CHAPTER  **1**

# Introduction: Larval Development, Evolution, and Ecology

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*No questions . . . are of greater importance for the embryologist than . . . the secondary changes likely to occur . . . in the larval state.*

(Balfour, 1880, p. 381)

## I. INTRODUCTION

The life history of many organisms includes a larval stage that is morphologically distinct from the adult and/or that inhabits a different environment from the adult. The aquatic tadpole and the terrestrial frog are prime examples. Other examples are less familiar (Fig. 1). Such species display indirect development; larvae must metamorphose to transform into, or be replaced by, adults.
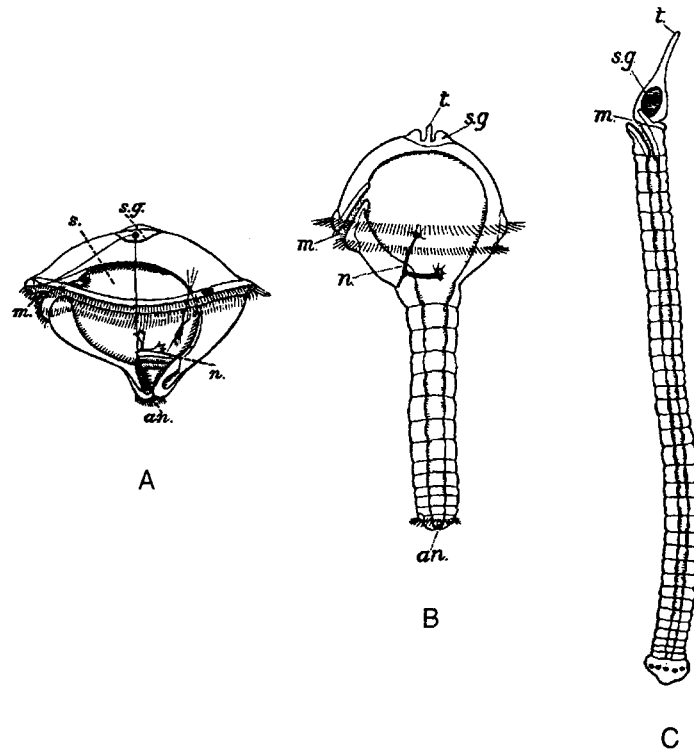
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FIGURE 1   The life history of *Polygordius,* a paedomorphic annelid. (A) Trochophore larva with the prominent ciliary band. (B) A later larval stage in which segments are beginning to form. (C) A mature stage. Abbreviations: an, anal opening; m, mouth; n, nephridium; s, stomach; s.g., brain; t, tentacle. (From Kerr, 1926.)

Larvae and metamorphosis therefore are inextricably linked, a larva being the "immature form of . . . animals that undergo some metamorphosis" (Oxford English Dictionary). Despite a long history of research, however, even such fundamental questions as "what is a larva?" and "what is metamorphosis?" occupy us today as they occupied naturalists, zoologists, marine biologists, and evolutionary biologists over a century and a half ago. It therefore seemed to us that there were ample reasons for revisiting these topics. This volume, our vehicle for that journey, deals with how vertebrate and invertebrate larvae develop and have evolved. Each author was asked to address the issue "what is a larva?" Comparative, functional morphological, physiological, and ecological aspects are included where appropriate and where data allow. The chapters are organized into sections that deal in turn with larval types and larval

evolution, mechanisms of larval development and evolution, and larval functional morphology, physiology, and ecology, highlighting four overarching themes: development, evolution, metamorphosis, and genetic mechanisms.

The title of the book is taken from the title of Walter Garstang's presidential address to Section D (Zoology) at the 96th Meeting of the British Association for the Advancement of Science, which was held in Glasgow, September 5–12, 1928. As Garstang reminded the audience in his opening statement, the evolution of larval transformations and metamorphoses had been featured in the presidential addresses of Milnes Marshall in 1890 and L. C. Miall in 1897 (Garstang, 1929). Garstang also could have mentioned the presidential address by Francis Balfour in 1880 on the same theme. During his long career, Garstang fought an energetic fight against Haeckel's biogenetic law—that ontogeny recapitulates phylogeny (Haeckel, 1866; Garstang, 1922)—and against contemporary recapitulationists such as Ernest MacBride, who was driven by notions of progress and for whom invertebrates were degenerate side branches from the central vertebrate line, which led inexorably to man. MacBride summed up his views on the proper ordering of life on earth in the following way: "It is, therefore, broadly speaking true that the invertebrates collectively represent those branches of the Vertebrate stock, which, at various times, have deserted their high vocation and fallen into lowlier habits of life" (1914, p. 662).

