The origins of insect metamorphosis

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Insect metamorphosis is a fascinating and highly successful biological adaptation, but there is much uncertainty as to how it evolved. Ancestral insect species did not undergo metamorphosis and there are still some existing species that lack metamorphosis or undergo only partial metamorphosis. Based on endocrine studies and morphological comparisons of the development of insect species with and without metamorphosis, a novel hypothesis for the evolution of metamorphosis is proposed. Changes in the endocrinology of development are central to this hypothesis. The three stages of the ancestral insect species—pronymph, nymph and adult—are proposed to be equivalent to the larva, pupa and adult stages of insects with complete metamorphosis. This proposal has general implications for insect developmental biology.

Metamorphosis is one of the most widely used life-history strategies of animals. The dramatic differences between larval and adult forms allow the stages to exploit different habitats and food sources, and also allow the extreme adaptation of one stage for a particular role, such as dispersal. In amphibians and many marine invertebrates, metamorphosis is an ancestral condition and its origins are buried deep in the evolution of these groups. In insects, however, the earliest forms showed direct development (were ametabolous) and the evolution of metamorphosis then fuelled their dramatic radiation[1,2]. The earliest true insects included some of the ametabolous orders that are still present today, the bristletails and the silverfish. Their juvenile stages look very much like the adult, except that they lack functional genitalia. Insects with 'incomplete' metamorphosis (hemimetabolous insects) are a polyphyletic assemblage which includes cockroaches, grasshoppers, dragonflies and true bugs. Their immature stages were originally called nymphs, and we will use that terminology here. Besides lacking genitalia, the nymphs of winged species bear wing buds folded over their backs, which are finally transformed into articulated, functional wings during the moult to the adult stage. Insects with 'complete metamorphosis' were first seen in the Permian and constitute a monophyletic group[3], the Holometabola (including beetles, flies, moths and bees). They have very different larval, pupal and adult stages, which allows them to separate the resources needed for growth from those needed for reproduction. They have also achieved extremely rapid life cycles.

How did the three-part life cycle that characterizes the Holometabola evolve from the nymph and adult stages of more basal insects? Two opposing hypotheses have been advanced. The first was formulated by Berlese[4], who noted a similarity between different larval body forms and the morphological transitions seen during embryogenesis of hemimetabolous insects. He proposed that the holometabolous larva arose by a process of 'de-embryonization' so that the larva was essentially a free-living, feeding embryo. The premature hatching was thought to be caused by a reduction in the amount of yolk stored in the egg, and hatching at different times generated a diversity of larval forms. As the larva took over the feeding responsibilities, the nymph was reduced to a single instar that became the pupa.

The alternative hypothesis for metamorphosis held that larvae and nymphs were equivalent, and that the pupal stage arose *de novo*, as the disparity between larva and adult widened[5,6]. Proponents of the latter hypothesis claimed that there was no difference in the amount of yolk in the eggs of holometabolous and hemimetabolous insects[7], and that some larval specializations, such as the abdominal prolegs of certain scorpionfly larvae, were derived structures that did not arise from the embryonic appendages[8]. The latter hypothesis, considering larvae and nymphs as equivalent stages, has been more widely followed[9,10]. Our examination of the endocrine control of embryonic and postembryonic development, though, suggests that the roots of metamorphosis are to be found in embryonic stages, more in line with the views of Berlese, and as recognized by the Czechoslovakian insect physiologist, V. Novak[11].

Form and function of the pronymph stage

In many arthropods, the stage that hatches from the egg has unique features that distinguish it from subsequent life stages. This is quite obvious in aquatic and marine crustaceans that have a specialized nauplius stage which serves as a primary dispersal stage. A unique hatchling stage is also seen in terrestrial arthropods, such as isopods

