

Evolution of viviparous reproduction in Paleozoic and Mesozoic reptiles

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ABSTRACT Although viviparity (live-bearing reproduction) is widely distributed among lizards and snakes, it is entirely absent from other extant Reptilia and many extinct forms. However, paleontological evidence reveals that viviparity was present in at least nine nominal groups of pre-Cenozoic reptiles, representing a minimum of six separate evolutionary origins of this reproductive mode. Two viviparous clades (sauropterygians and ichthyopterygians) lasted more than 155 million years, a figure that rivals the duration of mammalian viviparity. Circumstantial evidence indicates that extinct viviparous reptiles had internal fertilization, amniotic fetal membranes, and placentas that sustained developing embryos via provision of respiratory gases, water, calcium, and possibly organic nutrients. Production of offspring via viviparity facilitated the invasion of marine habitats in at least five reptilian lineages. Thus, this pattern of embryonic development and reproduction was central to the ecology and evolution of these ancient animals, much as it is to numerous extant species of vertebrates.

KEY WORDS: *viviparity, reproductive patterns, paleontology, placentas*

"The possibilities of existence run so deeply into the extravagant that there is scarcely any conception too extraordinary for Nature to realise."

Louis Agassiz. (Miller, 1865, p. 80)

Introduction

In viviparous vertebrates, pregnant females sustain developing embryos inside their reproductive tracts and give birth to their young. This mode of reproduction involves several specializations, including those by which the developing embryo is sustained during pregnancy. Viviparity is the product of numerous evolutionary experiments, and arose independently in more than 150 vertebrate lineages, including amphibians, reptiles, fishes, and mammals (Blackburn, 1999a, 2014). Remarkably, at least 115 of these origins of viviparity have occurred among squamates (lizards and snakes) (Blackburn, 2014). However, other extant Reptilia (turtles, crocodylians, sphenodontids, and birds) are entirely oviparous, as were (non-avian) dinosaurs and various other extinct reptilian groups. Viviparity also is absent in most actinopterygian fishes (Wourms, 1981; Wourms *et al.*, 1988), as well as most amphibians (Wake, 1993; Wake and Dickie, 1998; Wells, 2007).

The discontinuous distribution of viviparity among vertebrate

groups raises questions as to why this means of producing offspring has evolved so frequently in some groups and not in others. One possibility is that the presence of viviparity is simply a reflection of selection pressures for that reproductive pattern. An alternative possibility is that clades that lack viviparity were constrained by biological features that prevented maternal retention and maintenance of embryos (Packard *et al.*, 1977; Blackburn and Evans, 1986). Yet another possibility, one that applies to extinct forms, is that viviparity was much more widespread than is commonly recognized and has been overlooked due to the scarcity of fossils preserving evidence of reproductive mode.

Non-avian reptiles (extinct and extant) offer a valuable group for exploring such issues, for three major reasons. First, while most reptiles are oviparous, the great majority of the identified origins of vertebrate viviparity have occurred in this group (Blackburn, 2014). Second, much information has accumulated on how and why reptilian viviparity evolves (Shine, 1985, 2014; Blackburn, 2006; Blackburn and Stewart, 2011; Stewart and Blackburn, 2014). Third, the fossil record reveals evidence about the distribution of reproductive modes in major extinct groups, as well as inferences about the biology of those species that exhibited viviparity. A broad understanding of viviparity in the context of geological history allows reconstruction of features that have influenced as well as

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followed its evolution (e.g., Shine 1985; Carter, 2008; Organ *et al.*, 2009; Lynch and Wagner, 2010; Schulte and Moreno-Roark, 2010).

This paper explores evidence for viviparous reproduction among pre-Cenozoic reptiles. Each of the identifiable evolutionary origins of this pattern is defined in historical and phylogenetic terms. Through extrapolation from extant amniotes, the means by which pregnant females sustained their developing embryos is reconstructed. Likewise, consequences of viviparity for the ecology and life history of extinct reptiles are explored. An underlying theme of this review is that the viviparous production of embryos may have been as significant and widespread a pattern in extinct amniotes as in extant forms.

Types of reproductive modes

According to widespread contemporary usage, the terms “oviparity” and “viviparity” are used in their literal senses, in reference to “egg-laying” and “live-bearing” reproduction respectively. A second set of terms represents the sources of nutrients for embryonic development. In “lecithotrophy,” embryonic nutrients are derived from the ovulated yolk. In “matrotrophy,” nutrients are provided after ovulation by some alternative means such as a placenta -- the latter being known as “placentotrophy” (Wourms, 1981; Wourms *et al.*, 1988; Blackburn, 1992, 2000a, 2014). Viviparous vertebrates can be highly lecithotrophic (as in most live-bearing squamates), or highly placentotrophic (as in therian mammals and a few squamates), or rely on dual sources of nutrients. The archaic term “ovoviviparity” is seldom used in the primary literature because it embodies ambiguities and misconceptions and its use has produced much confusion (Wourms, 1981; Blackburn, 1994a, 2000a). Among other problems, the term implies that live-bearing species with lecithotrophic nutrition are not truly “viviparous,” thereby imposing a mammalian perspective inappropriate for most other species. One of the many advantages of the oviparity/viviparity dichotomy is its ready application to fossil forms for which data on fetal nutrient sources are unavailable.

Criteria for recognition of reproductive modes

A standard set of criteria has been established for recognition of oviparity and viviparity in extant reptile species (Blackburn, 1993a). Most (but not all) of these criteria can be modified for application to fossil specimens. Viviparity arguably would be indicated in fossil amniotes by the following, listed in approximate order of decreasing reliability: (A) specimens of adult females preserved during parturition or ejection of advanced fetuses; (B) pregnant female specimens with advanced embryos that are not surrounded by mineralized eggshells; and (C) pregnant specimens with less well-developed embryos that show no trace of eggshells. Oviparity would be indicated (again in decreasing order) by (D) fossilized developing eggs with identifiable embryos; (E) fossilized nests with identifiable hatchlings and eggshell remnants; (F) adult specimens and nests showing strong evidence of egg-tending behavior; and (G) gravid adult females that contain relatively undeveloped eggs with eggshells.

The rationale for most of these criteria is self-explanatory. For “B” above, one rationale is that in extant reptiles, advanced embryos almost always indicate viviparity, since oviparous deposition of advanced eggs is very rare (Blackburn, 1995; Andrews and Mathies, 2000; Smith and Shine, 1997; García-Collazo *et al.*, 2012).

However, an important caveat is that one should be able to rule out cannibalism/predation (Branca, 1908; McGowan, 1979; Deeming *et al.*, 1993; O’Keefe *et al.*, 2009), e.g., that the putative embryos not be confined to an esophageal and gastric region, and not show signs of maceration, digestion, or consumption. The rationale for “C” and “G” above is that mineralized eggshells indicate oviparity, since such shells are not deposited in extant viviparous reptiles (Blackburn, 1998a; Thompson *et al.*, 2004), where they would inhibit maternal-fetal gas exchange. An additional rationale for “B” and “C” is that in extant oviparous amniotes, eggshell deposition begins soon after fertilization and continues until the egg is laid (Packard and DeMarco, 1991; Palmer *et al.*, 1993). Problems in the inference of reproductive modes from fossil evidence are discussed by Deeming *et al.*, (1993).

Viviparity in extinct reptiles

Evidence for viviparity in various pre-Cenozoic reptiles is presented below. For readers unfamiliar with the taxa, many sources are available. Among them are accounts in the general and popular literature (McGowan, 1992; Norman, 1994; Cowan, 1995; Ellis, 2003; Everhart, 2007; Motani, 2000a, 2009) and the internet (Everhart, 1998-2014), as well as reviews of a more technical nature (e.g., Callaway and Nicholls, 1997; Sander, 2000; Mazin, 2001; Everhart, 2005). Comprehensive sources that deal with reproduction in other extinct reptiles include the following: Carpenter *et al.*, (1994), Carpenter (1999), Horner (2000), and Sánchez (2012).