Garstang was especially concerned with how larval evolution paralleled adult evolution, "subject to conspicuous deviations" (1929, p. 77). These conspicuous deviations confound any simple parallel between larval and adult evolution and bedevil us still. He championed the view that

- ancestry should be sought in larvae rather than in adults;
- ontogeny creates rather than recapitulates phylogeny; and
- many larval features are secondary adaptations to larval life.

Many of us were introduced to Garstang's thinking through his delightful verses, *Larval Forms*, first published in 1951. A single Garstang verse contains as much erudition on larval development and evolution as is found in far lengthier (and loftier) treatises, as the following examples testify.

Young Archi-mollusks went to sea with nothing but a velum—
A sort of autocycling hoop, instead of pram—to wheel 'em;
And, spinning round, they one by one acquired parental features,
A shell above, a foot below—the queerest little creatures.
(*The Ballard of the Veliger or How the Gastropod Got Its Twist*)

MacBride was in his garden settling pedigrees,
There came a baby Woodlouse and climbed upon his knees,
And said: 'Sir, if our six legs have such an ancient air,
Shall we be less ancestral when we've grown our mother's pair?'
(*Isopod Phylogeny*)

And newts Perennibranchiate have gone from bad to worse:
They think aquatic life a bliss, terrestrial a curse.
They do not even contemplate a change to suit the weather,
But live as tadpoles, breed as tadpoles, tadpoles altogether!
(The Axolotl and the Ammocoete)

Encapsulated in these verses are such issues as the relationship between ontogeny and phylogeny, larval adaptations, the transformation from larva to adult, retention of ancestral features, acquisition of new features, life history evolution, and neoteny. They raise major questions such as

- How far do larval and adult evolution run in parallel?
- How can we sort out secondary adaptations (caenogenesis) from primary features?
- How much of larval evolution has been an "escape from specialization," to use the title of a chapter by Sir Alister Hardy (1954) in a book devoted to evolution as a process?

In Garstang's day, many still regarded larval stages as foregone ancestors, evolution proceeding from adult to adult and/or through modifications at the end of ontogeny, a position Garstang roundly rejected. For Garstang, as with Wordsworth, "The Child is father of the Man." In adopting this view, Garstang was far ahead of his time; this was, after all, the man who coined the phrase "ontogeny does not recapitulate phylogeny, it creates it" (Garstang, 1922, pp. 21, 81). Garstang also coined the term "paedomorphosis," using it for the first time in his 1928 presidential address, with the origin of torsion in gastropods as his example. A paedomorphic annelid, Polygordius, is shown in Fig. 1.

Garstang saw larvae as a mechanism for dispersal, like the seeds of a plant. He saw secondary reduction of the free-swimming larval stage as a consequence of the adoption of an incubatory mode of development. Cephalopods lack larvae, bypassing the trochopore and veliger larvae and omitting metamorphosis, because the adult is locomotory—a dispersive larval stage is unnecessary. The relationship between larval and adult stages also is amply illustrated in organisms from groups that normally contain a larval stage as the primitive condition, but that have either modified or lost the larva. Such direct-developing organisms (e.g., many sea urchins, many frogs and salamanders, some ascidians) hatch as miniature adults, demonstrating the plasticity of early developmental processes and ontogenetic stages, as discussed by Rudy Raff in his chapter.

## II. LARVAL ADAPTATIONS AND EVOLUTION

Whole edifices of invertebrate relationships have been erected on the basis of larval similarities, and complex transformation sequences between dissimilar larvae and between similar larval and adult forms have been devised. (Willmer, 1990, p. 116)

Larvae may well be as ancient as the Metazoa; the oldest known fossil metazoan larvae are from early Cambrian deposits in China and Siberia (Bengtson and Zhao, 1997). Many early workers postulated that larval evolution provides the key to unlocking metazoan evolution and diversification [see Jägersten (1972) and Bowler (1996) for two monographic treatments on the origins of the Metazoa, and Wray (1992) for changes in larval morphology that accompanied echinoderm radiation after the Paleozoic era]. Yet because of larval adaptations (caenogenesis), only some larvae have provided useful information for reconstructing phylogenetic histories and evaluating evolutionary relationships (Strathmann, 1978, 1993). Ernst Haeckel introduced the concept of caenogenesis in 1866 to cover those situations in which recapitulation of phylogeny in ontogeny was obscured because of larval adaptations or the displacement of embryonic or larval stages in time or space during ontogeny. We have retained the term, but modern usage tends to follow de Beer (1958), who restricted caenogenesis to larval adaptations without any reference to recapitulation.

