The Palaeontology Newsletter

Contents

Association Business 2
News 8
Association Meetings 10
Meeting Reports 14
Mysterious Fossils 25
From our correspondents
   Inferring Developmental Mode 26
   Foiling vertebrate inversion 32
   PalaeoBioSuperstar 40
   Palaeo-math 101: Regression 4 44
Obituary: Ehrhard Voigt 54
Progressive Palaeontology 2005 57
Future meetings of other bodies 58
Book Reviews 72
Palaeontology
   vol 48 parts 1 & 2 92–93
Discounts for PalAss members 94

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Something Old, Something New: Inferring Developmental Mode from the Fossil Record

Continuing with our discussion of topics relevant both for developmental biologists and palaeontologists, this article addresses how mode of development can be interpreted from fossilized developmental stages of extinct metazoans, using knowledge from extant metazoans. We also present examples of how life history information from extant species can enhance our understanding of fossilized developmental stages, and discuss the importance of these fossils to modern biological research. Unlike living taxa, for which collection of embryos is at least possible (although admittedly, not always practical), among fossil forms such opportunities are extraordinarily limited at best. Where fortuitous taphonomic conditions preserve entire developmental series (e.g., Dong et al., 2004), such instances are the extreme exception to the rule, and cannot be expected for the majority of species. Fortunately, features of fossilized adult and juvenile skeletons, and traces and impressions of soft tissues, can provide clues to developmental mode.

*Mode of development* can be direct, when a miniature version of the adult form is born/hatched, or indirect, when one or more free-living larval stages undergo metamorphosis to attain the adult form. The presence of a larval stage is the defining characteristic of indirect development. Larvae are, by definition, morphologically distinct from the adult form, often possessing different structures and body plans from the adult, and typically make use of different ecological niches (see Hall and Wake, 1999 for further discussion of larval stages). One of the most widely recognized examples of indirect development is the metamorphosis of a larval caterpillar into an adult butterfly. Along with developmental mode, growth rates, feeding strategies, age and size at maturity, death rates, and reproductive mode are collectively referred to as life history traits (Wake, 2003). Together, these traits determine how an organism interacts with its environment and the roles it plays within the ecosystem.

Life history information is useful in clarifying relationships between metazoan taxa that would otherwise be obscured by drastic differences between adult and larval morphologies. A classic example is the realization that ascidians are chordates, which was discovered by looking at the morphological features of their tadpole larvae (Hall, 2005). Mode of development is also helpful in differentiating cryptic species with similar adult forms (e.g., the sea urchin genus *Heliocidaris*, in which adults of both species are morphologically identical, yet one species (*H. tuberculata*) has a feeding larval form while the other (*H. erythrogramma*) does not (Raff et al., 1999). Comprehensive surveys can also elucidate the evolution of differential developmental modes within a particular taxon. For example, ten of the approximately thirty extant anuran families exhibit direct development; parsimony dictates that indirect development is the ancestral state (Hanken, 1999).
Similar information can be gleaned from fossil embryos of both direct and indirect developers. In the discussion that follows, we highlight diagnostic features of direct and indirect developers from a host of metazoan taxa, and briefly discuss the implications of the recognition of developmental modes and fossilized developmental stages.

INVERTEBRATES

Echinoderms
Echinoderms, such as sea urchins, exhibit both direct and indirect development. Due to their well-mineralized skeletons both adults and larvae are commonly recognized in the fossil record (Déflandre-Rigaud 1946; Sprinkle, 1987). Calcium carbonate skeletal rods, called spicules, are characteristic of planktonic feeding (planktotrophic) echinoderm larvae. Spicules may be present in direct developing species, lacking a "true" larval stage (such as brooded embryos), or lecithotrophic species (nonfeeding larvae with yolk eggs; Emlet, 1995), but they are typically not as elaborate or well organized as those of indirect developing species.

