shades of grey. *CV1* caudal vertebrae of embryo 1; *H* humerus of adult lizard; *FL1*, *FL2* forelimbs of embryos 1 and 2; *HL1*, *HL2* hind limbs of embryos 1 and 2; *rb* ribs of adult lizard; *Sc* scapula of embryo 2; *SK1*, *SK2* skulls of embryos 1 and 2; *VC1*, *VC2* presacral vertebral columns of first and second embryo. Note that skull 1 is shown in more detail in Fig. 4



pterosaurs and birds and other dinosaurs (Zhou et al. 2010; X. L. Wang, personal communication, March 2011). V18005 consists of the part and counterpart of a medium-sized lizard (estimated 192 mm snout–pelvis length [SPL]) with skull, axial skeleton and the proximal parts of the fore- and hind limbs (Fig. 1). The lizard is about two thirds the size of the largest known individual of *Yabeinosaurus* (c. 300 mm SPL, IVPP V13285) and is not fully mature skeletally (long bone epiphyses still separate) but was obviously sexually mature given its gravid condition. The skull shows diagnostic characters of *Y. tenuis*: cranial sculpture, sharp conical teeth, a large postfrontal that partially closes the upper temporal fenestra, a reduced postorbital, and a hook-like angular process of the lower jaw (Evans et al. 2005). Given these, and the postcranial proportions, there is no doubt as to its attribution to *Y. tenuis*.

The specimen contains at least 15 (probably more) embryos distributed on both sides of the abdominal cavity between the humeri anteriorly and the femora posteriorly (Fig. 2). This distribution precludes their being gut contents (there are scattered fish remains in the posterior part of the abdomen) and instead corresponds to the position of the paired oviducts which in living lizards extend forward within the pleuroperitoneal cavity to roughly the level of the mid-lung (just behind the humeri in IVPP V 18005).

The embryos are all of the same kind and are of roughly the same size (given distortion and preservation) and level of ossification. Where the skeletons are most clearly visible

(Fig. 3), their morphology corresponds to that of the youngest known *Yabeinosaurus* skeletons, particularly with respect to the presence of the enlarged postfrontal bone (Fig. 4). The limb bone shafts are ossified, including those of the phalanges, as are the unguals, parts of the vertebrae, ribs, and pectoral girdle (dermal and endochondral), and many of the skull bones (frontal, parietal, maxilla, jugal, mandible, squamosal, pterygoid, postfrontal, possibly epipterygoid) as well as upper and lower teeth (Figs. 3 and 4). The frontals are ossified along their lateral margins but are separated by an unossified area posteriorly. The parietals are

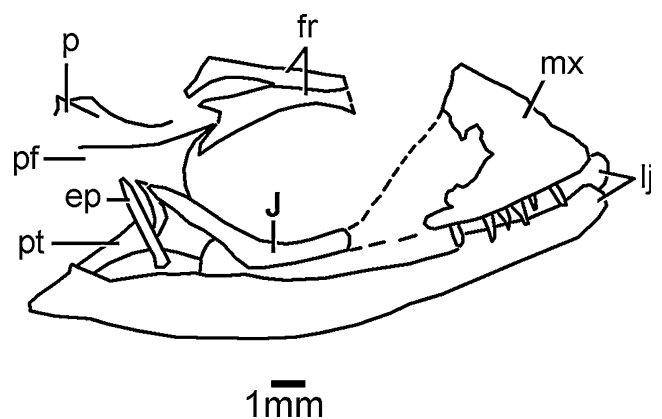


Fig. 4 Line drawing of the skull of an embryo in IVPP V 18005. *ep* epipterygoid, *fr* frontal, *j* jugal, *lj* lower jaw, *mx* maxilla, *p* parietal, *pf* postfrontal, *pt* pterygoid

ossified along their lateral margins but the central area is either unossified or very thin, and there is no development of the interdigitating frontoparietal suture found in the smallest known juveniles of *Yabeinosaurus* (e.g. IVPP V 12641). Behind the orbit, the jugal meets the postorbital series and the upper temporal bar seems to be complete, as is the facial process of the maxilla.