Paleozoic mesosaurs (Mesosauridae)

Mesosaurs are enigmatic, aquatic forms of the Early Permian, with a Gondwanan distribution in eastern South America and southern Africa (Modesto, 2006). Highly distinctive in form, mesosaurs are characterized by elongate skulls and jaws that are armed with many long, slender teeth; paddle-like forelimbs and hindlimbs; and an elongate body form with thick (pachyostotic) abdominal ribs and a long tail (Fig. 1A). Skeletal structure (Canoville and Laurin, 2010; Modesto, 2010) and geological location (Piñeiro *et al.*, 2011) unequivocally demonstrate that *Mesosaurus* was aquatic, living in a coastal or deep-water marine environment. Whether the animals could locomote on land (as required for terrestrial oviposition of amniotic eggs) is questionable (Modesto, 2010; Piñeiro *et al.*, 2012a).

Early sources assumed that mesosaurs were oviparous (Williston, 1914). However, nothing specific was known of their reproduction until the discovery of a pregnant *Mesosaurus* from the Early Permian in South America, one that contained a single, well-preserved embryo (Piñeiro *et al.*, 2012a). Cannibalism was ruled out for the specimen based on the position and state of preservation of the embryo. Also discovered was an isolated developmentally more-advanced embryo, as well as several disarticulated specimens (interpreted as late embryos or neonates) found in association with adult specimens (Piñeiro *et al.*, 2012a). No trace of eggshells was observed in any of the specimens. One explanation of the young, extra-uterine specimens was that they were fetuses displaced by post-mortem disruption. Two alternatives were that they represented late-stage eggs laid just before hatching (indicating viviparity) or that they were hatchlings or neonates that remained with parents after their emergence. Overall, the above evidence indicates that *Mesosaurus* was probably viviparous. Absence of visible eggshells suggests viviparity, as does the fact that amniotic eggs cannot de-

velop in water. Further support for viviparity comes from the fact that oviparous deposition of eggs with late stage embryos is very rare in extant reptiles, being found in only a few lizard species (Blackburn, 1995; Andrews and Mathies, 2000; Stewart and Blackburn, 2014).

That mesosaurs were probably viviparous is particularly notable given their phylogenetic position near the base of the sauropsid/reptilian clade (Reisz, 1997). Mesosaurs usually are considered either to be a sister group to all other reptiles or as basal parareptiles or anapsids (Laurin and Reisz, 1995; Modesto and Anderson, 2004; Müller and Reisz, 2006; Piñeiro *et al.*, 2012b). Each of these interpretations is consistent with the inference that they evolved

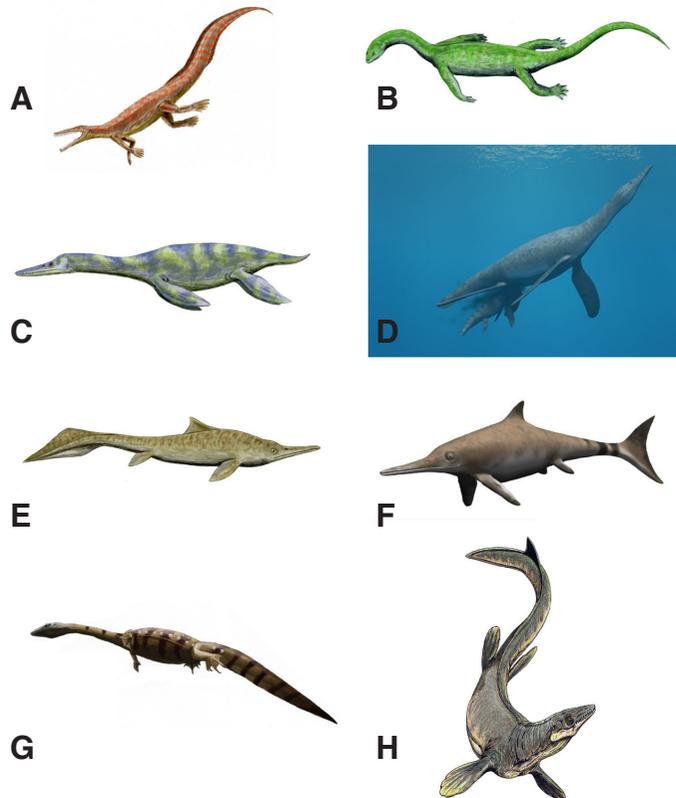


Fig. 1. Artistic reconstructions of viviparous aquatic reptiles. *Figures are not to scale, and coloration is conjectural.* (A) Mesosaurus. (B) The pachypleurosaur *Keichosaurus*. (C) The plesiosaur *Dolichorhynchops*. (D) The plesiosaur *Polycotylus* giving birth. (E) The ichthyosaur *Mixosaurus cornalianus*. (F) *Ichthyosaurus communis*. (G) The choristodere *Hyphalosaurius*. (H) The mosasaur *Plioplatecarpus*. Sources of figures. All figures used by permission under the terms of the GNU Free Documentation License and licensed under CC BY 2.5 or 3.0 via Wikimedia Commons. Figs. 1A–1F by Nobu Tamura (<http://spinops.blogspot.com>) – Own work. Fig. 1A. “Mesosaurus BW” – http://commons.wikimedia.org/wiki/File:Mesosaurus_BW.jpg. Fig. 1B. “*Keichosaurus* BW” – http://commons.wikimedia.org/wiki/File:3AKeichosaurus_BW.jpg. Fig. 1C. “*Dolichorhynchops* BW” – http://commons.wikimedia.org/wiki/File:3ADolichorhynchops_BW.jpg. Fig. 1D. “*Polycotylus* NT” – http://commons.wikimedia.org/wiki/File:Polycotylus_NT.jpg. Fig. 1E. “*Mixosaurus* BW” – http://commons.wikimedia.org/wiki/File:Mixosaurus_BW.jpg. Fig. 1F. “*Ichthyosaurus* BW” – http://en.wikipedia.org/wiki/Ichthyosaurus#mediaviewer/File:Ichthyosaurus_BW.jpg. Fig. 1G. “*Hyphalosaurius* mmartyniuk wiki” by Matt Martyniuk – Own work. http://commons.wikimedia.org/wiki/File:Hyphalosaurius_mmartyniuk_wiki.png. Fig. 1H. “*Plioplatecarpus*DB” by DiBgd at the English language Wikipedia – <http://commons.wikimedia.org/wiki/File:PlioplatecarpusDB.jpg>.

viviparity independently of other reptiles. As Early Permian forms, mesosaurs represent the earliest known evolutionary origin of viviparity among tetrapods, at about 280 MA (million years ago).

Pachypleurosaurs and Nothosaurs (Sauropterygia)

Sauropterygians were an enormously successful group of aquatic reptiles with a worldwide distribution and a stratigraphic range that spanned the entire Mesozoic (for basic information, see Storrs, 1993; Rieppel, 1997; Lin and Rieppel, 1998; Benton, 2000; Ellis, 2003; Everhart, 2005). Within the diversity of sauropterygians, the relatively advanced plesiosaurs are the most familiar to general readers. Early sauropterygians were the Triassic pachypleurosaurs, which were aquatic, lizard-shaped animals of <1m in length, with small heads, long necks and limbs, sinuous bodies, and deep tails (Rieppel and Kebang, 1995; Rieppel and Hagdorn, 1997). Triassic “nothosaurs” (*sensu* Benton, 2000), a paraphyletic group, were larger (3 to 4m) marine forms with long necks and flattened snouts, and paddle-like webbed feet. They have been compared anatomically to a cross between a seal and a crocodile. Pachypleurosaurs and nothosaurs were extinct by the end of the Triassic, but were survived by sauropterygian placodonts and plesiosaurs (Carroll, 1988; Benton, 2000).

