Reproductive modes, ontogenies, and the evolution of body form

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Abstract—The evolution and development of complex morphological structures, and of body form, can now be addressed hierarchically, using diverse techniques from multiple theoretical perspectives. Such an ‘integrative’ or ‘holistic’ approach is likely to provide more complete insight into the origin of patterns and processes of evolution than the more traditional reductionist mode. Current work on the implications of reproductive mode on the ontogenies of amphibians and the evolution of their body form is an example of that approach. Genome size, egg and clutch size, and a number of other life history traits are involved with developmental rate and pattern (including loss of larval features, ontogenetic repatterning, and modified patterns of organogenesis), and reproductive mode (the presumed ancestral egg-laying vs. direct development and viviparity) is correlated and potentially causal for certain patterns. Such correlations are being explored using a variety of approaches, and examples of this work-in-progress are provided.

Keywords: amphibians; direct development; genome sizes; viviparity.

INTRODUCTION

The ‘Leiden School’ has, for a long time, led an intellectual synthesis of modelling, functional approaches, development, behaviour, ecology and, recently, evolution, in its holistic approach to ideographic studies of morphology. This holism has both developed and summarised the approach and enabled conceptual advances, as new methods and tools are meshed with new ideas. It was adopted as a model by many of us, either consciously or unconsciously. The Leiden School’s holistic approach to studies which are primarily morphological, but which integrate many ideas and techniques from all areas of biology, engineering, physics, and mathematics, in order to understand biological complexity, was a forerunner of the ‘integrative biology’ that many of us now espouse, and try to institute.

An important factor in the Leiden School’s approach to holistic studies has been the selection of interesting animals as objects of research and study. Many were
chosen, apparently, because of their complexity — such as the rattlesnakes for Pieter Dullemeijer’s brilliant analysis of the functional morphology of the head (see Dullemeijer, 1974), and Gart Zweers’ work on feeding and drinking in birds (e.g., Zweers, 1991; Zweers et al., 1994). Was an inductive logic that developed the problem also involved in the selection of the organism of study?

It is of concern that organisms currently considered to be ‘model’ are rarely good choices as study organisms for evolutionary biologists interested in issues of complexity. Model animals usually become such because they represent particular species with particular characteristics. Model animals for developmental biology, for example, are usually characterised by the following criteria: rapid development and short generation time, relative insensitivity to environmental perturbation, assumptions of universality, and practicality of breeding and maintenance (Bolker, 1995). Not only is phylogeny “rarely or never a factor in the choice of model systems” (Bolker, 1995), but such species are rarely members of lineages for which there are robust phylogenetic hypotheses, so evolutionary trends cannot be mapped on phylogenies in order to assess direction of evolutionary change. Furthermore, model species are usually derived members of lineages, with unique characters, that give no information about relationships to other species (Cannatella and de Sá, 1993). Studies of individual species give no information about the ancestral condition (Hanken, 1993; Kellogg and Shaffer, 1993). Bolker (1995) recommends that more attention be given to developing research on non-model species, with the integration of results of that work into current theories and research agendas, which will test the universality of model system data by providing a comparative base.

I do not know whether the Leiden School has intuitively rejected the model systems approach, or chosen species with the idea that they should become model systems because of their particular characteristics. However, their research has illustrated that choice of study organism is critical to holistic, integrative science, and that non-model organisms have features that make them appropriate to many kinds of studies, despite practical difficulties. Significantly, such studies illustrate that science can expand because of non-model systems, rather than be constrained by them.

My approach to questions of complexity in biology has been parallel to and, I think, influenced by, the Leiden approach. I have concentrated much of my research on a little known, difficult to obtain and maintain, lineage of animals — far from ‘model animals’. I have chosen to do broadly comparative research, but I have tried to deal with issues of complexity from both a taxon- and systems-driven approach and a question-driven thesis, and inductive and deductive methods. I will illustrate this with a consideration of the implications of reproductive mode on ontogenies of animals, and the evolution of their body form.

Reproductive modes and ontogenies

I would propose that we currently focus too narrowly on the evolution of adult body form; the ontogeny of body form, not the final adult form, may be a more
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profitable source of study in order to understand patterns of evolution. As de Queiroz stated (1985), “the ontogenetic transformation is the character”, and he laid out an explicit methodology for examining ontogenies as characters in analyses of phylogenetic reconstruction. It has rarely been utilised (but see Wake and Larson, 1987; D. Wake, 1989). The evolution of the body form of larvae to the free-living, pre-metamorphic phase, the modifications and their costs of metamorphosis, and the form of embryos/foetuses to effect survival by direct development and viviparity are equally important (if not more so) to survival (see Hall and Wake, 1999; Richardson, 1999).