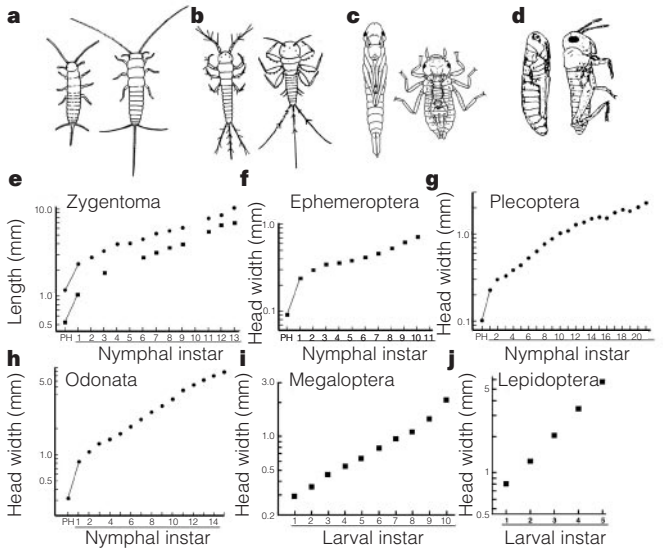

Figure 1 Comparison of the early immature stages of ametabolous, hemimetabolous and holometabolous insect species. **a**–**d**, Drawings of the pronymph (left) and first-instar nymph (right) of ametabolous (**a**) and hemimetabolous (**b**–**d**) insects: **a**, the silverfish *Ctenolepisma longicaudata*; **b**, the mayfly *Stenonema interpunctatum*[55]; **c**, the dragonfly *Epiophlebia superstes*[56]; and **d**, *L. migratoria*[30]. **e**–**j**, Comparison of the dimensions of the head or body parts of the immature instars of various insects during postembryonic life. In the ametabolous (**e**) and hemimetabolous (**f**–**h**) species, there is a marked shift in body proportions between the pronymph (PN) and the first nymphal instar. Typically, no such shift is seen in the immature series of holometabolous species (**i**, **j**). **e**, Lengths of the antenna (circles) and the cercal filaments at the end of the abdomen for the *C. longicaudata* (Zygentoma)[14]. **f**, Head width of *S. interpunctatum* (Ephemeroptera)[55]. **g**, Head width of a stonefly, *Neoperla clymene* (Plecoptera)[57]. **h**, Head width of the dragonfly *Anax imperator* (Odonata)[58]. **i**, Head width of the alderfly *Sialis rotunda* (Megaloptera)[59]. **j**, Head width of the tobacco hornworm *M. sexta* (Lepidoptera). The *Manduca* data are from measurements of 10 individuals; s.e.m.s were smaller than the data points.

(Crustacea), arachnids and myriapods, although it is not adapted for dispersal. It typically does not feed, and is often helpless and the object of maternal care (for example, in scorpions and woodlice[12,13]). It subsists on its yolk supply and represents a continuation of embryonic development, but outside the confines of the egg shell. The first postembryonic moult finally transforms it into an active, feeding juvenile.

Our hypothesis for the evolution of metamorphosis focuses on a corresponding stage in the ametabolous and hemimetabolous insects. This is a largely ignored stage that we will call the pronymph. In the ametabolous insects, such as silverfish, it lasts for 3 to 4 days after hatching[14], but in the hemimetabolous groups the pronymph becomes less obvious. In basal hemimetabolous orders (mayflies, dragonflies, stoneflies and grasshoppers), the pronymph stage is passed primarily in the egg and lasts for only minutes to a few hours after hatching[15]. In more derived hemimetabolous orders (such as true bugs and lice), the shedding of the pronymphal cuticle occurs during hatching and it is the first-stage nymph that actually emerges from the shell.

The pronymph has a number of characteristics that make it unique[15]. Its bodily proportions differ from those of the nymph (Fig. 1a–h) and probably reflect a developmental compromise for growing long appendages within the confined space of the egg shell. Its cuticle has a distinctive ultrastructure[16] and lacks the rigid, tanned plates (sclerites) that characterize nymphal and adult cuticles. Its mandibles are typically unsclerotized, and it may possess specialized hatching devices such as 'egg bursters'. It lacks the wing buds that feature prominently in the growing nymph and, as detailed below, its endocrinology is distinct from that of the nymph. The embryo begins to secrete its pronymphal cuticle around the time of dorsal closure[17–19] when it has achieved its full size (at about 48–60% of embryogenesis; %E). Although the embryo may have secreted cuticle before this time, the pronymphal cuticle is the first one that is sufficiently tough to require coordinated muscular activity for its shedding. The first nymphal cuticle is finally deposited at 75–85%E.