Larvae of extant sea urchins metamorphose into juveniles that grow in size to become adults. The juvenile develops as a cluster of cells within the larva, and the juvenile skeleton is deposited within this cluster as a series of calcium carbonate plates. Some of these plates develop in association with the proximal end of the spicules. Studies using polarized light have shown that the crystallographic axes of the calcium carbonate crystals that form the larval spicules determine the axes of these plates (Emlet, 1985). In general, if a juvenile plate has formed from a spicule, as it would in indirect developers, the plate will have a crystallographic axis that is nearly parallel to that of the spicule from which the plate originates. Alternatively, in direct developing species, the juvenile plates do not form from spicules and the crystallographic pattern of the affected plates would be expected to be nearly perpendicular to that of the plate surface (Jeffery and Emlet, 2003). Consequently, the developmental mode of a fossilized adult sea urchin can then be determined by placing the fossil under polarized light and observing the axes of the plates.

Molluscs
In molluscs that secrete an external, calcified shell, the shell forms early in development, and mode of development can be inferred from scanning electron microscopical studies of the shell at nearly any time during ontogeny (see review by Jablonski and Lutz, 1980). Among snails (Gastropoda), shells can be classified into three sections: protoconch-1, protoconch-2 and teleoconch, each secreted at a different stage in development (pre- and post-hatching, and post-metamorphosis, respectively). One can infer egg size and amount of yolk, which indicates larval type, from each segment. In general, a small, well-defined protoconch-1 indicates a small (<200μm) egg with a small amount of yolk, typical of planktotrophic larvae. A large protoconch-1, and protoconch 1-2 boundary that is not readily discernable indicates that the specimen was likely a product of a larger, more yolk-filled egg; this is typical of nonplanktotrophic developers (including lecithotrophic and brooded embryos).

A similar analysis can be applied to bivalves. The trochoophore (first larval stage) and veliger (second larval stage) shells, formed prior to metamorphosis, are termed prodissoconchs 1 and 2, respectively; the dissoconch is formed post-metamorphosis. Again, shells that have distinct boundaries between sections, have a small (<150μm in length) prodissoconch-1
and a relatively smooth prodissocochn-2 surface suggests planktotrophic development (see also Moran, 2004), while a large (>135μm) prodissocochn-1 and a small or nonexistent prodissocochn-2 is indicative of lecithotrophic development. Shells of brooded embryos often have a very large (>>230μm) and rough prodissocochn-1. It may be difficult, however, to classify shells of a direct versus an indirect developer when sections fall in an intermediate size range (135–150 μm).

Bryozoans
Bryozoans are yet another marine invertebrate group exhibiting diverse modes of development and having mineralized elements which fossilize well. Although colonial bryozoans most often reproduce asexually, extant species are also known to produce both lecithotrophic and planktotrophic forms. Lecithotrophic bryozoan larvae are usually larger than planktotrophic larvae, and may exhibit brood chambers (McGinnis, 1997). The first larva to settle to the substrate, metamorphose and start a colony is called the ancestrula (Pechenik, 2000). Examining and measuring the size of fossil ancestrulae can therefore provide some insights into mode of development of particular taxa. This information must be used in combination with knowledge of the palaeogeographic and palaeogeologic distributions of the taxa in question further to corroborate mode of development (Pachut and Fisherkeller, 2005).

Many other invertebrate groups have also been found as fossils, and inferences have been made as to their development (see Raff, 1996; Morris, 1998; Budd, 2004; Dong et al., 2004).

**VERTEBRATES**

**Fish**
Of course, indirect development is not limited to the invertebrates; a number of fossil fish larvae are now known. In fact, the oldest known vertebrate larva is a lungfish larva from the Middle Devonian (Thomson et al., 2003). Some groups of fish have unique larval characteristics providing clues to their taxonomic affiliations and life histories. For example, the cranial adhesive glands common to larvae of substrate-brooding cichlids are reduced or entirely lacking in larvae of extant mouth-brooding cichlids (Richards and Leis, 1984; Meijide and Guerrero, 2000). Klett and Meyer (2002) show that substrate-brooding and larval cranial adhesive discs are primitive, and that mouth-brooding and larval regressed cranial adhesive discs are derived for African cichlids when these characters are mapped onto a molecular phylogeny. Knowledge of these life history strategies and larval characteristics in cichlids would enable palaeontologists to recognize the existence of fossil cichlid larvae should they be discovered.