However, Smith (1997) has taken a new approach to larval characters in systematics. He has examined echinoderms using new phylogenies based on several data sets to trace the evolution of life-history strategies and to compare rates and patterns of larval and adult morphological change. Smith agrees that larval characters used exclusively can "mislead phylogenetic analysis" because of caenogenesis, expressed in the form of the extensive homoplasy (convergence) found in nonfeeding larvae through their loss of structures. His examination of larval and adult morphologies together indicates that larval morphology evolves independently of adult morphology, that larval morphology includes considerably more homoplasy than does adult morphology, and that patterns of early development are highly flexible.

Larvae came to prominence because Johannes Müller and other 19th century naturalists identified many types of marine larvae in plankton samples and raised major questions about animal diversity, relationships, and origins. Given that the larvae of marine invertebrates of all phyla display a profound tendency toward convergence, Müller's ability to recognize so many larval types was a staggering accomplishment.

The importance ascribed to larvae in the 19th century can be seen from Francis Balfour's treatment of larvae in a major review (Balfour, 1880), reproduced in his two-volume "Treatise on Comparative Embryology" (1880–1881). Balfour's definition of larvae and his view of their evolutionary importance were straightforward. Larvae are those animals "born in a condition differing to a greater or less extent from the adult" (Balfour, 1880, p. 381, and see the epigraph for this chapter). This line of thinking persisted for many decades.[1]

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[1]Kerr (1921, p. 94) defined a larva as "a young developing individual, differing in form from the adult, but *not* contained within the body of the parent or other protective envelope," contrasting larvae with adults and embryos, the latter being "a young developing individual, which is contained within the body of the parent or within a protective shell or other envelope."

In the "Department of Phylogeny" Balfour saw the aim of embryological research as

> (1) To test how far Comparative Embryology brings to light ancestral forms common to the whole of the Metazoa.
>
> (2) How far some special embryonic larval form is constantly reproduced in the ontogeny of the members of one or more groups of the animal kingdom; and how such larval forms may be interpreted as the ancestral type of those groups.
>
> (3) How far such forms [larvae] agree with living or fossil forms in the adult state; such an agreement being held to imply that the living or fossil form in question is closely related to the parent stock of the group in which the larval form occurs.
>
> (4) How far organs appear in the embryo or larva which either atrophy or become functionless in the adult state, and which persist permanently in members of some other group or in lower members of the same group. (Balfour, 1880–1981, Vol. 1, pp. 4–5)

Balfour saw natural selection operating early in embryonic stages:

> I see no reason for doubting that the embryo in the earliest periods of development is as subject to the laws of natural selection as is the animal at any other period. Indeed, there appear to me grounds for the thinking that it is more so. (Balfour, 1874, p. 343)

> The principles which govern the perpetuation of variations which occur in either the larval or the foetal state are the same as those for the adult state. Variations favorable to the survival of the species are equally likely to be perpetuated, at whatever period of life they occur, prior to the loss of the reproductive powers. (Balfour, 1880, p. 381)

According to Balfour, development that included a larval stage was more likely to repeat ancestral history than was direct development. Production of a larva requires that organs be maintained without interruption of function to allow independent larval existence. Even though secondary larval adaptations occur, larval development is a closer representation of the evolutionary history of the group than is the life cycle of a direct-developing species. Direct development appears simpler because it is abbreviated, but direct development is a secondary modification of a primarily indirectly developing ontogeny, just as the yolk-free mammalian egg is a secondary modification of a yolk-containing egg. "There is a greater chance of the ancestral history being lost in forms which develop in the egg; and masked in those which are hatched as larvae" (Balfour, 1880, p. 383).

Adam Sedgwick, who wrote the extensive entry on larval forms for the 11th edition of the "Encyclopædia Britannica" (1911) and who succeeded Balfour at Cambridge, used Balfour's argument that direct development was more likely to preserve ancestral features than development without a larval stage, but came to quite different conclusions with respect to natural selection. Balfour saw natural selection operating throughout development. For Sedgwick

"embryonic variations are not for the most part acted upon by natural selection, because they concern rudimentary organs only" (Sedgwick, 1894, p. 88).