The first evidence of viviparity in sauropterygians came in the form of enigmatic reports of embryonic specimens. An embryo of the aquatic nothosaur *Neusticosaurus* was discovered in Triassic shale (230 MA) of central Europe (Sander, 1988, 1989). At 51mm in body length, the specimen was smaller than neonatal size, but with a well-developed skeletal system. The specimen was not associated with an eggshell, leaving the question of reproductive mode open. A subsequent study described a cluster of four embryos of the nothosaur *Lariosaurus* (Renesto *et al.*, 2003). At 4 cm in snout-vent length (SVL), the embryos were far smaller than adult size (~50 cm SVL); they also lacked any trace of eggshell. The authors considered this discovery to be strong evidence of viviparity, with the embryos having been expelled prematurely. Another relevant report came from study of the pachypleurosaur *Keichosaurus hui* (Fig. 1B), from the Middle Triassic of China. Lin and Rieppel (1998) described a late stage embryo, a specimen 48mm in length that lacked any trace of eggshell. The authors tentatively inferred this species to be viviparous, based on morphology of the embryo and the fact that adults seemed too well adapted for aquatic life to come to land.

Concrete evidence of viviparity in *Keichosaurus* was presented in a report on two pregnant females, one with four embryos and the other with at least six embryos (Cheng *et al.*, 2004). In both females, the embryos were arranged in two longitudinal rows along the body axis, as in paired oviducts. This study noted that adults lacked a solid connection between the pelvis and the sacral ribs. The authors interpreted this feature as a specialization for aquatic habits that would hamper terrestrial locomotion but potentially allow for a widening of the pelvic canal during the birth of offspring (Cheng *et al.*, 2004). Based on the fact that a similar skeletal arrangement occurs in pachypleurosaurs, nothosaurs, and plesiosaurs, the authors suggested that viviparity was widespread among sauropterygians.

Plesiosaurs (Sauropterygia)

Plesiosaurs were a diverse clade of aquatic reptiles that along with ichthyosaurs, dominated marine environments during the Jurassic and Cretaceous; they went extinct at the end-Cretaceous

mass extinction (Benton, 2000; Ellis, 2003; Everhart, 2005). Adult body size commonly ranged from 2 to 15 meters (depending on the species) making them among the largest marine tetrapods of the Mesozoic. Plesiosaurs were highly adapted for aquatic life, with broad flat bodies and strong paddle-shaped limbs. Two main body types can be recognized – “plesiomorphs” with small skulls and long necks, and “pliosauromorphs” with elongated heads and relatively short necks (Ellis, 2003; Everhart, 2005, 2007), the latter of which evolved convergently multiple times (O’Keefe, 2002).

Prior to direct evidence being available, several sources considered it very likely that plesiosaurs were viviparous (Williston, 1914; Taylor, 1986; Cheng *et al.*, 2004; *contra* Colagrande and Felder, 2000). The chief rationale for this inference was that adult females could not have come to land to lay their amniotic eggs. The inference of viviparity gained empirical support from observations on a specimen of the short-necked polycotyloid *Dolichorhynchops osborni* (Fig. 1C) that contained a developing fetus (Rothschild and Martin, 1993; Everhart, 2005; also see Everhart, 2007). Cannibalism was ruled out because the developing offspring showed no signs of digestion and was too large to have been ingested.

Further evidence of plesiosaur viviparity came from description of a pregnant short-necked plesiosaur, *Polycotylus latipinnus* (Fig. 1D), from the Late Cretaceous (O’Keefe and Chiappe, 2011). This remarkable specimen was associated with a single, well-preserved fetus evidently spilled from the maternal body cavity. The fetus was estimated to be about 2/3 of the way through development, with a body length of 1.5m. The authors ruled out explanations other than viviparity given that the offspring was partly articulated, still in embryonic state, and showed no sign of having been ingested.

Phylogenetic information indicates *Polycotylus* and *Dolichorhynchops* are relatively derived plesiosaurs (O’Keefe, 2001, 2002, 2004), and of a group that is distantly related to the pachypleurosaurs and nothosaurs (Storrs, 1993; Rieppel, 1997, 1999). The broad phylogenetic and temporal distribution of viviparity among sauropterygians raises two possibilities. One is that viviparity had multiple origins within this large, diverse group. A more conservative explanation is that viviparity arose in Triassic pachypleurosaurs and was retained during the Jurassic and Cretaceous radiations of sauropterygians to become widespread in the group. The latter possibility would explain how amniotes so highly specialized for aquatic life were able to reproduce.

Ichthyosaurs (Ichthyopterygia)

Ichthyosaurs were another highly successful and diverse group of Mesozoic marine reptiles (Figs. 1 E,F). Like sauropterygians, they exhibited a worldwide distribution and a broad stratigraphic range, one that extended from the Early Triassic to beyond the mid-Cretaceous (Callaway, 1997; Motani, 2000a, 2009; Ellis, 2003). Easily recognizable from their dolphin-like body shape, they ranged from small (< 1m long), snub-nosed forms through enormous, long snouted types that reached as much as 20m in body length (Ellis, 2003; Motani, 2005). Ichthyosaurs are combined with basal forms of the Early Triassic in the clade Ichthyopterygia (Motani *et al.*, 2014).

Empirical evidence for viviparity in ichthyosaurs dates back to the 1800s, in the form of adult specimens that contained developing embryos (von Jäger, 1828; Pearce 1846; Seeley, 1880; Woodward, 1906). Several early sources attributed the association of adults and young to instances of cannibalism (e.g., Branca, 1907, 1908).

Many years elapsed before evidence of viviparity was viewed as sufficient to rule out other explanations (see Benton, 1991; Deeming *et al.*, 1993). Some fossils showed pregnant adults with partially developed offspring coiled in an embryonic posture (Deeming *et al.*, 1993). Several specimens show an adult female with a late stage fetus being extruded via the pelvic canal (for photographs, see Osborn 1901; Romer, 1974; Carroll, 1988; Organ *et al.*, 2009). A common interpretation of the latter situation is that the females died due to complications during birth (Deeming *et al.*, 1993; Brinkman, 1996). An alternative view is that offspring were expelled after the female died through *post mortem* decay (McGowan, 1992; see Reisdorf *et al.*, 2014 for discussion).

Accumulated evidence indicates that viviparity was widespread and probably universal among ichthyosaurs (Sander, 2000; Motani, 2005). Fossil specimens of adults with developing embryos date from the Middle Triassic (Brinkman, 1996) and Late Triassic (Xiaofeng *et al.*, 2008). Such documentation of viviparity likewise extends from the Early Jurassic (McGowan, 1979; Deeming *et al.*, 1993; Dal Sasso and Pinna, 1996; Lomax and Massare, 2012; Maxwell, 2012) and Late Jurassic (O’Keefe *et al.*, 2009) into the Cretaceous (Kear *et al.*, 2003; Maxwell and Caldwell, 2003; Kear and Zammit, 2014). Viviparity was recently discovered in the basal ichthyopterygian *Chaohusaurus* (Motani *et al.*, 2014). This finding extends the record of ichthyopterygian viviparity back another 10 million years. Accordingly, viviparity is now known to span at least 158 million years of ichthyopterygian history.