I focus my concern on the evolutionary morphology of amphibians because, as a group, those non-model organisms have many ‘natural experiments’ in progress that may give insight into whether examination of entire ontogenies might be productive. Taxa and lineages reveal many alterations in reproductive mode, ontogeny and life history, and consequently form and function. Many of the modifications of body form (e.g., miniaturisation, secondary simplification, ontogenetic repatterning) occur in taxa that have derived reproductive modes relative to more basal members of their lineages. As indicated above, the ancestral reproductive mode is generally believed to be that of external fertilisation of eggs laid in water, with a free-living, feeding larval stage that then undergoes metamorphosis to the adult morphology, physiology, and ecology. Frog tadpoles and salamander and caecilian larvae are examples of that free-living, pre-adult phase of the life history. Derived reproductive modes typically are those that obviate aspects of the aquatic aspects of reproduction and development, such as internal fertilisation, eggs laid on land or in trees, direct development (eggs laid on land, with embryonic development through metamorphosis before hatching, so that a juvenile emerges), live-bearing (embryos retained in or on the body of a parent, sometimes with parental nutrition after yolk is exhausted, and ‘birth’ at various stages from larval through completely metamorphosed juveniles), and parental care. Assessment of the pattern of evolution of features is now usually carried out by assessing phylogenetically-related groups (= lineages), such that taxa basal in the lineage are those with predominately ancestral characters, and derived taxa are those that have features presumed to be a consequence of the evolution of the lineage (possessing synapomorphies — shared, derived characters, which bear upon relatedness, and autapomorphies — derived features unique to the taxon examined, which do not give evidence of relatedness, but only of derivation). Derived reproductive modes that I will emphasise are direct development and ovo-viviparity/viviparity, although there are many others, especially among frogs. I pose several questions. How many times has direct development evolved? What are the physical, physiological, and ecological correlates of its evolution? How many times has live-bearing evolved? What are the correlates of its evolution? What modifications of form are consequences of alteration of reproductive mode, and what may be ‘drivers’ of that alteration? What came first, change in reproductive mode, or change in developmental rate or ecological responses?
I consider direct development and live-bearing to be alternative, and very different, paths to terrestriality and obviation of the free-living larval phase. Some workers (e.g., Hanken, 1992) consider that viviparity can be subsumed within direct development because of the loss of the larval period. I do not believe that this is appropriate, because direct developers deposit on land a clutch of fertilised ova that has the maternal contribution of nutrients, hormones, etc., contained within it. Conversely, live-bearers carry their developing embryos in or on their bodies, and thus many species can moderate the nutrient, hormonal, and ecological regimes throughout gestation, providing a much more fine-tuned developmental environment. I will compare correlation of genome size, cell size, egg size, rate of cell proliferation, developmental trajectories, and adult form in amphibians with direct development and viviparity in order to assess correlation among these features.

Direct development has evolved in several lineages of frogs and salamanders and is relatively well studied (Del Pino and Elinson, 1983; Elinson, 1987, 1989; Del Pino, 1989; Hanken, 1992, 1999; Collazo, 1996; Callery et al., 2001, and other references herein); study of the relatively few direct-developing caecilians is limited (e.g., Brauer, 1897, 1899; Wake, 1986). Viviparity is rare in frogs (but well studied for one of the few species — see Xavier, 1977, 1986) and salamanders (constrained to a very few salamandrids [See Joly, 1986; Guex and Greven, 1994; Dopazo and Korenblum, 2000, for summaries]). Conversely, a number of species of caecilians are viviparous (Wake, 1977a, b, 1989). (See Wake, 1977, 1982, 1993; in press a, b, c; Wake and Dickie, 1998, for summaries of aspects of the evolution of viviparity in amphibians, and Blackburn, 1992; Guillette, 1987; Packard et al., 1989, and Wake, 1989, for summaries for vertebrates.) I will first examine what is known of the correlation of genome and cell size with developmental patterns and effects on adult morphology in direct-developing amphibians, and then compare these correlations with those that occur among viviparous taxa.