We propose that the hemimetabolous pronymph has become the holometabolous larva. This proposed relationship is reflected in a number of similarities between the two stages. (1) In holometabolous embryos, the secretion of the first-instar larval cuticle[20–22] begins around the time of dorsal closure (45–55%E), which would correspond to the time of pronymphal cuticle secretion in hemimetabolous forms. A late bout of cuticle production, which would correspond to the nymphal moult[17,19], is absent in the Holometabola. (2) The larval body cuticle is typically soft and lacks sclerites, similar to that of the pronymph. (3) The larval sensory nervous system also shows similarities to that of the pronymph. At the beginning of its pronymphal stage, a grasshopper embryo has a stereotyped set of early-born neurons in each body segment[23] and appendage[24]. Some of these neurons are 'pioneer' neurons that provide the pathways that are later used for the growth of nymphal sensory axons into the central nervous system (CNS). Importantly, the sensory neurons in the body wall of newly hatched larvae of both *Drosophila* and the moth *Manduca sexta* correspond to this early set of cells[23,25]. Similarly, we think that the small number of sensory neurons that are found in the appendages of larvae are homologous to the set of pioneer neurons present at the start of the pronymphal stage in hemimetabolous species. In the pronymph, some of these neurons apparently die after completing their pioneering function[26]. In the larva, in contrast, we expect that these cells survive as functional, larval sensory neurons. They may, however, eventually die at metamorphosis after they help to guide the adult sensory axons into the CNS. Therefore, rather than being a derived condition[27], the reduced sensory systems of holometabolous larvae seem to be a primitive condition that they share with the pronymph.

A major difference between a pronymph and a larva is that the former lasts for a single instar before transforming into the nymph (Fig. 1e–h), whereas, with the exception of some derived parasitic species, the latter maintains its form through successive instars until finally reaching the pupal stage (Fig. 1i, j). A shift in hormone secretion during embryogenesis may have been instrumental in

