Seminars in Cell & Developmental Biology 21 (2010) 432–440

Contents lists available at ScienceDirect

Seminars in Cell & Developmental Biology

journal homepage: www.elsevier.com/locate/semcdb

Review

A survey of the rock record of reptilian ontogeny

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ARTICLE INFO

Article history:
Available online 11 November 2009

Keywords:
Growth
Development
Heterochrony
Allometry
Dinosaur

ABSTRACT

Given the large diversity and long stratigraphical range of fossil reptiles, their development is a fundamental aspect of the evolution of ontogeny in vertebrates. Eggs, juveniles, embryos and growth series document different aspects of fossilized ontogenies. About three-fifths of the more than 850 available publications on these topics concern dinosaurs. Non-invasive imaging techniques have facilitated the study of embryos *in ovo*. Examination of ontogenetic trajectories is used to establish criteria to identify fossil growth series and solve taxonomic issues. Many morphological innovations in reptilian skeletal structures are associated with growth heterochronic changes, whereas sequence heterochronic changes remain largely unstudied but are a potential avenue of research. Relative age assessments via not only palaeohistology but also comparative anatomy have been used to reconstruct life history patterns in fossil archosaurs. Several fossil marine reptiles evolved viviparity convergently. Extinct adult phenotypes can reveal information on development, as in the discovery of polydactyly in diapsids, the examination of vertebral number evolution, and its relation to somitgenesis and *Hox*-gene boundaries, and signs of tissue regeneration provided by anatomical peculiarities following caudal autotomy.

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1. Introduction—a database of developmental palaeontology in reptiles

The extant radiation Reptilia includes over 18,000 species: about 8700 species commonly referred to reptiles and over 9600 species to birds [1]. This clade originated in the Carboniferous period about 320 Ma [2]. The rich diversity of fossil reptiles includes not only non-avian dinosaurs, but also radiations of marine forms (e.g., Sauropterygia), an extinct clade of flying forms (Pterosauria), a clade of wholly extinct forms including armoured and marine reptiles (Parareptilia), as well as many groups related to extant reptiles which exhibit many kinds of variations in size, shape, and ecology [3,4]. Such a large clade must have had a diversity of developmental strategies and life histories, deeming ontogenetic studies of fossils relevant to understand this radiation.

The integration of embryological and palaeontological data to understand evolutionary transformations in reptiles has a long tradition [5] and is currently exemplified by the ongoing discussions on the origin of the bird digit identities from theropod ancestors [6–10] and that of the turtle shell [11,12]. One of the few quantitative methods to compare ontogenetic and evolutionary transformations of an anatomical complex was developed using crocodiles as subject of study [13].

In this paper we provide an overview of how the fossil record informs about the evolution of development in reptiles; previous treatments of this topic have mostly concentrated on dinosaurs

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1084-9521/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.semcdb.2009.11.007