We now know that natural selection can act separately on larval and adult stages. Consequently, larvae and adults can evolve on different schedules and with considerable independence from each other; witness direct development. Indeed, natural selection acts throughout ontogeny, as Charles Darwin discussed. The role played by natural selection on different parts of the life cycle has attracted considerable interest (Wilbur et al., 1974; Calow, 1983; Mayo, 1983; Nielsen, 1995; Olive, 1985; Roff, 1992, 1996; Stearns, 1980, 1992; Ebenman, 1992; Williams, 1992).

## III. LARVAL AND ADULT DEVELOPMENTAL PROGRAMS

Embryos contain cells and developmental programs for both larval and adult structures. These may be completely separate, as in insects (in which adult cells are set aside in imaginal disks within the larval body), or they may be admixed, as in amphibians. We know quite a bit about the former and astonishingly little about the latter. Specific larval structures can be retained as adult structures. As tadpoles metamorphose into frogs, larval jaw muscles are resorbed and new adult jaw muscles develop. In at least some frogs, however, adult muscles are innervated by larval nerves that persist through metamorphosis (Alley, 1989, 1990). Such equivalence or lack of equivalence between larval and adult body parts creates some interesting problems for the identification of homologous structures and for the analysis of serial homology (Cowley, 1991; Minelli and Peruffo, 1991; Minelli, 1996).

In Chapter 6 of this volume, Chris Rose calls attention to the paucity of information on mechanisms responsible for musculoskeletal remodeling during metamorphosis in amphibians. Although changes in rate of production of thyroid hormone have been implicated, we still know little of the hormonal changes associated with the evolution of larvae or of metamorphosis. Similarly, we currently are unable to explain the phylogenetic distribution of muscoskeletal remodeling within amphibians, why larval reproduction (neoteny) is found in salamanders but not in frogs, or how metamorphosis is linked with sexual maturation.

## IV. KINDS OF LARVAE

Balfour summarized the evidence for two kinds of larvae: (1) primary larvae as modified ancestral forms that have existed as free larvae "from the time

when they constituted the adult form of the species" (1880, p. 383); and
(2) secondary larvae, introduced secondarily into the life history of a species
that previously developed directly (Fig. 2). Balfour set the primary larva, the
Planula (the ancestral form of coelenterates), apart from all other larval forms,
which he regarded as secondary. Secondary larval adaptations were thought
to arise from changes in larval life or changes in the order of appearance of
structures or to be related to the struggle for existence. Garstang saw secondary
larval characters as mainly anticipating adult characters. Do we still see them
in this light? He viewed primary larvae as "limited to the lower of more
primitive sections of the class" (1929, p. 77). Is this so?

Nowadays, zoologists recognize two fundamental types of invertebrate lar-
vae, corresponding to protostome and deuterostome modes of development
and the superphyla that comprise protostomes and deuterostomes:

- The trochophore (trochosphere) found in animals with a protostome
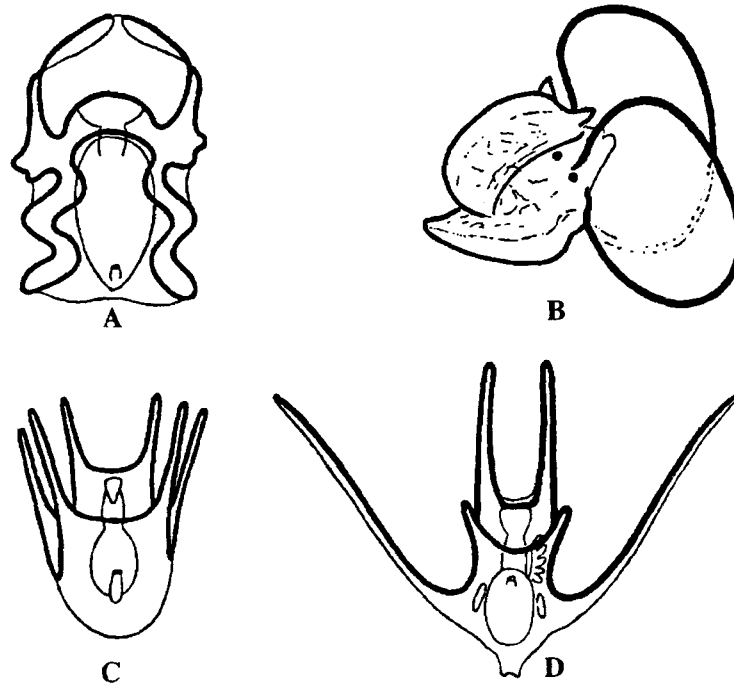  mode of embryonic development and spiral cleavage (Fig. 1A). Cladistic



FIGURE 2   Representative larvae of echinoderms (A, C, D) and a gastropod (B). The thick black
line on each larva marks the location of the ciliary band. (Modified from Kerr, 1926.)

analyses of the distribution of larvae are consistent with the trochophore as the type of larva possessed by the last common ancestor of arthropods and chordates (Peterson et al., 1997).