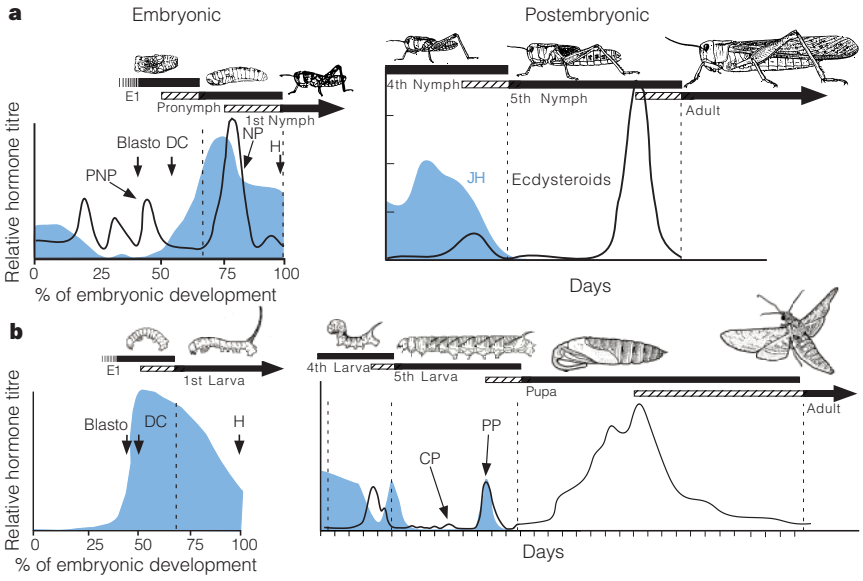

Figure 2 Endocrinology of embryonic and post-embryonic insect development. Comparison of the embryonic and postembryonic titres of ecdysteroids (black) and juvenile hormone (blue) for **a**, hemimetabolous insects, the grasshoppers *L. migratoria* (embryonic) and *Schistocerca gregaria* (postembryonic) and for **b**, a holometabolous insect, the sphinx moth *M. sexta*. The bars over the hormone titres show the times when the cuticles of the particular instars are present; cross-hatching represents the pharate stage when the insect is still covered by the old cuticle of the preceding stage. Detailed ecdysteroid titres are not available for embryos of *Manduca*. Vertical dashed lines show the times of ecdysis (shedding of the old cuticle); Blasto, blastokinesis; DC, dorsal closure; E1, first embryonic instar; H, hatch. Ecdysteroid peaks: CP, commitment peak; PP, prepupal peak; PNP, pronymphal peak; NP, nymphal peak. The *Schistocerca* titre references are cited in ref. 60; more recent citations are supplied for *Locusta* showing embryonic ecdysteroid[30] and JH[31] titres, and *Manduca* showing embryonic JH titres[37] and postembryonic titres for ecdysteroids[61] and JH[62,63].

changing the transitional pronymphal stage into a stable larval stage.

Endocrinology of pronymph formation

Two families of hormones, the ecdysteroids and the juvenile hormones (JH), control moulting and metamorphosis during postembryonic life[28]. The former induce the production of a new cuticle during a moult, whereas the latter regulate the character of that moult. For both larvae and nymphs, moults that occur in the presence of JH are 'status quo' moults that result in a new instar which retains its former morphology[29]. The withdrawal of JH then allows metamorphosis to ensue. In hemimetabolous insects, the first moult after the decline of JH is to the adult (Fig. 2a). In holometabolous insects, by contrast, the endocrine interactions are more complex (Fig. 2b). After the initial disappearance of JH, a small peak of ecdysteroids 'commits' certain tissues to pupal differentiation[29]. The pupal moult, though, is induced only later in response to a large surge of ecdysteroids. JH reappears during this ecdysteroid surge but then disappears before the large ecdysteroid peak that drives adult differentiation. The origin of this pattern of JH secretion has been unclear.

These hormones are also involved in the embryonic development of insects. In accord with its postembryonic function, peaks of ecdysteroids are also seen during the embryonic moults[30] (Fig. 2a). The JH titre, though, is unusual. For example, in the grasshopper *Locusta migratoria*, JH is found in newly laid eggs but disappears before the first embryonic moult and the initial phases of the pronymphal moult[31]. It then rises to its highest levels during nymph formation. Data from the embryos of other hemimetabolous insects, such as cockroaches[32] and true bugs[33], also show low or no JH at the start of the pronymphal stage followed by high JH levels during nymphal differentiation.

That a JH-free period is essential for normal embryogenesis was shown by applying JH or JH mimics to embryos of hemimetabolous insects[34]. In contrast to its 'status quo' action during postembryonic life, JH acts embryonically to promote precocious maturation. For example, our treatment of embryos of *L. migratoria* with the JH mimic pyriproxifen just before the pronymphal moult redirected development to produce precocious nymphs that had sclerotized mandibles, cuticular bristles and wing buds (Fig. 3a, b). Their body proportions fit these extrapolated for a '0'-instar nymph (Fig. 3c–f). Similarly treated embryos produced cuticle with a nymphal ultrastructure[35]. The developmental window during which treatment with JH can induce a precocious nymph closes just before dorsal closure, after the pronymphal moult has commenced. Treatment with JH mimics very early in embryogenesis (at 15–20%E) resulted in tiny nymphs (Fig. 3b, right) bearing wing buds and having sclerotized mandibles appropriate for a '–1'-instar nymph. Importantly, both the '0'- and '–1'-instar nymphs were terminal embryonic stages that showed no further moulting.

An alternative approach is to deny developing embryos their normal JH by treating them with precocenes to destroy the embryonic corpora allata, the source of JH. In both cockroaches[36] and crickets (D. Erezyilmaz, L.M.R. & J.W.T., unpublished results), such treated embryos eventually became nymphs but the maturation of their internal tissues was severely suppressed. Thus, in these hemimetabolous embryos, JH seems to be involved in regulating the shift between growth and tissue maturation.

In the Holometabola, detailed embryonic JH titres are available for only a few species of moths[37]. Interestingly, these embryos already show a high JH titre when they initiate their moult at dorsal closure. This precocious appearance of JH is probably associated with this moult's now leading to a fully differentiated form—the larva—rather than to the transitional pronymph stage of hemimetabolous insects.