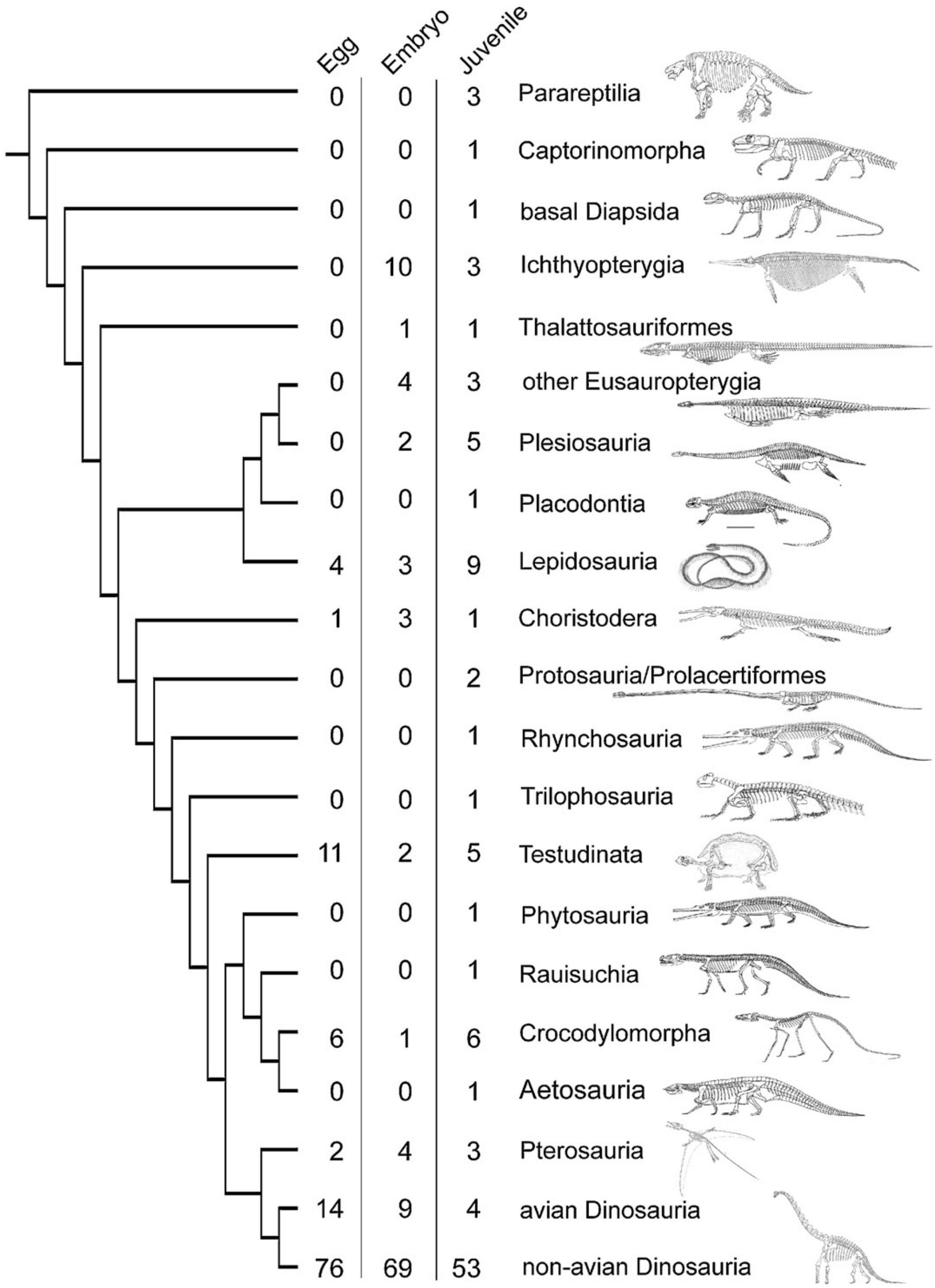

Fig. 1. Summary of the relative frequency of fossilized embryos, juveniles, and eggs in major clades of reptiles. These numbers were calculated based on data presented in www.developmental-palaeontology.net (version July 2009). There are no reports of eggs of aetosaurs, but there is possible evidence for their nests [21].

(e.g. [14]). We reviewed the literature concerning developmental palaeontology in reptiles and found more than 850 papers dealing with fossil eggs, embryos, and juveniles (see www.developmental-palaeontology.net). A summary of the relative frequency of selected taxa is reported in Fig. 1. Knowledge of fossilized ontogenies is taxonomically skewed and does not represent all windows of development. About three-fifths of the papers deal with avian and non-avian dinosaurs, with non-avian dinosaurs being 10 times more represented than birds. Turtles and crocodylomorphs are discussed in about 5% of the papers. Most of the information available at present concerns juvenile stages. Direct investigations in fossil reptiles, and amniotes in general, are usually hampered by their mode of reproduction involving the amniote egg, with the embryo having poor potential for fossilization.

There are also indirect ways to study ontogeny in fossils. Fossils of adult individuals can provide ontogenetic information because of records of development in skeletal tissues, for example via palaeohistology [15]. They can also be informative on the development by virtue of preserving phenotypes with features that can be one-to-one related to a developmental process [16] or by expanding the morphological space [17] occupied by a clade.