Although the phylogenetic origins of ichthyosaurs have long been uncertain, their viviparity has almost certainly originated independently of that of other reptiles. Several recent analyses have concluded that ichthyosaurs have diapsid affinities (e.g., Massare and Callaway, 1990; Motani, 2000b; Liu *et al.*, 2011), being (for example) a sister clade to a group that contains archosaurs, lepidosaurs, and sauropterygians (Motani *et al.*, 1998). A minority view nests ichthyosaurs among parareptiles along with Testudines (turtles and allies), or links them to mesosaurs (Maisch, 2010), or even with a non-amniote origin (Maisch, 1997). These postulated relationships, possibly excluding the tentative link to mesosaurs, would require that viviparity in ichthyopterygians resulted an independent origin of that reproductive mode.

Choristoderans (Choristodera)

Choristoderes were aquatic diapsids with a long stratigraphic range (from the Upper Triassic through the Miocene) and a broad geographical distribution (eastern Asia, Europe, and North America) (Gao and Fox, 1998; Gao *et al.*, 2000; Matsumo and Evans, 2010). The most familiar members of the group are the champsosaurs, large crocodylian-like forms with long, narrow snouts and paddle-shaped limbs. However, choristoderes also include the Cretaceous *Hyphalosaur* from China, a highly distinctive freshwater form with extremely long necks, tiny heads, and long tails (Fig. 1G) (Gao and Ksepka, 2008; Matsumoto *et al.*, 2007). The post-cranial skeleton of *Hyphalosaur* was specialized for aquatic habitat, and whether the animals could locomote on land is highly questionable (Gao and Ksepka, 2008; Ji *et al.*, 2010).

Viviparity was suggested for *Hyphalosaur baitaigouensis* based on the discovery of an adult specimen (the holotype) that lay surrounded by 11 egg-like nodules of variable shapes (Ji *et al.*, 2006). The “eggs” lacked shells, and at least some contained early embryos. The authors considered it likely that this species repro-

duced by viviparity and gave birth in the water, and speculated that the embryos of this particular specimen were prematurely expelled. Viviparity in *H. baitaigouensis* was confirmed through discovery of a pregnant female containing approximately 18 embryos filling the body cavity (Ji *et al.*, 2010). Likewise, re-examination of the holotype revealed two eggs that lay inside the body cavity (Ji *et al.*, 2010). An independent study described a specimen of this species associated with two external, flexible shelled eggs, one with an embryo and the other with a partially hatched neonate (Hou *et al.*, 2010). This study examined the structure of the eggshells with scanning electron microscopy. A later paper suggested that perhaps these eggs were deposited on land immediately prior to birth (Lü *et al.*, 2014). However, observations of a putative eggshell are hard to reconcile with the inference of viviparity. Thus, one might wonder if the specimens are from similar species, in view of the fact that numerous squamate genera contain both oviparous and viviparous representatives (Stewart and Blackburn, 2014).

Viviparity may have been widespread among choristoderes. An adult specimen of the monjurosuchid *Monjurosuchus splendens* from the Early Cretaceous contained skulls of seven juveniles; although originally interpreted as cannibalism (Wang *et al.*, 2005), it was reinterpreted as viviparity (Wang and Evans, 2011). Yet another study described a monjurosuchid *Philydrosaurus* associated with six smaller individuals, which the authors speculated to be a reflection of viviparity or parental care (Lü *et al.*, 2014).

Although the position of choristoderans within the Diapsida is uncertain, they are distantly related to any of the other viviparous reptiles known from the Mesozoic. They have variously been placed as basal archosauromorphs, a sister group of archosauromorphs, or basal archosauromorphs + lepidosauromorphs, each possibility of which predicts an origin by the late Paleozoic or very early in the Mesozoic (Matsumo and Evans, 2010). Hyphalosaurids and monjurosuchids are early forms that diverged prior to development of neochoristoderans such as the champsosaurs (Matsumo *et al.*, 2007). Given evidence that viviparity evolved very early in the group, this reproductive mode possibly was widespread in choristoderans, in which case it may have extended from the Cretaceous (if not before) until well into the Cenozoic, when the group went extinct. This hypothesis currently lacks empirical support.

Mosasaur (Mosasauroidea)

Mosasaur were enormous marine lizards of the Cretaceous, the largest of which ranged up to 17m in length (Fig. 1H) (Lingham-Soliar, 1995; Everhart, 2005). They evolved to become the dominant oceanic predators after the decline of plesiosaurs and extinction of ichthyosaurs (Bell, 1997a; Ellis, 2003; Everhart, 2000, 2005). "Aigialosaurs" are smaller-bodied, semi-aquatic forms that are commonly included with mosasaur in the superfamily Mosasauroidea (Bell, 1997b; Conrad, 2008). Classification of these forms is in flux, reflecting uncertainties and shifts in cladistic relationships (Caldwell and Palci, 2007; Conrad *et al.*, 2011; Caldwell, 2012). Likewise, clarification of relationships has challenged monophyly of the tradition distinction between aigialosaurs and mosasaur (Bell, 1997b; Bell and Polcyn, 2005; Caldwell, 2012).

Questions over the reproductive habits of mosasaur and their allies date back for more than a century. Despite the extreme specializations of mosasaur to aquatic habitats, Williston (1898, 1904, 1914) considered viviparity unlikely since no adult specimens had been discovered to contain embryos. A study on the mosasaur

Clidastes suggested viviparity based on a mobile sacroiliac joint thought by the authors to allow a widening of the pelvic canal at birth (Dobie *et al.*, 1986).

The first direct evidence of mosasaur viviparity came from a brief report on a specimen of *Plioplatecarpus* collected from South Dakota that contained unborn embryos in its abdomen (Bell *et al.*, 1996; Everhart, 2000). Viviparity was confirmed for mosasauroids by analysis of a type specimen of the semi-aquatic aigialosaur *Carsosaurus* from Slovenia (Caldwell and Lee, 2001). Compared to other aigialosaurs, *Carsosaurus* is relatively large (~2m in total length) with proportionately larger limbs (Caldwell *et al.*, 1995). The pregnant specimen contained at least four advanced embryos, three spaced evenly as if in the right oviduct, and one within the pelvic canal (Caldwell and Lee, 2001). Embryos were in a curled-up posture as if enclosed within their fetal membranes, and were near term, as indicated by their size and state of development. No trace of eggshell was apparent. The embryos were oriented as if to be born tail-first (as occurs in cetaceans and ichthyosaurs), a feature that the authors interpreted as an adaptation to aquatic habitat.

Viviparity may well have been widespread among the Cretaceous mosasauroids, given its presence among a plesiomorphic aigialosaur as well as the highly derived mosasaur *Plioplatecarpus* (for cladograms, see Dutchak, 2005; Caldwell and Palci, 2007; Conrad, 2008; Conrad *et al.*, 2011). The most conservative interpretation is that these animals stem from a single origin of viviparity. An alternative (but less parsimonious) possibility is that viviparity arose independently in the two groups. The distant phylogenetic relationship between mosasauroids and other squamates indicates that their viviparity arose independently of extant forms. Mosasauroids often have been considered to be allied with varanoid lizards (Evans and Wang, 2005; Conrad, 2008; Conrad *et al.*, 2011), a group whose extant members are entirely oviparous (Vitt and Caldwell, 2009). In other interpretations, mosasauroids are allied with basal anguimorphs, scleroglossans, or snakes (Lee and Caldwell, 2009; Caldwell, 2012; Gauthier *et al.*, 2012). For each of these groups, oviparity is ancestral (Blackburn, 1982, 1985, 1999b; Shine, 1985). Thus, under each of these interpretations, viviparity in mosasauroids must have originated independently of viviparous squamate groups with extant representatives.