Application of exogenous JH or JH mimics to embryos of flies and moths has only minor effects on embryonic growth and morphogenesis, although it does interfere with some morphogenetic movements such as blastokinesis[38–40]. We think that these holometabolous embryos are relatively insensitive to exogenous JH because much of the embryonic growth that was ancestrally sensitive to JH has been shifted into postembryonic life during the evolution of the larval form.

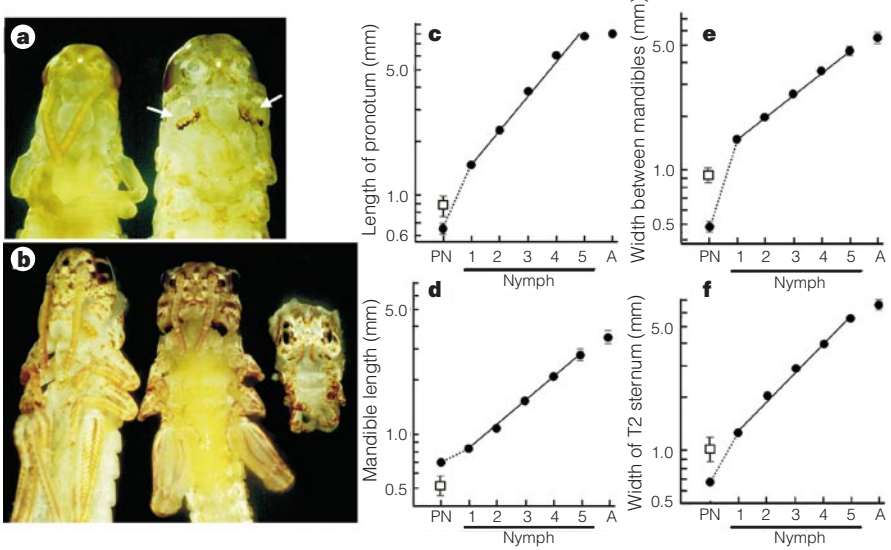

Figure 3 The effects of the JH mimic pyriproxifen on *Locusta* embryos. **a**, A ventral view of the anterior end of embryos three days after treatment with acetone (left) or pyriproxifen (right) at about 47%E. The acetone-treated embryo is a newly ecdysed pronymph (~68%E). Its clutchmate, treated with the JH mimic, shows sclerotized mandibles (arrows) and the dimensions of a head and thorax predicted for a '0'-instar nymph. **b**, Ventral views of (left) control embryo about 1 day before hatching, (middle) a '0'-instar nymph of comparable age produced by JH mimic treatment before dorsal closure, and (right) a '–1'-instar nymph formed after JH mimic treatment before blastokinesis. **c**–**f**, Quantification of the result of treating embryos with the JH mimic at 45%E. The normal progression of the size of various structures between the pronymph (PN) and nymphal instars is represented as in Fig. 1. Points are the means ± s.e.m. for 10 individuals; s.e.ms smaller than the data points are not shown. The treatment with the JH mimic (squares, ±s.e.m. for $n = 14$) redirected the pronymphal moult to produce animals with proportions that were shifted towards those predicted for a hypothetical '0'-instar nymph. Similar results are seen after treatment with physiological dosages of JHIII.

JH and postembryonic development

At first glance, the effects of JH in promoting tissue maturation in hemimetabolous insect embryos seem contrary to its 'status quo' action during postembryonic life. The action of JH on embryos, though, might be better contrasted with its action on imaginal discs—tissues that are in an 'embryonic' condition in the larva and will give rise to the structures of the adult. Over the years most of the studies of imaginal discs have focused on Lepidoptera and higher flies. In these insects the imaginal discs arise from cells that are set aside late in embryogenesis and grow actively through much of larval life[41]. Their formation and growth are not blocked by JH, although JH may influence the rate of growth[42,43].