DIRECT DEVELOPMENT

Wake and Hanken (1996) list several ‘developmental consequences’ and correlates associated with the evolution of direct development. They include: increase in egg size and development time, loss of larval structures, ontogenetic repatterning, altered pattern formation in organogenesis, evolutionary and phylogenetic consequences and correlates (are certain patterns characteristic of particular lineages?), loss of larval constraints, conservation of ontogenetic trajectories, and homoplasy. Much can be learned about mechanisms of the evolution of ontogeny and of adult form by comparing features at several levels of organisation (DNA quantity, cell size, cell number, processes of cell movement and differentiation), especially in non-model organisms that have derived reproductive modes, to obtain information on patterns (and processes) of evolution.
Genome size, cell size, and egg size

There is a developing literature on the correlation of genome size, cell size, developmental rates and adult morphology and the correlation of egg size with developmental rates and products, and on hormonal mediation of development, but these are rarely comparative studies, and even more rarely include analysis of the reproductive modes that influence them. Most of our knowledge of correlation of genome size, cell size, and effects on development is based on comparisons among oviparous species with the ancestral reproductive mode, and a few comparisons of direct-developing frogs and salamanders with related species that have a larval phase: little attention has been paid to live-bearing modes in this context.

Chipman et al. (2001) reviewed the correlations of genome size in seven species of frogs, such as a larger genome providing longer cell cycle time, slower cell division rate, and lower metabolic rate. They investigated cell size/cell number and cell size and rate of development and cell proliferation in order to sort the differences that influence evolutionary processes via changes in genome size. Their seven species have a $3 \times$ difference in genome size; all have ancestral reproductive modes, not derived. Some genome size differences among their species are a result of polyploidy, but most are not. Genome size is thought to correlate with slower developmental rate, but large genome size is not necessarily causal, and the complexity of development must be considered. Chipman et al. found that interspecific variations in cell size or density are evident only at relatively late stages of development, but differences in rate of proliferation and development are evident throughout development. Their results were inconclusive regarding support for the hypothesis that increased genome size has a selective role and is one of the mechanisms for changing growth rates and metabolic rates during evolution, vs. whether changes in genome size are random events to which the organism as a whole must adapt. They state that genome size is not only correlated with, but is causally linked to, general growth rate; that variation of different kinds of cells (late vs. early cell density during development, a negative correlation of genome size with CNS development, that the notochord does not proliferate during development, etc.) confounds the problem, and that embryo size is not correlated with genome size, etc. They concluded that evolutionary changes in genome size must occur concomitantly with adjustment of development to compensate for differences in cell size and proliferation rate. They might have gained different insights if they had sampled different reproductive modes.

Egg size and development

The correlation of egg size and developmental time has long been known both in general and specifically for amphibians (see Wake and Hanken, 1996, for summary). Wake and Hanken suggest that large egg size may be the ancestral point of departure for the evolution of direct development. Large egg size typically results in slow development relative to congeners with smaller eggs; however, large eggs and slow
development can occur in species with larvae, so it is necessary but not sufficient for direct development. In the direct-developing salamanders and frogs (see Del Pino and Elinson, 1983; Elinson and Del Pino, 1985; Elinson, 1987, 1989; Del Pino, 1989; Collazo and Marks, 1994; Collazo, 1996), and in caecilians with large yolky eggs, whether direct-developers or not (Duenker et al., 2000), the large eggs have meroblastic rather than holoblastic cleavage, the early embryos form a disk on the top of the yolk (similar to that of the large, yolky eggs of birds), and morphogenetic movements are modified. The correlation of egg size and genome size with developmental rate in salamanders is complicated, but it is clear that direct developers have long hatching times (79-251 da: Wake and Hanken, 1996), with the shorter times being characteristic of direct developers with relatively smaller eggs and smaller genomes.

Collazo (1996) examined the correlation between early development and life history in plethodontid salamanders, and found that they have large eggs and slow development. Large egg size influences several aspects of early development, including time of holoblastic cleavage (as a barrier to cytokinesis), thickness of the blastocoel roof, gastrulation process and timing, early developmental rate (Collazo and Wake [unpubl. data] found that rate of early development correlates with egg size but correlates more strongly with genome size), formation of an embryonic disk, and percentage of egg volume contributing to embryonic structures. Collazo (1996) examined 28 species of plethodontids, and found that oviposition in fall or winter is the derived condition (all plethodontids have internal fertilisation), suggesting that many features of life history are correlated with cell size/egg size phenomena. Elinson (1989) found that increases in egg size may have led to the transition from monospermic to polyspermic fertilisation, eliminating blocks to polyspermy.