The Cretaceous lizard *Yabeinosaurus*

Yabeinosaurus tenuis was a large-bodied (~350 mm SVL) pre-Cretaceous lizard recorded from the Early Cretaceous of northeastern China. The lizards had thin, flexible bodies covered with scattered osteoderms, with short powerful limbs and a substantial tail (Evans and Wang, 2012). Unlike other taxa discussed above, *Yabeinosaurus* does not show specializations for an aquatic lifestyle. However, presence of fish bones in the gut of some specimens indicates that it could forage in water (Wang and Evans, 2011; Evans and Wang, 2012) and may therefore have been semi-aquatic. Analysis of a developmental series has revealed a prolonged period of post-natal growth and skeletal development (Evans and Wang, 2012). This species is thought to be a relict of a Jurassic clade with a broad geographical distribution (Evans and Wang, 2010, 2012).

Viviparity was documented in *Yabeinosaurus tenuis* based on discovery of a pregnant female that contained ≥15 late-stage fetuses (Wang and Evans, 2011). The pregnant specimen (at ~300 mm SVL) was at less than maximum size, and its skeleton was not fully mature. The fetuses were distributed anteriorly in two

longitudinal rows, presumably in the paired oviducts. In general morphology, the fetuses were judged to be at advanced development (stage 37 to 40, where 40 is the stage at birth) (Wang and Evans, 2011).

As to whether viviparity in *Yabeinosaurus* represents an independent origin, this lizard genus evidently is not closely related to any extant squamate clade (Evans *et al.*, 2005). *Yabeinosaurus* has been variously classified as a basal anguimorph (Conrad, 2008; Conrad *et al.*, 2011) and as basal to all extant, non-iguianian crown group squamates (Wang and Evans, 2011; Evans and Wang, 2012). Regardless, its distant relationship to extant lineages of viviparous squamates clearly indicates that it represents an independent evolutionary origin of viviparity (Wang and Evans, 2011).

Other extinct reptiles

As shown above, viviparity in fossil reptiles is commonly associated with aquatic habits. One rationale is that amniotic eggs cannot develop in water. The other is that reptiles highly adapted for aquatic locomotion may be unable to come to land to lay their eggs. Accordingly, viviparity has been suggested for various other marine Reptilia including thalattosuchians (Williston, 1914; Neill, 1971; Fernández *et al.*, 2014) and the aquatic bird *Hesperornis* (Currie, 1991; Feduccia, 1991), both of the Cretaceous. Viviparity has also been raised as a possibility in two Triassic lineages, the Hupehsuchia (Carroll and Zhi-Ming, 1991) and Tanystropheidae (Rieppel *et al.*, 2010). Approximately 20 reptilian clades have become well-adapted to aquatic habitats, most during the Mesozoic (Carroll, 1997; also see Mazin, 2001). Among them, other candidates for viviparity arguably include the placodonts and

pleurosaurs.

Viviparity also has been suggested on occasion among sauropsid dinosaurs (Bakker, 1980, 1986). However, this hypothesis is countered by abundant evidence for sauropod eggs and nests (Carpenter *et al.*, 1994; Carpenter, 1999; Horner, 2000) and has not been well-accepted (e.g., Dunham *et al.*, 1989; Paul, 1994). Thus, aquatic non-dinosaurian forms offer the best prospects for undiscovered evidence of reptilian viviparity.

Origins of viviparity

The foregoing review of the literature shows that contrary to traditional assumptions (see Fernández *et al.*, 2014), viviparity was widespread among extinct reptiles in terms of phylogeny, geological age, and geographical distribution (Table 1). Viviparity occurred in species of nine nominal groups, some of which are paraphyletic (e.g., aigialosaurs, nothosaurs). These nominal groups form six separate viviparous clades (Fig. 2). These six clades are widely distributed phylogenetically among extinct reptiles of the Mesozoic and Paleozoic, and are presumed to represent a minimum of six separate evolutionary origins of this pattern, as follows: mesosaurs, sauropterygians, ichthyopterygians, choristoderans, mosasauroids, and the Cretaceous lizard *Yabeinosaurus* (Fig. 2).

The inference of a single origin of viviparity in sauropterygians is highly conservative. It assumes that two Triassic nothosaurs of central Europe, a Triassic pachypleurosaurs from China, and two Late Cretaceous plesiosaurs all stemmed from a single origin of viviparity. A plausible alternative is that more than one origin of live-bearing habits is represented (Sander, 2012). However, two

points can be marshalled in favor of the more conservative interpretation: the absence of convincing evidence of oviparity in any sauropterygian, and (more significantly) the presence of structural specializations for aquatic habits that seemingly would make it difficult or impossible for adult females to come to land to lay eggs. In contrast to the sauropterygian situation, the derivation of live-bearing ichthyopterygians from a single origin of viviparity is strongly supported. As outlined above, compelling evidence for viviparity is available in forms that range from the Early Triassic through the mid-Cretaceous. The interpretations above do not assume that basal members of each of the identified groups were viviparous. To

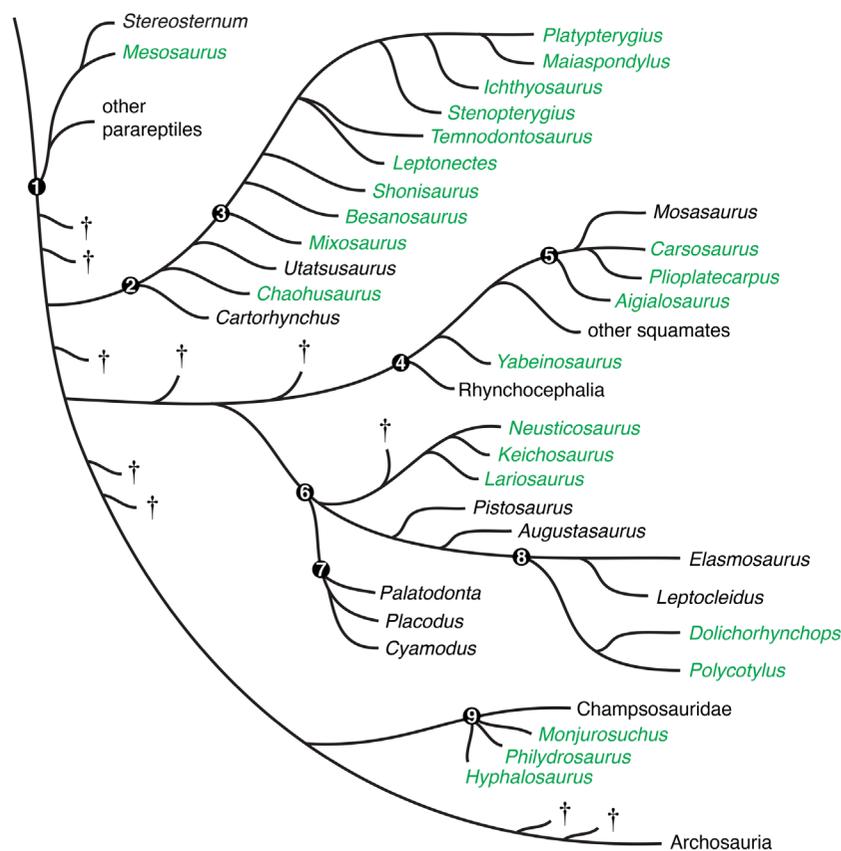


Fig. 2. Cladogram of representative Permian-to-Cretaceous reptile taxa. Taxa indicated in green are those for which viviparity has been inferred by direct evidence (see text). For taxa in black, reproductive mode is unknown. Nodes 1–9 correspond to the following clades: (1) Reptilia; (2) Ichthyosauriformes; (3) Ichthyopterygia; (4) Lepidosauria; (5) Mosasauroida; (6) Sauropterygia; (7) Placodontiformes; (8) Plesiosauria; (9) Choristodera. Dagggers denote additional major reptilian clades whose positions support the inference that viviparity evolved multiple times. Cladistic relationships are based on the following sources: Benson and Druckenmiller (2014); Leblanc *et al.*, (2012); Matsumoto *et al.*, (2007); Modesto *et al.*, (2014b); Motani (2005); Motani *et al.*, (2015); Neenan *et al.*, (2013); Rieppel (2000).

infer that viviparity was universal in mosasauroids, mesosaurs, or choristoderans goes beyond the available evidence.