* The dipleurula (pluteus) found in animals with a deuterostome mode of embryonic development. The tornaria larvae found in hemichordates and the auricularia larvae of echinoderms are perhaps the least modified dipleurula larvae [Fig. 2; see Willmer (1990) for a discussion]. The divergence of the deuterostomes may well have started with the transformation of the protostome trochophore larva to the dipleurula larva (Peterson et al., 1997).

The origin and evolution of vertebrate larvae have been considered by many authors, often in the context of the evolution of metamorphosis. A particularly cogent (and little cited) discussion is that of Szarski (1957). He thought it likely that a larval stage was present in the ancestor of all chordates and endorsed Garstang's (1928) view that chordates arose from sessile tunicate ancestors through neoteny of their larvae. Szarski compared fish and amphibian larvae, citing many similarities (e.g., external gills, lateral line system and large neurons in the central nervous system, pronephric kidney, and other features). He explored the significance of direct development in amphibians (but not in fishes, unfortunately) and questioned whether direct development was a "secondary adaptation" or ancestral for amphibians—a question that persists, although most workers maintain that direct development is a derived state (see Hanken's Chapter 3 in this volume). Szarski particularly was interested in the role of thyroxin primarily, but not only, in metamorphosis in fishes and amphibians; he also considered the role of thyroxin in development (presaging some of the work Rose reports in Chapter 6), in reproductive migrations, and in the maternal aspect of gestation in live-bearing taxa. He found that several assumptions about the origin of the Amphibia are not justified (e.g., that amphibians arose from a group of fishes that had increased thyroxin secretion and that larvae and metamorphosis in amphibians are "recent acquirements"). Though all larvae of the "Ichthyopsida" have many similarities, Szarski (1957) recognized that "amphibian larvae . . . have a considerable number of characteristics, which can be considered as comparatively new caenogenetic adaptations. They are most numerous in larvae of Anura."

Szarski (1957) concluded that the ancestors of Amphibia must have had a larval stage, that "a great evolutionary gain" was achieved by amphibians through prolongation of the larval period, acquisition of larval adaptations, and shortening and synchronizing metamorphosis. To this day, the variation in larval period, functions of many larval features (see Cohen, 1984; Kendall et al., 1984), larval endocrinology, and modifications of metamorphosis are not well-understood in fishes or amphibians and provide an arena that might shed light on the origin of chordates.

## V. LARVAE AND PHYLOGENY

Do the fundamental features of primary larvae provide any clues to the evolutionary origins of larvae, life histories that include larvae, the adults that derive from those larvae following metamorphosis, or even the Metazoa? Examples from studies on crustaceans and vertebrates illustrate how larvae have influenced approaches to relationships and origins.

Fritz Müller, who believed that he could identify a nauplius stage in all members of the Crustacea, identified the nauplius larva as the crustacean ancestor. He hypothesized that more advanced crustaceans, such as crabs, shrimps, and lobsters, had an additional larval stage that would be expected to appear later in ontogeny and be restricted to the life cycles of those higher forms. The zoea stage that he found in crabs and shrimp fit these expectations precisely: an additional stage inserted into the life cycle between nauplius and adult. Müller's book, "Für Darwin" (1864), which contained his studies on crustacean larvae, was the first explicit test of Darwin's theory of descent with modification. Darwin had the book translated in 1869 under the title "Facts and Arguments for Darwin" (Müller, 1869); see Bowler (1994, 1996) who has analyzed Müller's use of larvae to unravel crustacean relationships and therefore crustacean evolution.

Theories on the ancestors of vertebrates also bear witness to the importance attributed to larvae and larval evolution (Bowler, 1996; Gee, 1996). To cite only one instance: the gill slits of *Balanoglossus* were discovered by Kovalevsky in 1866 (Kovalevsky, 1866, 1867); Metschnikoff (1869) saw the resemblance of *Balanoglossus* and echinoderm larvae to the free-swimming Tornaria larvae, and by the early 1880s *Balanoglossus* was grouped with the echinoderms on the basis of the resemblance of their larvae, shared features of their embryonic development, and lack of segmentation. Garstang (1894, 1896) used these larval findings to propose an entirely novel theory for the origin of the chordates: they had an echinoderm ancestor and arose through neoteny, with the tornarian larva becoming an adult chordate.