In general morphology, the *Yabeinosaurus* embryos correspond to late embryonic stages (stages 37 to 40) of *Lacerta* (*Zootoca*) *vivipara* (Dufaure and Hubert 1961). This is also consistent with descriptions of the osteological development of *L. vivipara* and *Lacerta agilis* (Rieppel 1992, 1994), and of the viviparous skink, *Liopholis whitii* (Hugi et al. 2010). The skull of the most clearly preserved embryos (Fig. 4) is at a similar level of development to the ~stage 37 *L. agilis* figured by Rieppel (1994, Fig. 1c) and the late embryo/newborn stage (~stage 40) of *L. vivipara* (Rieppel 1992, Fig. 4), and this is matched by the presence of ossified ungual phalanges and a small scapula, but not carpal or tarsal bones, or an obvious coracoid ossification. With estimated skull lengths in the range of 11–14 mm, the embryos are some 61–79% of the size of the smallest known juvenile specimens of *Yabeinosaurus* (IVPP V 12641 at 17.8-mm skull length, Ji et al.'s 2001 neotype at 19.8 mm skull length; Endo and Shikama's 1942 specimen at c. 23 mm skull length). Skeletal development at hatching/parturition varies between taxa (Maisano 2001), but the embryos within IVPP V 18005 were probably quite close to term.

Discussion

Squamate viviparity has generated considerable interest in recent years in terms of its evolutionary advantages and ecological relevance (e.g. Blackburn 2000, 2006; Davis et al. 2011; Lee and Shine 1998; Shine 1995) as well as its relationship to sex determination (genetic or temperature dependent, e.g. Organ et al. 2009; Robert and Thompson 2010; Wapstra et al. 2004). In living taxa, the evolution of viviparity is most commonly associated with cold climate (whether through latitude or altitude) as it allows the mother to maintain the developing embryos at a higher than ambient temperature and also increases their survival chances once born. For the mother, viviparity has the disadvantage of increasing her metabolic needs, decreasing her speed and mobility, and necessitating longer periods of potentially dangerous exposure during basking. In compensation, viviparous species usually have only one clutch per year, or even in alternate years (Blackburn 2000).

Yabeinosaurus is represented by a good range of specimens from juvenile to mature adult. The largest known specimen has an estimated snout–pelvis length of 300 mm

and is heavily ossified (Evans et al. 2005). However, given the number of juvenile and subadult specimens in collections, it probably reached skeletal maturity over several seasons. This is the kind of large lizard for which the advantages of viviparity (giving the young a ‘head-start’, protecting them from potential egg predators and removing the need to find suitable nest sites, Shine 1985) may have outweighed the disadvantages for the mother, although the environment was warm rather than cold (Wang and Zhou 2003). According to Shine (1985), gravid female lizards at full term lose about 25% of their running speed thus increasing their vulnerability to predators, but this would have been less of a problem for a lizard that could escape into water. From the fish bones in the gut of IVPP V 18005 (Fig. 4), and at least one other specimen (IVPP V 16361), it seems likely that *Yabeinosaurus* did sometimes forage in water. Nothing in the skeleton of *Yabeinosaurus* suggests it was predominantly aquatic, but most living lizards swim with ease. However, fish eating is rare (Mattison 1992). It occurs in the Chinese Crocodile lizard, *Shinisaurus*, which is also viviparous (Blackburn 2006) and in the Monitor lizards *Varanus* and *Lanthanotus* which are not.

The presence of viviparity in the Early Cretaceous *Yabeinosaurus* demonstrates that squamates had evolved the anatomical and physiological adaptations necessary for this reproductive strategy by at least 125 mya (Swisher et al. 1999; Zhou 2006), at a time probably not markedly different from that of therian mammals (contra Blackburn 2006). Unlike mammals, squamates retained oviparity as their primary reproductive mode, but their ability to switch to viviparity may have contributed to their survival, at least on land, during times of environmental stress.

Acknowledgements This work formed part of a joint Anglo-Chinese project funded by the Royal Society, London and the National Natural Science Foundation of China. Field work was also supported by grant 41072015 from the NNSF, China. Our thanks go to Jie Zhang (IVPP) for photographing the fossil and to Jack Conrad, Marcelo Sánchez-Villagra and an anonymous reviewer for comments on an earlier draft.

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