Underlying postulates

The inference of independent origins of viviparity is based on the postulate that no two of the six live-bearing clades defined above were derived from a common viviparous ancestor. The widespread phylogenetic and temporal distribution of these groups (Fig. 2) supports this postulate, since most are linked to forms with oviparous representatives. For example, mosasauroids and *Yabeinosaurus* are each linked to squamate groups that ancestrally were oviparous (see above). Likewise, regardless of whether choristoderans are basal archosauromorphs or stem neo-diapsids that diverged in the Permian or Early Triassic (Matsumo and Evans, 2010), their viviparous habits (which are not known before the Cretaceous) presumably evolved independently of other major reptilian clades. The same argument applies to sauropterygians, which have been placed as either basal archosauromorphs or basal lepidosauromorphs (Rieppel, 1999), both of which were ancestrally oviparous. As for the ichthyopterygians, while their phylogenetic origins remain obscure, little to no evidence ties them to any other group known to have been viviparous.

The inference of separate origins of viviparity also is based on the postulate that viviparity evolves irreversibly from oviparity. This postulate is widely supported by studies on viviparity in squamate reptiles (Blackburn, 1985, 1999b; Shine, 1985; Lee and Doughty, 1997; Lee and Shine, 1998; Shine and Lee, 1999; Stewart and Blackburn, 2014) and other vertebrates (Blackburn, 2014). A few putative cases of viviparity to oviparity reversals have been suggested in chondrichthyans (Dulvy and Reynolds, 1997; cf. Blackburn, 2014) and snakes (Lynch and Wagner, 2010; Fenwick *et al.*, 2012). One recent work on squamates has suggested many such reversals (Pyron and Burbrink, 2013), a view that has elicited multiple rebuttals (e.g. Griffith *et al.*, 2015; Blackburn, 2015).

To relax the operative assumption of reversibility for extinct reptiles has little consequence for the present analysis. Possibly one might conjecture from the presence of viviparity in a mesosaur species that this reproductive mode was ancestral for parareptiles, or reptiles, or even for amniotes (requiring multiple reversions to oviparity). This viewpoint might be taken as consistent with the scarcity of fossilized amniotic eggs prior to the Late Triassic. However, the scarcity of early fossil eggs is explained by the fact that the mineralized eggshell was a later innovation (Stewart, 1997; Sander, 2012). Further, given the frequency and apparent ease with which viviparity evolves in reptiles, its early evolution in Paleozoic forms like mesosaurs is entirely understandable.

Historical and geographical distribution

The recognized origins of viviparity are widely distributed in space and time. Fossils indicating viviparity in mesosaurs date from the Early Permian in South America, of 278 MA (Piñeiro *et al.*, 2012a). The next-oldest origin of reptilian viviparity is represented by a Middle Triassic ichthyopterygian from China (~248 MA) (Motani *et al.*, 2014), an origin that is presumably homologous with viviparity in the highly derived ichthyosaurs of the Cretaceous in North America. Viviparity in sauropterygians is only a little younger (relatively speaking), dating to ~230 MA (Sander, 1988; Renesto *et al.*, 2003; Cheng *et al.*, 2004). Viviparity has a lengthy history in these two lineages: ≥158 million years in ichthyopterygians

and ≥165 million years in sauropterygians. Chronologically, the next two origins of viviparity are represented by two Early Cretaceous groups of eastern Asia from about 121 MA -- freshwater choristoderans and the lizard *Yabeinosaurus* (Wang and Evans, 2011). The duration of viviparity in these two groups cannot be assessed from present evidence. Mosasauroids represent the most recent of the six origins of viviparity, based on a specimen from North America dating to 95 MA (Caldwell and Lee, 2001; Wang and Evans, 2011). Although viviparity was present in mosasauroids by 72 MA (Wang and Evans, 2011) (suggesting that viviparity lasted ≥23 million years), the group was extinct by the end of the Cretaceous.

Most of the origins of viviparity identified herein long predate those from which extant squamates have descended. Viviparity in lizards and snakes commonly evolved at subgeneric levels, and sometimes, at subspecific levels (Shine, 1985; Blackburn, 1999b; Stewart and Blackburn, 2014). Most of the origins of squamate viviparity for which quantitative data are available are scattered throughout the Cenozoic (Schulte and Moreno-Roark, 2010), with some having occurred as recently as the Pliocene and Pleistocene (Surget-Groba *et al.*, 2001; Calderon-Espinoza *et al.*, 2006). At least a few squamate origins of this pattern may date to the Late Cretaceous (Caldwell and Lee, 2001; Schulte and Moreno-Roark, 2010). However, the six origins of reptilian viviparity represented in the fossil record, including that of the Cretaceous

TABLE 1

EXTINCT REPTILE SPECIES FOR WHICH VIVIPARITY HAS BEEN INFERRED BASED ON DIRECT EVIDENCE

Reptile Subclade	Species	Age	Literature Reference
Mesosauridae	<i>Mesosaurus tenuidens</i>	Early Permian	Piñeiro <i>et al.</i> (2012a)
Sauropterygia	<i>Neusticosaurus peyeri</i>	Middle Triassic	Sander (1989)
Sauropterygia	<i>Lariosaurus</i> sp.	Middle Triassic	Renesto <i>et al.</i> (2003)
Sauropterygia	<i>Keichosaurus hui</i>	Middle Triassic	Cheng <i>et al.</i> (2004)
Sauropterygia	<i>Dolichorhynchops osborni</i>	Late Cretaceous	Rothschild & Martin (1993)
Sauropterygia	<i>Polycotylus latipinnus</i>	Late Cretaceous	O'Keefe and Chiappe (2011)
Ichthyopterygia	<i>Chaohusaurus geishanensis</i>	Early Triassic	Motani <i>et al.</i> (2014)
Ichthyopterygia	<i>Mixosaurus</i> sp.	Middle Triassic	Brinkman (1996)
Ichthyopterygia	<i>Qianichthosaurus zhoui</i>	Late Triassic	Xiaofeng <i>et al.</i> (2008)
Ichthyopterygia	<i>Shonisaurus popularis</i>	Late Triassic	Camp (1980) [as cited by Lomax & Massare 2012]
Ichthyopterygia	<i>Ichthyosaurus communis</i>	Early Jurassic	Deeming <i>et al.</i> (1993)
Ichthyopterygia	<i>Besanosaurus leptorhynchus</i>	Early Jurassic	Dal Sasso & Pinna (1996)
Ichthyopterygia	<i>Leptoneustes</i> cf. <i>L. tenuirostris</i>	Early Jurassic	Lomax & Massare (2012)
Ichthyopterygia	<i>Stenopterygius quadriscissus</i>	Early Jurassic	McGowan (1979); Maxwell (2012)
Ichthyopterygia	<i>Stenopterygius triscissus</i>	Early Jurassic	Maxwell (2012)
Ichthyopterygia	<i>Stenopterygius</i> spp.	Early Jurassic	Deeming <i>et al.</i> (1993)
Ichthyopterygia	<i>Temnodontosaurus</i>	Early Jurassic	Böttcher (1990) [as reported by Motani 2005]
Ichthyopterygia	<i>Platypterygius australis</i>	Early Cretaceous	Kear & Zammit (2014)
Ichthyopterygia	<i>Platypterygius longmani</i>	Early Cretaceous	Kear <i>et al.</i> (2003)
Ichthyopterygia	<i>Maiaespondylus lindoei</i>	Early Cretaceous	Maxwell & Caldwell (2003, 2006)
Choristodera	<i>Hyphalosaurus baitaigouensis</i>	Early Cretaceous	Ji <i>et al.</i> (2006)
Choristodera	<i>Monjurosuchus splendens</i>	Early Cretaceous	Wang <i>et al.</i> (2005)
Choristodera	<i>Philydrosaurus proseilus</i>	Early Cretaceous	Lü <i>et al.</i> (2014)
Mosasauroida	<i>Carsosaurus marchesetti</i>	Late Cretaceous	Caldwell & Lee (2001)
Mosasauroida	<i>Plioplatecarpus primaevus</i>	Late Cretaceous	Bell <i>et al.</i> (1996)
Squamata	<i>Yabeinosaurus tenuis</i>	Early Cretaceous	Wang & Evans (2011)