Balfour ended his lengthy discussion of larval types with some phylogenetic conclusions. They hinge on the central notion that groups that share a common larval type are "descended from a common stem" (Balfour, 1880, p. 405). Common larval types can be used to deduce the form of the common ancestor for all triploblastic animals, which Balfour and others saw as a radially symmetrical, medusa-like organism.

More recently, Eric Davidson and colleagues have approached metazoan origins by searching for the evolutionary origins of the basic developmental regulatory mechanisms within embryonic and larval metazoans (Davidson, 1990, 1991, 1993; Davidson *et al.*, 1995; Peterson *et al.*, 1997). Davidson

molded 19th century classification of larvae as primary and secondary into a modern approach to metazoan origins, because in his view, metazoans initially would have resembled modern, marine, microscopic invertebrate larvae.

Most invertebrate phyla have what Davidson calls type 1 embryogenesis and share common mechanisms for specification of cells and cell lineages (Table I). Clusters of genes encoding cell autonomous regions are expressed from cleavage onward. lin (cell lineage abnormal) genes in Caenorhabditis elegans (lin-4, lin-14, lin-28, and lin-29) control the "larva-to-adult switch" when adult genes are activated and larval genes repressed (Ambros, 1989). The importance of cell lineages in larval development and evolution is reflected in the two chapters devoted to them in this volume, in which Raff (Chapter 8) and Nagy and Grbic (Chapter 9) discuss cell lineages in echinoderms and in insects, respectively.

Cell lineages in indirect-developing sea urchins that specify only larval cell types are not needed in direct-developing embryos. Rather than being eliminated (a disruptive developmental event), they are respecified to form adult structures. In Heliocidaris erythrogramma, a direct-developing Australian sea urchin, for example, respecification occurs as early as the 16-cell stage. Cells that produce mesoderm in indirectly developing species form ectodermal and endodermal cells in the direct-developing species (Wray and Raff, 1990; Wray, 1994).

An interesting and possibly significant correlation is that no species with indirect development sets aside its germ line early in development (Ransick et al., 1996). The germ line often only arises after both embryonic and larval structures are established.

Davidson and his colleagues regard type 1 embryogenesis (and therefore set-aside cells) as having arisen only once, i.e., as being homologous throughout the Metazoa (Peterson et al., 1997). Primary larvae derived from type I embryogenesis are proposed to represent basic metazoan organization. (The embryo-

TABLE I   The Essential Features of Type 1 Embryogenesis as Enumerated by Davidson (1991)

- The type of embryogenesis characteristic of most invertebrate taxa
- Patterns of cleavage are invariant and specify cell lineages
- Spatial organization of embryo and larva primarily is specified by cell lineages
- Cell lineage plays an important role in specification of cell fate so that cell lineage normally is equivalent to cell fate
- Maternal cytoplasmic factors deposited in the ovum during oogenesis are important in specification of cell lineages and therefore cell fate
- Extensive movement of cells within the embryos is not required to specify cells
- One embryonic axis is specified during oogenesis and the second after fertilization
- Regulation (compensation for lost cells or portions of the embryos) is possible
- Selective gene expression occurs early in embryogenesis

genesis of advanced insects and vertebrates is derived and their larvae are secondary. Such larvae are unlikely to yield information pertinent to initial conditions.) The first essential element of Davidson's scenario therefore is that larvae of extant indirect-developing marine invertebrates with type 1 embryogenesis are surrogates of the Precambrian genetic regulatory systems that formed the basis for the evolution of metazoan body plans. The second and third elements are the evolution of set-aside cells and hierarchical, regulatory, developmental programs necessary for the diversification of metazoan body plans. Each lineage of set-aside cells evolved its own hierarchical program of gene expression. Elaboration of upstream regulatory processes within cell lineages or set-aside cells provides the basis for rapid specialization and evolution of novel cells and subsequent morphogenetic diversification. Such approaches demonstrate that the search for the origin and evolution of larval forms is as alive and active as it was 150 years ago.

## VI. LARVAE IN CONTEXT

How are larvae to be viewed in functional, community, and ecological contexts?

