First record of live birth in Cretaceous ichthyosaurs: closing an 80 million year gap

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New fossils of embryonic ichthyosaurs are both the geologically youngest and the physically smallest known ichthyosaur embryos. The embryos are articulated, though only partially preserved, and are located within the body cavity of an adult, presumably the mother. The embryos and adult were found in association with several other individuals of differing size classes, all of which appear to be a new taxon of Cretaceous ichthyosaur. The material was collected from units of the Loon River Formation, Hay River, Northwest Territories, Canada. The implications of this new material to ichthyosaurian reproductive biology are discussed.

Keywords: ichthyosaurs; viviparity; Cretaceous; diapsids

1. INTRODUCTION

Two recently discovered Lower Cretaceous ichthyosaur embryos, found within the body cavity of a single pregnant female, close an 80 million year gap in the fossil record of ichthyosaur viviparity. Evidence of live birth (viviparity) in fossil reptiles is known only for marine reptiles even though many living species of terrestrial reptiles are viviparous (Shine 1985). Embryos associated with adults have been reported for some marine lizards (Bell *et al.* 1996; Caldwell & Lee 2001) but are most common in ichthyosaurs (four taxa ranging in age from the Upper Triassic to the Lower Jurassic). Three of these ichthyosaur occurrences are isolated—only a single specimen of each taxon has been found in association with embryos (Böttcher 1990; Brinkman 1996; Dal Sasso & Pinna 1996). The fourth occurrence, *Stenopterygius*, from the Lower Jurassic of Germany, includes hundreds of specimens of pregnant females with embryos at all stages of development (Böttcher 1990).

Oviparity is the most common mode of reproduction among extant aquatic reptiles, with the exception of some groups of aquatic snakes. Viviparity has arisen many times in both aquatic and non-aquatic squamates (snakes and lizards). However, in the fossil record viviparity has been reported only in marine diapsid reptiles (Böttcher 1990; Bell *et al.* 1996; Brinkman 1996; Dal Sasso & Pinna 1996; Caldwell & Lee 2001). The usual interpretation is that extreme modifications to an aquatic habitat result in physical limitations to terrestrial locomotion and egg laying (Andrews & Mathies 2000).

Over the course of ichthyosaur evolution, the limbs were modified as paddles, with the pelvic girdle and hind limbs being reduced in size but never lost (Sander 2000). These modifications, when coupled with large size, make it improbable that ichthyosaurs could have crawled out onto land to lay eggs. The presence of fossilized embryos in the body cavity of supposed female ichthyosaurs has been cited as evidence of viviparity in these marine reptiles; embryos have been reported in some Triassic ichthyosaurs (Brinkman 1996; Dal Sasso & Pinna 1996), and in many specimens of Jurassic ichthyosaurs (Dal Sasso & Pinna 1996). Viviparity in Cretaceous ichthyosaurs is predicted, but has never been confirmed by the discovery of fossil evidence.

The Loon River Formation at Hay River (Northwest Territories, Canada), is Albian in age (Singh 1971) and has yielded several ichthyosaur specimens, representing at least two separate taxa. One of these appears to be an adult *Platypterygius*, historically considered to be the only genus of ichthyosaur that survived into the Cretaceous (Maisch & Matzke 2000). However, the specimens associated with the embryos (two large adults, two juveniles and two embryos) appear to represent a new taxon, quite distinct from *Platypterygius*. The description and diagnosis of this new species of Cretaceous ichthyosaur and of the associated specimen of *Platypterygius*, will be presented elsewhere.

2. MATERIAL AND METHODS

Digital photographs were made using a Nikon Coolpix 990 digital camera in two formats: (i) attached via a Nikon Photographic system to a Nikon SMZ 1500 dissecting microscope for close-up photography; (ii) hand-held for non-macro photography. All the drawings and other graphics were made by manipulating the digital camera images in ADOBE PHOTOSHOP 5.5 for MacIntosh.