Loss of larval features

Direct development is characterised by the embryonic development of adult features before hatching, given the absence of the larval stage. Hanken (1992) and Hanken et al. (1992) have conjectured about the extent to which ancestral larval features are recapitulated by direct developers. Loss of larval components (e.g., bones, muscles, neuromast organs) is demonstrated in a number of salamander and frog species (summarised in Wake and Hanken, 1996). In addition, loss of larval structures is characterised by extensive changes in the embryonic patterning of the remaining components, and the appearance of novel adult features.

Ontogenetic repatterning

Apparently new sets of morphogenetic processes occur in direct-developing salamanders (and frogs) that have large cell sizes; this has been called ‘ontogenetic repatterning’ (Roth and Wake, 1985; Wake and Roth, 1989). The evolution of the highly projectile tongue of many direct-developing plethodontid salamanders as a
consequence of loss of lungs (D. Wake, 1982) and reorganisation of the tectum mesencephali (Roth et al., 1994) and the brainstem motor nuclei (Nishikawa et al., 1991) are examples of such repatterning.

**Pattern formation**

Altered pattern formation in organogenesis is another feature of direct-developers relative to related taxa. Limb development patterning is an example. In direct developing frogs and salamanders, limb development is accelerated, so that hind limbs develop rather early and nearly simultaneously with the forelimbs (summarised in Wake and Hanken, 1996). Hanken et al. (2001) note that the assumption that limb development is highly conserved among vertebrates is based on study of very few species, virtually none with derived reproductive modes, “which might be expected to affect developmental pattern or process”. In direct developing frogs, many of the features that form after hatching in metamorphic frogs, such as limbs, appear during embryogenesis in direct-developers. They studied *Eleutherodactylus coqui*, a Puerto Rican leptodactylyid frog that has a mosaic of conserved and novel features. Conserved are the basic sequence and the pattern of limb chondrogenesis, expression of distal-less protein in distal ectoderm, expression of sonic hedgehog in the zone of polarising activity (ZPA), and the ZPA inducing supernumerary digits when transplanted to a host limb bud. Novel features (Richardson et al., 1998) include absence of a morphologically distinct apical ectodermal ridge, the ability of the limb to continue distal outgrowth and differentiation of the distal ectoderm, and earlier cessation of the induction by the ZPA. Attempts to represent tetrapod limb development as a developmental module must take into account evolutionary variation among species.

**Effects on adult body form**

Adult body forms correlated with direct development include miniaturisation; this phenomenon occurs relatively frequently in direct developers, but not always (Hanken and Wake, 1993; M. Wake, 1986). Roth et al. (1988, 1990) cite direct development and large cell size as key factors in miniaturisation and other aspects of adult body form. For example, Roth et al. (1994) found that cell size is a predictor of the morphological complexity of the amphibian tectum mesencephali. Cell size is correlated with genome size in amphibians. Frogs with small cells have more complex tecta than frogs with large cells, independent of body and brain size. Salamanders, however, have brain-body size relationships that are correlated with tectal complexity. Small salamanders with large cells have simple tecta; large salamanders with small cells have the most complex tectal morphologies. Increases in the genome and, therefore, cell size, are associated with a decrease in the differentiation rate of nervous tissue, which leads to the differences in brain morphology. Therefore they concluded that features of the structure of the brain can arise independently of functional demands as a consequence of changes at lower
levels of organisation; increase in genome size apparently induces simplification in brain morphology.

As noted above, ontogenetic repatterning can have either subtle (such as the above example of brain structure) or more profound consequences for adult form, including miniaturisation, or lung loss resulting in modification of feeding morphology (the projectile tongue in lungless plethodontids (D. Wake, 1982)). These effects have primarily been observed in salamanders among the amphibians; there is little evidence of such effects on adult forms in frogs or caecilians, although the development of only one elongate lung in most caecilians, with secondary reacquisition of the second lung to some degree in the aquatic caecilians, may be a consequence of ontogenetic repatterning concomitant with elongate body form and the physiological demands. Most taxa have not been studied in terms of ontogenetic repatterning (and most of the phenomena in question).