## A. FEEDING

Although most larvae feed, some coelenterate and sponge larvae and tunicate tadpoles are nonfeeding and therefore short-lived. They stand in sharp contrast to the ammocete larvae of lampreys, which can exist for 6 years or more buried in lake sediment during which time organs such as the lens grow exponentially (Hendrix and Rubinson, 1996). In Chapter 10 in this volume, Laurie Sanderson and Sarah Kupferberg discuss larval feeding mechanisms in amphibians and fishes, providing a physiological and ecological perspective to the chapters on the development and evolution of amphibian and fish larvae by Jim Hanken (Chapter 3) and Jackie Webb (Chapter 4), respectively. The authors of these three chapters call for studies that integrate development, physiology, ecology, and evolution and that are conducted against the background of a well-resolved phylogeny. Sanderson and Kupferberg especially emphasize approaches that take into account both ontogenetic changes in individual organs systems and the progressive integration between organ systems that occurs during ontogeny. Hunt von Herbing *et al.* (1996a,b) undertook an analysis of both aspects using larval cod; Hall (1998) discusses the importance of such studies for understanding embryonic and larval development and evolution.

Several authors have developed the theme that heterochrony, accompanied by developmental plasticity, was important in the evolution of nonfeeding

larvae [Strathmann *et al.*, 1992; Ponder and Lindberg, 1997; see Hall (1998) for a discussion of heterochrony and the even more important mechanism of heterotopy]. In Chapter 5 in this volume, Mike Hart and Greg Wray critically evaluate heterochrony and question its role in larval evolution. They could find only one example in which heterochrony was responsible for the evolution of a derived larva—the study of Strathmann *et al.* (1992) of feeding sea urchin larvae—and conclude that heterochrony has not been important in larval origins or larval evolution. Their analysis indicates that we have a long way to go in understanding the generative mechanisms underlying larval evolution.

## B. MULTIPLE STAGES AND PLASTICITY

Whereas a life cycle may consist of a single larva that metamorphoses into the adult, many organisms have multiple larval stages, and some have multiple adult stages. The multiple larval stages of some parasitic insects each are specialized for different aspects of parasitic life. Barnacles may have as many as six nauplius feeding-stage larvae, the last of which transforms into the nonfeeding cypris larva, which settles and metamorphoses into the subadult (Walley, 1969). Insects that display larval heteromorphosis (different larval stages within the life cycle) include blister beetles (family Meloidae) and mantispids (Wilson, 1971). Other insects have different morphological types as adults—worker and soldier ants, for example. The two adult forms of the lancelet *Epigonichthys lucayanum* develop from two different larvae— amphioxides and amphioxus, originally thought to be distinct adult forms, even separate species—with larval features that are adapted for dispersal and nondispersal, respectively (Willey, 1894; Bone, 1957; Gibbs and Wickstead, 1996). Larval polymorphism therefore is an important topic (Hall, 1998), treated in depth by Erick Greene in Chapter 11 of this volume, in which he emphasizes evolutionary causes and consequences of phenotypic plasticity and phenotypic variation. As Greene notes and illustrates in his Fig. 1, colony mates of the Asian ant *Pheidologeton diversus* can vary by as much as 500-fold in dry weight!

One experimental approach to understanding phenotypic plasticity discussed by Greene is to combine experimental manipulation with field studies of natural patterns. Larval patterns in sea urchins can be altered by experimentally manipulating the volume of the egg (Sinervo and McEdward, 1988; McEdward, 1996). Consequences of egg cytoplasm reduction are the slowing of development and the production of smaller, simpler larvae. Egg size affects larval morphology, development and growth rate, feeding capacity, size, stage of maturation–size at metamorphosis, and timing of the metamorphic transition; see Hall (1998) for further discussion and examples.

Possession of a larval stage in the life cycle offers many organisms an opportunity for asexual reproduction. Alternatively, reproductive organs can mature precociously in the larva. When accompanied by failure of metamorphosis, the larva becomes the reproductive stage. The process, neoteny, is especially prevalent among salamanders, as Rose discusses in Chapter 6. Correlations between such life history traits as timing of metamorphosis, size at metamorphosis, attainment of sexual maturity, and development rate are discussed by McLaren (1965), Raff (1992), and McEdward and Janies (1997).

Complex life cycles—those that include multiple stages—have received considerable attention in studies of life history evolution. The heteromorphosis mentioned earlier is one example. Istock (1967) provided an ecological perspective on the evolution of complex life cycles. He characterized such cycles as those that include two or more ecologically distinct phases, without overlap among the factors that limit abundance in each phase. Consequently, each of the phases has its own set of interactions in terms of competition, predation, resource allocation, and environmental factors. Istock (1967) used several life table characters (e.g., age at first reproduction, age at change in life history phase) to evaluate the evolution and maintenance of complex life cycles in diverse invertebrate and vertebrate species, concluding that complex life cycles are inherently unstable over evolutionary time and that such life cycles lead to major changes if extinction does not occur first. He stressed that the evolution of the different phases of a complex life cycle are largely independent and that this independence would make complexity unstable by "moving the population away from maximum realization of the ecological advantages of such a life cycle" (Istock, 1967). Istock (1967) also stated that selective forces that promote the reduction or loss of one phase or another thus would be generated and that such selective forces have generated the diverse characteristics seen in many species that may once have had more complex life cycles (e.g., loss of feeding larvae in echinoderms, paedomorphic salamanders).