3. RESULTS

(a) *Systematic palaeontology: Ichthyosauria* *Blainville, 1835; cf. Ophthalmosauria Motani, 1999*

(i) *Material studied*

Embryos, UALVP 45639 (figures 1*b,c*, 2 and 3*a*), two embryos agglutinated to eight articulated vertebrae (adult). Other specimens: UALVP 45635, a disarticulated individual preserved in three dimensions; UALVP 45640, 14 articulated vertebrae (juvenile); UALVP 45640, 12 articulated vertebrae; UALVP 45642, a fragmentary snout including right and left maxillae with teeth, partial premaxillae, right and left dentaries with teeth, possible left splenial; UALVP 45643, a fragmentary snout including right maxilla, partial lacrimal, partial jugal, partial prefrontal. All specimens were collected from an outcrop of the Loon River Formation, Lower Cretaceous (Albian; 110 million years ago; Singh 1971), along the Hay River (60°01' N, 116°57' W), Northwest Territories, Canada.

(ii) *Description of embryos*

UALVP 45639 (figure 1*a*) is interpreted as a string of eight mid-thoracic vertebrae (height of 6 cm, width of 2.5 cm) from a large adult ichthyosaur. Agglutinated to the left ventral surface of these vertebrae are the remains of two small ichthyosaurs both of which are oriented parallel to the adult vertebrae (figures 1*b,c*, 2*a-c* and 3*a*). The anterior-most embryo is well preserved and extends the length of two centra. This embryo preserves some skull

Figure 1. Embryo associated with the northern Canadian opthalmosaur (UALVP 45639). (a) Vertebrae of UALVP 45639, anterior is to the left. The boxed in regions indicate the area where the embryos were found. (b,d) Anterior-most embryo, the skull is partially covered by the vertebral column. (c,e) Posterior-most embryo, 14 centra preserved. Scale bars, 1 cm.

elements, visible in ventral view and partially overlain by its own vertebral column. The skull bones appear to have rotated posteriorly, suggesting that the embryo was curled. Several of the embryo's teeth are preserved in the posterior region of its skull.

The second embryo is represented by only a short string of vertebrae located posterior to a damaged region of the adult vertebral column. The two embryos appear to be separated by a distance equal to the length of one adult centrum. The embryonic centra retain a notochordal canal.

4. DISCUSSION

(a) Embryos

The small individuals preserved on UALVP 45639 are interpreted as embryos because of their articulated state, their orientation relative to the vertebral column, their small size and their embryonic features (i.e. a dispro-

portionately large skull relative to the post-cranium and partially ossified centra; figure 3a,b). Their serial distribution and similar size also support their status as embryos. Gut contents would show some evidence of trauma incurred during consumption, and there would be other taxa mixed with the remains of the small ichthyosaurs (Swinton 1930). The small size of the individuals, as well as their embryonic features, strengthens the hypothesis that the specimens were never free-living (Deeming *et al.* 1993).

While the second string of embryonic vertebrae is very incomplete, we interpret these remains as indicative of the presence of a second embryo based on metric comparisons to *Stenopterygius* embryos. The skull of the anterior specimen, UALVP 45639 measures 4.2 cm, and if the two strings of centra were from the same embryo, the post-cranium would be disproportionately long (11.3 cm). Examination of early embryos of *Stenopterygius*, in which

Figure 2. Details of vertebral and skull structure from the anterior-most embryo associated with the adult opthalmosaur (UALVP 45639). (a) Vertebrae of UALVP 45639, anterior is to the left. (b) Anterior-most embryo, detail of partial skull, jaws and anterior-most vertebrae and ribs (arrows pointing to (c) indicate enlarged area). (a,b) Scale bars, 5 mm. (c) Details of the teeth from the middle left of (b). Scale bar, 1 mm.

the cranial region and the post-cranial region are of approximately equal length, indicates that the skull should be as long or longer than the ossified post-cranial skeleton (figure 3b; Deeming *et al.* 1993).