**Anuran amphibians**
Indirect development is also common to many amphibians. Although rare, fossilized anuran tadpoles representing several species, including extant genera (e.g., Pelobates from the Miocene of Turkey; Wassersug and Wake, 1995), are known. Larval forms resembling tadpoles and salamander larvae have been found dating back to the Carboniferous (Milner, 1982). Two recent studies (Chipman and Tchernov, 2002; Baez and Pugener, 2003) reveal beautifully preserved ontogenetic series of anuran species – one from a large grouping of soft tissue imprints and skeletons from the Lower Cretaceous (the pipid Shomronella jordanica), and the other a soft tissue assemblage from the mid-Eocene to early Oligocene.
(reportedly representing a new pipid taxon). The presence of tadpoles confirms that these species exhibited indirect development and corroborates an ancestral designation for indirect development in anurans.

Direct development in amphibians is not represented in the fossil record (Elinson, 2001). This is more likely a failure of fossilization of early developmental stages of amphibians than it is of their recognition, as direct- and indirect-developing amphibians can be readily distinguished based on discrepancies in skeletal development. For example, the elongation and ossification of jaw cartilage occur sequentially in anuran larvae, but simultaneously in the direct developer *Eleutherodactylus coqui* (Elinson, 2001).

**Urodèle amphibia**

Early descriptions of various salamander-like taxa separated those forms with external gills (so-called Phyllospondyli) from those without external gills ('branchiosaurids'). More detailed studies have since amended this notion, and now several temnospondyl amphibian groups are known from partial ontogenetic series that include larvae.

A study of the temnospondyl *Micromelerpeton credneri* (Witzmann and Pfretzschner, 2003) identified a series of ontogenetic characteristics that suggest adaptation to a terrestrial habitat from an aquatic environment. These features include sequential ossification of the postcranium (in craniocaudal and proximodistal fashion), relative shortening of the external gills, relative increase in the diameter of the sclerotic ring (and consequently the eye) and formation of a palpebral bone (indicating the presence of an eyelid, a feature not seen in larval/neotenic salamanders; see Witzmann and Pfretzschner, 2003 and references therein).

Other putatively transitional characteristics, such as changes in dermal sculpturing, are now considered to be individually variable and not necessarily linked with the adoption of a terrestrial lifestyle (Witzmann and Pfretzschner, 2003; Schoch, 2004). In *Micromelerpeton*, ontogenetic growth of the skull appears to be gradual, and the appearance of 'adult' characters (such as eyelids) simultaneous with the ongoing loss of larval features (such as the presence of external gills) suggesting that in at least some forms the transformation from larval to adult was prolonged (see Albrech, 1989).

Analysis of fossil larvae is also useful in inferring the phylogeny and evolutionary origins of amphibians. For instance, Roček's (2003) comparison of larval development in *Palaeobatrachus* and *Xenopus laevis* suggests that the two taxa are closely related. Similarly, Carroll and colleagues (1999) have extrapolated patterns of ontogeny, specifically the ossification rates of vertebral elements, from fossilized Palaeozoic tetrapods and compared them with those in modern amphibians. They note that ossification of the centra is expedited in caecilians, urodeles and lepospondyls relative to anurans and labyrinthodonts, and suggest that the anuran lineage split from basal tetrapods earlier than urodeles and caecilians.

All of these examples underscore the utility of early developmental stages of all metazoans (fossil and extant) for elucidating the taxonomic affinities, ecology and evolution of both extant and extinct taxa. The potential applications for information gleaned from fossil developmental stages, however, are not limited to the realm of palaeobiology. For instance,
fossil larvae may provide information useful to the geologist interested in climate variation or palaeotectonism. We hope this paper will serve as a general introduction on how knowledge of life history information allows us to distinguish developmental modes within the fossil record, and how fossil developmental stages contribute to discussions of the evolution of developmental forms and metazoans.

References


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