Istock's (1967) view of the instability of complex life cycles was challenged by several workers. In reviews of the maintenance of biphasic life cycles in frogs and the modification of the cycles in direct developers, Wassersug (1974, 1975) emphasized that larval ecology is the key to understanding these phenomena and that the specialized morphology and feeding behavior of tadpoles is the key to maintenance of their life cycles. Tadpoles are adapted to specific food resources that typically are temporary, and so they can deal with environmental fluctuations. Wassersug makes the case that living in an environment with marked changes in productivity makes it advantageous to have different morphological phases, so that different resources can be assimilated. He notes that environmental modification, temperature and moisture changes, and seasonality have characterized evolutionary time, so that biphasic life cycles are adaptive and provide stability for many species.

Wilbur *et al.* (1974), Werner (1988), and Ebenman (1992), among others, also challenged Istock's conclusions. Istock (1967) had focused on the several lineages that had secondary losses of phases of their life cycles; Werner (1988) noted that approximately 80% of extant animal species are bi- or multiphasic, suggesting long-term stability of the cycles. Further, the duration of different stages, the timing of metamorphosis, and the concomitant niche shift can be modified without complete loss of a life cycle phase. By using quantitative genetic models to assess the stability of complex life cycles, Ebenman (1992) found that trade-offs in the efficiency of resource utilization by larvae vs adults, caused by different selection on the two phases, select for a disruption of the genetic correlation between juvenile and adult traits so that they evolve independently. Ebenman asks for further research on the evolution of life cycle diversification and phenotypic evolution, especially using mechanistic and dynamic models that include quantitative genetic parameters.

## C. LARVAL ECOLOGY

Clearly, larvae must also be viewed in ecological context. Take, for example, the production of soldier ants in *Pheidole bicarinata*, discussed by Fred Nijhout in Chapter 7. The number of soldiers is regulated by both interactions between individuals and the nutritional status of the colony. Adult soldiers release a pheromone that inhibits production of further soldiers by regulating the threshold of the larvae to juvenile hormone, the hormone that triggers development of soldiers. Size of individual soldiers and allometric relationships between soldiers are regulated by programming the growth patterns of imaginal disks. Hormone levels also are sensitive to colony nutritional status. Consequently, a balance of nutritional status and the number of soldiers already present determines whether additional soldiers will be produced (Wilson, 1971; Wheeler and Nijhout, 1983, 1986; Nijhout and Wheeler, 1996). In an analogous way—but where nutrition alone determines transformation from the larval phenotype—the development of larval bees into workers or queen depends on whether or not they are fed the "royal jelly" secreted by the workers' salivary glands. Hormonal control of larval development and evolution in both insects and amphibians is treated in the chapters by Nijhout (Chapter 7) and Rose (Chapter 6). Nijhout emphasizes the significance of the modularity of postembryonic insect development for the independent evolution of body parts and stages of the life cycle.

Some larvae, especially those of insects, can enter a phase of dormancy that permits them (and indeed the population or species) to survive what otherwise would be lethal environmental conditions. Dormancy is broken when conditions improve. Larval variation in many organisms is correlated with patterns

of dispersal, involving a wonderfully complex interplay between seasonal signals that trigger larval development, physiological attributes of (marine) larvae such as positive or negative photo- and geotaxis, and larvae–environment interactions that determine both competence for site selection and the particular site(s) selected (Chia and Rice, 1978; Morse, 1991; Fell, 1997). The release, by females, of larvae that feed on phytoplankton within the water column is both coordinated with seasonal blooms of phytoplankton and controlled by phenolic compounds released by the phytoplankton (Starr et al., 1990). This example of what one of us has called environmentally mediated induction (Hall, 1998) represents a major class of evidence in support of Van Valen's (1973) aphorism that evolution is the control of development by ecology and provides yet another reason for revisiting the origin and evolution of larval forms. Our journey ends with a final chapter including an inquiry into the accomplishments of recent research and the questions and research arenas that require attention if we are to more fully understand and appreciate the origin and evolution of larval forms.

## ACKNOWLEDGMENTS

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