VIVIPARITY

It is instructive to compare the features of direct development with those of development of viviparous species; nearly all we know about derived reproductive modes and developmental correlates pertains to direct developers. Viviparity with maternal nutrition involves reduced egg sizes: ovoviviparous taxa that simply retain their developing young in or on the bodies of a parent usually do not have reduced egg sizes (= yolk volumes). The yolk reduction/egg size reduction appears to be independent of genome size; the constraint on genome size appears to be phylogenetic. However, only *Salamandra atra*, *S. salamandra*, and a few caecilians among live-bearing taxa, have been subject to genome size measurements (Gregory, 2002; M. Wake, unpubl. data). In amphibians with derived reproductive modes, developmental rates are usually longer than in related species with ancestral reproductive modes, and this seems particularly true of viviparous taxa. In the viviparous frogs and salamanders, there appears to be an ecological correlation: they live at high altitudes, and temperature and rainfall distribution are thought to influence the gestation period, either by a tight correlation (*Nectophrynoides occidentalis* [Xavier, 1977, 1986]) or a loose one (*Salamandra atra* [summarised in Guex and Greven, 1994]). However, there is no such ecological correlation with viviparity in caecilians; lowland tropical species are viviparous.

*Egg size*

Very few species of either frogs or salamanders are live-bearers; even fewer provide maternal nutrition after the yolk of the egg is resorbed (obligate viviparity in contrast to ovoviviparity — see above). (Parenthetically, it is important to note that ovoviviparity in amphibians is clear-cut, with such taxa having ‘typical’ [unreduced] to large egg sizes, being yolk-dependent throughout development and metamorphosis; that is, not providing additional maternal nutrition, and retaining their internally-fertilised eggs and embryos for varying amounts of developmental time, often giving
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birth to larvae. Viviparous taxa are those that have reduced yolk volumes, provide maternal nutrition during gestation after the yolk is exhausted, are aplacental, and give birth to fully metamorphosed young.) However, viviparity with maternal nutrition is relatively more common among caecilians. In the viviparous species, egg size characteristically is reduced (a direct-developing caecilian, *Hypogeophis rostratus*, has among the largest of ovarian ova [8 × 10 mm]; viviparous species have ova that are appx 2 mm diam. [Wake, 1977b]), and the assumption is that nutrient supply is ‘deflected’ from the ova to the longer-term provision during gestation. Rates of development are inferred for only one oviparous and two viviparous species of caecilians (Duenker et al., 2000), one species of viviparous frog (Xavier, 1977, 1986), and not well known for the viviparous salamander. However, rates of development are well known for certain direct-developing frogs and salamanders (see above) and for oviparous taxa in both clades. Consequently, within-clade comparisons of cell size/genome size with developmental rates and reproductive modes that include viviparity are at best speculative.

**Developmental rate**

There are modifications of developmental rate and even of body form during gestation in viviparous species that have received little attention, in contrast to those of direct developers and oviparous taxa. The viviparous *Nectophrynoides occidentalis* has small eggs, a 9-month intra-oviductal gestation, and a prolonged intra-oviductal metamorphosis. The embryos develop modifications of the mouth and the gut thought to be involved in ingestion of the nutrient secretions (Xavier, 1977, 1986; Wake, 1980), and other alterations relative to oviparous relatives. Similarly (but differently), viviparous caecilians have prolonged gestation periods (7-9 months in typhlonectids; 11 months in *Dermophis mexicanus*). Metamorphosis is a disjunctive and prolonged series of events (Exbrayat and Hraoui-Bloquet, 1994; Wake, 1994; note that Breckenridge et al. [1987] found metamorphosis to be somewhat prolonged in the oviparous *Ichthyophis glutinosus*); the foetuses modify rates and trajectories of development (heterochrony relative to species with ancestral reproductive and life history modes: Wake and Hanken, 1982), the foetal dentition develops, and typhlonectids modify their gill structure, presumably for gaseous exchange and perhaps for nutrient transport (Delsol et al., 1981). Most data regarding cell sizes in caecilians are my own, published and unpublished; genome sizes are reported for only a few species (summarised in Gregory, 2002) and I have unpublished data for several species. This renders correlation difficult, and speculative.