lizard *Yabeinosaurus*, predate most of those recognizable among extant squamates.

Comparison to other vertebrates

To consider the reptilian origins of viviparity in the broad context of vertebrate evolution offers a useful perspective. Given the time of divergence of eutherians and marsupials (Luo *et al.*, 2011), mammalian viviparity dates back to at least 160 MA. Thus the three oldest origins of this pattern among reptiles (230 to 278 MA) are of much greater antiquity, representing the oldest known origins of this pattern among tetrapods. However, the duration of viviparity in mammals rivals that of the two longest-lived clades of viviparous reptiles, sauropterygians and ichthyopterygians.

Of the >150 origins of viviparity that have occurred in vertebrate history (Blackburn, 2014), that of mesosaurs is one of a very few that date to the Paleozoic. It is preceded historically by origins of viviparity in a Devonian placoderm (Long *et al.*, 2008), a Carboniferous holocephalan (Grogan and Lund, 2011), and possibly some selachian clades (Blackburn, 2005). Likewise, outside of reptiles, very few vertebrate origins of viviparity can be traced to the early Mesozoic. These are represented by coelacanth (Wen *et al.*, 2013) and an actinopterygian (Bürgin, 1990), both from the Triassic, and some elasmobranchs (Blackburn, 2005).

In sum, viviparity in reptiles is remarkable in multiple ways. Quantitatively, reptiles are responsible for the great majority of origins of vertebrate viviparity, with at least 121 of ~150 identifiable vertebrate origins (Blackburn, 2014). Geologically, reptiles account for two of the longest-lived viviparous clades ever to have evolved. Finally, historically, reptiles represent by far the oldest known origin of viviparity in tetrapods, and three of the oldest to have occurred in all of vertebrate history.

How did ancient viviparous reptiles sustain their embryos?

For a reptilian embryo to develop to term inside its mother's reproductive tract requires that its needs for gas exchange, water, and calcium be met by the pregnant female (Thompson *et al.*, 2004). Provision of organic nutrients is not a minimal requirement of viviparity. In lecithotrophic viviparous forms, organic nutrients are provided by the yolk, and only small amounts of these nutrients are provided after ovulation (Blackburn, 2000b; van Dyke and Beaupre, 2012; Stewart and Blackburn, 2014). How the three essential requirements of viviparity are met in extant viviparous reptiles is discussed below to provide a background for understanding extinct reptiles.

Evidence from extant reptiles

Gas exchange involves the provision of oxygen for aerobic respiration of the embryo and the removal of carbon dioxide as a waste product. In embryos of both oviparous and viviparous reptiles, the need for oxygen progressively increases, and becomes accentuated towards the end of development (Thompson, 1989; Vleck and Hoyt, 1991; DeMarco, 1993; Thompson and Stewart, 1997; Robert and Thompson, 2000; Parker *et al.*, 2004). Maternal-fetal gas exchange poses a particular problem in viviparous reptiles due to the hypoxic nature of the uterine oviduct. In fact, the capacity for maternal-fetal gas exchange is thought to constrain the evolution of viviparity (Andrews and Mathies, 2000;

Andrews, 2002; Parker *et al.*, 2004; Parker and Andrews, 2006). Furthermore, in chelonians, limitations on gas exchange arrest development of the oviductal egg, with the result that the egg is laid at a very early stage of development (Rafferty *et al.*, 2013).

In viviparous squamates, gas exchange is accomplished between capillaries of the uterine oviduct and the fetal chorioallantois, an arrangement that constitutes the chorioallantoic placenta (Blackburn, 1993b; Blackburn and Stewart, 2011; Stewart and Blackburn, 2014). Several specializations facilitate maternal-fetal gas exchange (Blackburn, 2000b). These include the following: increased vascularity of the chorioallantois and pregnant oviduct (Murphy *et al.*, 2010; Parker *et al.*, 2010a, b; Ramírez-Pinilla *et al.*, 2012); evolutionary loss or reduction of the eggshell and the glands that secrete it (Blackburn, 1998a; Heulin *et al.*, 2002; Stewart *et al.*, 2004a; Thompson *et al.*, 2004; Blackburn *et al.*, 2009, 2010; Anderson *et al.*, 2011); a reduction in the interhemal diffusion distance through attenuation of intervening fetal and maternal epithelia (Blackburn, 1993b; Blackburn and Lorenz, 2003; Stewart and Brasch, 2003; Adams *et al.*, 2005; Blackburn *et al.*, 2010; Ramírez-Pinilla, 2014); and the development of higher oxygen affinity of fetal blood over maternal blood (Birchard *et al.*, 1984; Berner and Ingermann, 1988; Ingermann, 1992; Ragsdale and Ingermann, 1993; Ragsdale *et al.*, 1993).

A second major need of viviparous embryos is that of calcium. In all oviparous reptiles (including chelonians, crocodylians, and squamates), the eggshell provides a substantial amount of calcium for embryonic development (Packard and Packard, 1991; Packard, 1994; Shadrix *et al.*, 1994; Packard and Clark, 1996; Stewart and Ecaj, 2010). Eggshell calcium is delivered via the fetal membranes (Ecaj *et al.*, 2004; Stewart *et al.*, 2004b). However, under conditions of viviparity, loss of the eggshell requires that calcium be replaced by the pregnant uterus and be taken up by these same fetal membranes, i.e., by placental means (Stewart *et al.*, 2009a, b; Linville *et al.*, 2010; Fregoso *et al.*, 2012; Stewart and Ecaj, 2010; Stinnett *et al.*, 2012; Stewart, 2013). As is the case with oxygen, embryonic needs for calcium are accentuated late in development when the skeleton becomes ossified (Fregoso *et al.*, 2010; Stewart, 2013).

A third major embryonic need is water. In oviparous reptiles, developing eggs typically absorb water from the substrate during development (Packard *et al.*, 1982; Packard and Packard, 1988; Packard, 1991; Thompson and Speake, 2004), which allows liquefaction of the yolk and contributes substantially to the wet mass of the hatchling. In viviparous squamates, water is taken up from the maternal oviduct via the fetal membranes. The amount of water uptake can be substantial, although in each reproductive mode it varies considerable between species (Blackburn, 1994b; Stewart and Thompson, 2000; Thompson *et al.*, 2000).