Based on a comparison with vertebral dimensions as published for other opthalmosaurs, the mother is estimated as having been between 2.2 and 2.5 m long; this is well within the size range of gravid stenopterygiids (Böttcher 1990). *Stenopterygius* embryos remained *in utero* until they were 75 cm long in some cases and, presumably, the young of the northern Canadian opthalmosaur would have been a similar size at birth (Deeming *et al.* 1993). Therefore, the embryos of UALVP 45639 represent the earliest known stage of ichthyosaur embryonic development.

In *Stenopterygius*, the head of the embryo is usually found to be directed anteriorly, except in extremely small stenopterygiid embryos (figure 3a,b) and UALVP 45639 (Böttcher 1990); both of which demonstrate that early-stage ichthyosaur embryos were curled or enroled. It has

been suggested for ichthyosaurs that the uncurling of embryos *in utero* is a response to constraints imposed by uterine morphology (Deeming *et al.* 1993). By contrast, we propose that uncurling results from biomechanical constraints imposed on the developing embryonic vertebral column and has little or nothing to do with uterine morphology.

For ichthyosaurs to use caudal propulsion effectively, the length of individual centra must decrease relative to their width. The result is that the vertebral column becomes very stiff (Sander 2000). In early ontogenetic stages, the vertebral elements consisted of the notochordal and cartilaginous precursors of the centra. These precursor elements have a high degree of elasticity and were flexible enough to allow the embryo to assume the foetal position. However, as the centra enlarge and ossify, their shape and relationships to each other do not permit the embryo to remain in a curled position. The opisthocelous vertebrae lack condyles on which the vertebrae can pivot, limiting dorsoventral and lateral movement. The relatively broad anterior and posterior faces of the vertebral bodies, relative to their width, also further restrict bending of the torso. We see these biomechanical features as having a greater influence on the uncured position of late-stage ichthyosaur embryos than maternal characteristics of the uterus. That being said, ichthyosaurs probably had elongate, paired uteri located dorsal to the digestive tract (Böttcher 1990), similar to the uterine system found in many other reptiles. For example, in viviparous snakes (Saint-Girons 1994) the oviducts are elongate, but the developing embryos remain curled within the amniotic sac as they would do within the egg, whether or not that egg is laid on the ground or retained within the oviduct (ovoviparous snakes). That the embryos of viviparous snakes remain curled within the amniotic sac reflects two features of snake anatomy and reproduction: (i) adult snakes are capable of coiling owing to their musculoskeletal anatomy; and (ii) curled embryos reflect the biomechanics of the adult musculoskeletal system. Our biomechanical argument for ichthyosaur uncurling is purely inductive. However, we find explanatory power in our scenario as it refers to the anatomy and biomechanical constraints of an endpoint of ontogeny, the adult condition.

Very little is known about ichthyosaur reproductive biology, aside from the temporally isolated Jurassic genus *Stenopterygius*. However, it is not surprising to find evidence of viviparity in Cretaceous ichthyosaurs, given their phylogenetic history (Deeming *et al.* 1993; Brinkman 1996; Dal Sasso & Pinna 1996) and obvious aquatic specializations. The northern Canadian opthalmosaur embryos (UALVP 45639) are the smallest ichthyosaur embryos ever found, and, as such, increase the amount of information available on the early ontogenetic stages of Cretaceous ichthyosaurs. Having embryonic and juvenile specimens of any taxon gives new insights into the patterns of development of some of the adaptations seen in that group. In this case, the embryonic structure reveals some constraints imposed on development as a result of stiffening the axial skeleton to facilitate caudal propulsion.

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Figure 3. (a) Anterior-most embryo, UALVP 45639, anterior is to the left. Scale bar, 1 cm. (b) Embryo of *Stenopterygius hauffianus*, SMNS 10460. Scale bar, 5 cm. (SMNS—Staatliches Museum für Naturkunde, Stuttgart, Germany).

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