The only viviparous species for which genome size data exist (*Salamandra* and some caecilians) suggest that their genomes are similar to those of related taxa, no matter what the reproductive mode. Consequently, the secondarily-reduced egg sizes, presumably correlated with prolonged maternal nutrition, suggest that genome size is a phylogenetic (lineage-based) effect that does not influence egg size per se, and prolonged gestation is an effect of reproductive mode but not
of cell size or cell number, in contrast to the situation in direct developing taxa. Furthermore, there is no indication of any cell size effects that might be correlated with reduced egg sizes and yolk volumes. However, Wake and Wake (2000) provide food for thought in their examination of vertebrogenesis, including segmentation and resegmentation. We observed that gymnophiones have many more cells per segment than do salamanders or frogs. We compared directly the same stages of vertebrogenesis in a direct-developing salamander, *Pseudoeurycea juarezi*, and a viviparous gymnophione, *Dermophis mexicanus*. The two species have approximately the same genome size (22-27 pc DNA/haploid nucleus [Sessions and Larson, 1991; Wake, unpubl. data]) and the same nuclear dimensions (Wake and Wake, 2000), but *Dermophis* has nearly three times the number of cells in each sclerotome half and more segments per cm than the salamander (segments at the same stages of development were compared). Therefore the higher density of sclerotomites in caecilians relative to that in salamanders is a phenomenon of increased cell number, which makes the events of resegmentation apparent. This may be a consequence of phylogenetic effects, or of a genome size effect in the direct-developing salamander but not the viviparous caecilian. Gatherer and Del Pino (1992) compared cell numbers per somite in three species of frogs. They found that large-egged species (*Gastrotheca*, a direct-developer in which the female carries the embryos through metamorphosis in a dorsal pouch, and *Bombina*, an oviparous species) have six times the number of cells per somite than the small-egged *Xenopus*. They note that the oviparous salamander *Ambystoma mexicanum* has few, large cells with a much larger genome size than frogs; they speculate that this is an attribute of somitogenesis, rather than a function of genome size itself. I suggest that the data of Wake and Wake and of Gatherer and Del Pino might be better interpreted in terms of differences in reproductive modes, than correlated with cell size. Of course, there is also a phylogenetic effect that renders the correlation more complex (and obscure).

CONCLUSIONS

Delving ever deeper into these issues reveals that many kinds of data are strikingly few for species with derived reproductive modes, and that studies to date of the relationships of genome size, cell size, egg size, proliferation rates, developmental phenomena, and life history features have concentrated on appropriate parts of the issues that I wish to address, but that the data do not lend themselves to a complete analysis of the correlation of reproductive mode with such phenomena. At the same time, the data and the several examples of complex developmental phenomena are tantalising, and some tentative conclusions can be offered. Most lend themselves to testable hypotheses, and reveal new directions of study. I infer that:

1. Data on genome size, cell size, etc. for many more species with derived reproductive modes must be gathered.
2. There is a pronounced phylogenetic effect, such that the genome size-cell size relationship is often not a correlate of reproductive mode within lineages.

3. Egg size is not strongly correlated with genome size and cell size, owing to its dependence on amount of yolk. Consequently genome size and cell size are for that reason also not predictors of reproductive mode.

4. Increased egg size appears to be essential to the evolution of direct development; in contrast, the reduced egg size of live-bearing taxa that have maternal nutrition is a consequence of the evolution of viviparity.

5. Increased genome size and the concomitant decrease in cell proliferation rate early in development does have consequences for adult morphology, but it is often tissue-specific (e.g., neural), or at least more pronounced in certain tissues, perhaps dependent on the developmental timing of their differentiation.

6. The developmental regimes of direct development and viviparity, probably because of the obviation of the free-living larval phase, influence body form throughout ontogeny, with effects on the assumption of adult form.

7. Direct development and viviparity are different pathways for obviating the larval period and increasing terrestriality.

8. Direct developers alter a conserved developmental trajectory relative to taxa with free-living larvae, often making use of ‘larval’ structures as exaptations; the embryos and foetuses of viviparous species use similar exaptations, but also develop structures and functions specific to the viviparous condition (e.g., foetal teeth) that are lost at birth.

9. The effects of derived reproductive modes, directly or indirectly, on adult form range from little difference between related taxa with ancestral and derived reproductive modes to profoundly different ‘key innovations’ that alter adult form and function in feeding, locomotion, respiration, and other major properties.

Testing these ideas opens up a new direction of research, one that should be profitable in identifying aspects of the mechanistic basis of patterns of evolution. Both pattern and process should be better understood through careful analysis of the correlates and non-correlates of reproductive modes with developmental trajectories and adult body form within and among lineages. Amphibians remain exemplary, non-model organisms by which to examine such features.

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