Maternal-fetal transfer in viviparous squamates is not limited to gas exchange and the provision of calcium and water. Typically, small amounts of organic and inorganic nutrients are transferred to the developing embryos across the placental membranes (Stewart, 1992; Blackburn, 2000b; Stewart and Thompson, 2000; Thompson *et al.*, 2000; Stewart, 2013). Four lizard clades are highly placentotrophic, and placental transfer accounts for virtually all of the nutrients for embryonic development (Blackburn *et al.*, 1984; Ghiara *et al.*, 1987; Flemming and Branch, 2001; Ramírez-Pinilla, 2006; Blackburn and Flemming, 2012). In two other clades of lizards, nutrients are provided to the embryos by yolk as well as

placental means (Stewart and Thompson, 1993; Thompson *et al.*, 2000, 2001; Thompson and Speake, 2006; Itonaga *et al.*, 2012a) and placental provision has a facultative component (Swain and Jones, 1997, 2000; Itonaga *et al.*, 2012b; van Dyke *et al.*, 2014)

Reproduction in extinct reptiles

As amniotes, extant Reptilia and mammalian monotremes bracket extinct reptiles phylogenetically. Thus, one can extrapolate from extant forms the shared, derived features of the crown group amniote clade (Benton, 2000). Such features include the following: oviparity; internal fertilization; paired maternal oviducts that house the eggs between fertilization and oviposition; a fibrous eggshell that resists egg dehydration; a vascular chorioallantois that lines the eggshell; a vascularized yolk sac that surrounds a relatively large yolk; and direct development, i.e., absence of an aquatic larval stage (for relevant discussions, see Elinson, 1989; Packard and Seymour, 1997; Stewart, 1997). Additional synapomorphic features of extant Reptilia include albumen provision and a mineralized eggshell (Stewart, 1997). However, whether these two features were shared by relatively plesiomorphic Reptilia is not known.

Based on our detailed understanding of extant reptiles, extinct viviparous forms must have addressed the same basic physiological needs of their developing embryos. The need for maternal-fetal gas exchange would have required an evolutionary loss of the eggshell (or its reduction to a vestige). In fact, the absence of an eggshell is widespread in extinct viviparous reptiles, and is routinely used as a criterion for recognizing viviparity (see above). Eggshell loss in turn entails placental formation for the following reasons. The reptilian oviduct is a very thin-walled, collapsible tube that closely envelops the eggs. Without an eggshell, the uterine lining is brought into apposition with the fetal membranes, thereby forming the chorioallantoic and the yolk sac placentas (Blackburn, 1998a). Being highly vascularized, the chorioallantois in particular would be ideally suited to accomplish gas exchange. Thus, as in squamates, placenta formation presumably would be an indirect consequence of viviparity, and would evolve simultaneously with that pattern (Blackburn, 1995, 2006). Given that placentas originated more than 100 times among extant squamate reptiles, their convergent evolution in extinct reptiles is readily understandable.

The placental arrangement necessitated by loss of the eggshell not only would permit gas exchange, but would allow the other two basic needs of embryos to be met. In the absence of a mineralized eggshell, calcium for embryonic development could have been supplied in part via the placental membranes, as in all extant viviparous reptiles. Likewise, the close apposition of fetal and maternal tissues would have provided a ready means of water transfer to the embryos, as it does in extant viviparous tetrapods.

As for nutrient provision, the simplest situation one can envision would be lecithotrophic viviparity, in which the ovulated yolk provides lipids, proteins, and carbohydrates for fetal development. However, no reason exists to rule out the possibility of placentotrophic nutrition of either minor or major extent. Maternal provision of large quantities of nutrients to viviparous embryos (matrotrophy) has evolved at least 33 times among vertebrates. Seven of these origins have occurred among amniotes (six in viviparous squamates and one in mammals) (Blackburn, 2014). No direct evidence of placentotrophy is available for any extinct reptiles. However, for an ovulated yolk to give rise to a fetus as large as that of the plesiosaur

Polycotylus would be unprecedented in vertebrate history. Thus, based on neonatal size, placentotrophy remains highly plausible for plesiosaurs, and possibly ichthyosaurs as well.

Consequences of viviparous reproduction

Studies on extant squamates offer insight into how viviparity may have arisen in the extinct reptilian lineages. According to a popular scenario, reptile viviparity evolves via incremental evolutionary increases in how long developing eggs reside in the maternal oviduct (Packard *et al.*, 1977). Gravid females retain their eggs for progressively longer periods of time, laying them in later and later stages of development. Viviparity represents the culmination of this trend, in which the female gives birth to her offspring. In a modification to this scenario, maternal retention of advanced embryos is evolutionarily unstable and the transition to viviparity occurs via a punctuated equilibrium transformation (Blackburn, 1995, 1998b). In both versions of the scenario, selection on intermediate evolutionary stages must occur. Thus, oviparous egg retention must be viable and progressive increases in the duration of egg retention must be adaptive (Packard *et al.*, 1977; Shine and Bull, 1979; Shine, 1985; Stewart and Blackburn, 2014).

This scenario may explain the association of viviparity with aquatic habits in the extinct reptilian lineages. The transformation from typical oviparity to viviparity could not occur in a fully aquatic lineage, since the evolutionarily intermediate stages of oviparous egg-retention (requiring terrestrial oviposition) would not be possible. However, in a semi-aquatic form that was able to return to land to lay its eggs, progressive evolutionary increases in egg-retention could be adaptive. Potential advantages to the embryos such as thermoregulatory benefits (Shine, 2014) would accrue, and the gravid female would gain freedom as to when and where to find a suitable site on land in which to deposit her eggs. Thus, viviparity could have arisen under semi-aquatic conditions and in descendant forms, exerted a permissive effect on the evolution of fully aquatic habits. Thus, a semi-aquatic, viviparous lizard such as *Yabeinosaurus* could reflect an intermediate stage in the sort of transformation that lies in the deep history of fully aquatic forms such as plesiosaurs and ichthyosaurs. Consistent with this scenario is the fact that the basal ichthyopterygian *Chaohusaurus* is thought to have evolved its viviparous habits under more terrestrial conditions (Motani *et al.*, 2014).

Conclusion

Far from being confined to extant squamates reptiles, viviparity characterized several groups of pre-Cenozoic reptiles, reflecting at least six separate evolutionary origins. In each case, the pregnant females must have sustained their developing embryos via placental gas exchange and possibly nutrient provision, most likely by means similar to those of extant reptiles. In five of the identified extinct clades, viviparity was an essential component of the ecology and life history of the animals, by permitting reproduction in water and the evolution of fully aquatic habits. Viviparity probably was more widespread among the extinct groups than we currently recognize. After all, much of the definitive documentation of live-bearing reproduction has only become available in the past 15 years, and in some key fossil specimens, evidence for viviparity was initially overlooked. Thus, future research on extinct reptiles

should remain open to the possibility of viviparity in groups for which evidence is not yet available.

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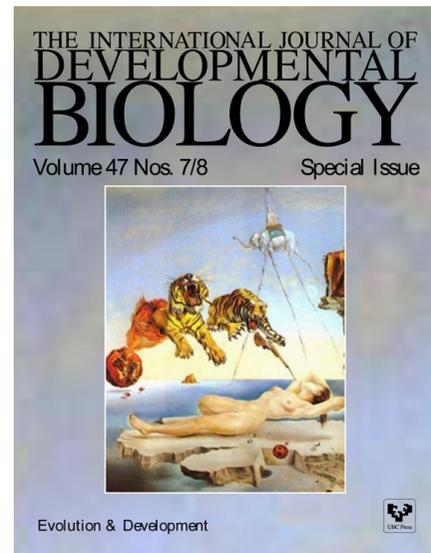
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