These 'classic' imaginal discs, though, seem to be derived structures[44], and may not be the proper type of imaginal primordia to compare with embryos. The ancestral condition for imaginal growth is thought to be similar to that seen for formation of the wing in the mealworm beetle, *Tenebrio molitor*[45]. In the preterminal instars, the beetle larvae show no imaginal discs and the cells that will form the wing primordium simply secrete larval cuticle. Only in the last larval instar do these cells become columnar, detach from the overlying larval cuticle and begin their imaginal proliferation.

Figure 4 maps the pattern of wing growth onto a phylogenetic tree for the Holometabola. If we assume that the onset of imaginal growth in the last larval stage is the ancestral condition, then early-developing wing discs evolved independently at least six times. In contrast, if we assume that early-developing wing discs were ancestral, then this capacity would have been lost at least ten times. Moreover, it would have been lost in the most primitive orders, Neuroptera (lacewings and antlions), Mecoptera (scorpion-flies) and Megaloptera (alderflies), and also in the more basal members of the Diptera (the Nematocera: midges and mosquitoes) and the Hymenoptera (the Symphyta: sawflies) but preserved in the more derived groups. We think that the latter model is unlikely and accept the proposal[10] that the ancestral holometabolous larva postponed their imaginal growth until the last larval stage.

In caterpillars of *M. sexta*, the wing primordia show a derived pattern of growth, but the primordia for the adult eyes show an ancestral growth pattern, in that they form only in the final larval instar[46,47]. Studies both *in vivo* and *in vitro* show that JH directly inhibits eye primordium formation, whereas the premature removal of JH, even in preterminal larval instars, results in its precocious formation (D. Champlin, L.M.R. & J.W.T., unpublished results). Importantly, this action of JH is independent of the ecdysteroids.

We think that the control of the formation of the eye primordium represents a general model for the ancestral pattern of control over imaginal growth. JH tonically suppresses primordium formation throughout the preterminal instars, but its decline in the final instar removes the inhibition and allows rapid growth to begin. For the subsequent evolution of classic imaginal discs, the appropriate regions of the epidermis would have to escape this JH-mediated suppression so that they could form and proliferate despite the high JH titres that maintain the larval character of the rest of the animal. The mechanism(s) by which this was accomplished has not been determined but it could have involved the local loss of JH receptors or the acquisition of high levels of enzymes that locally inactivate JH. Consistent with the latter possibility, the wing discs of the wax moth *Galleria mellonella* express high levels of JH esterase activity[48] early in the last larval stage, which may facilitate their growth in an environment that still has circulating JH. Thus, the insensitivity of classic imaginal discs to JH is not surprising and, indeed, was a prerequisite to allowing imaginal growth throughout larval life and thereby shortening the life cycle.

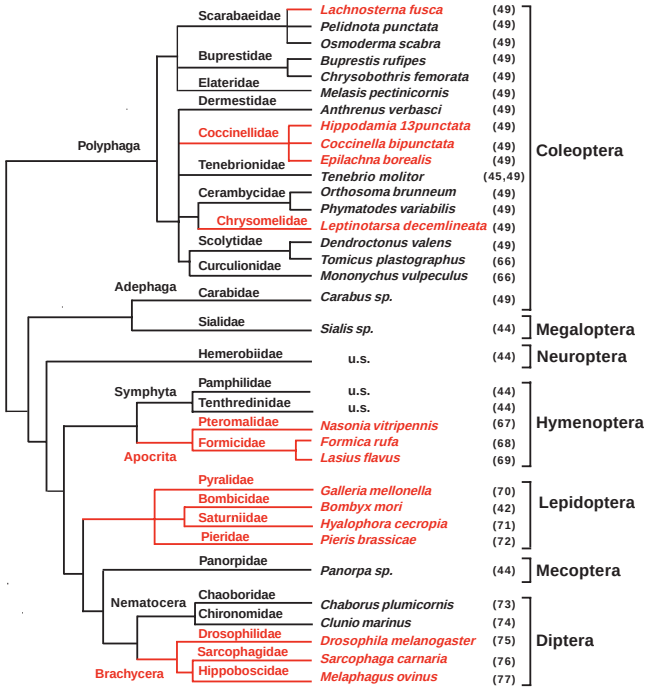

Figure 4 Relationship of the phylogeny of the Holometabola to the pattern of imaginal disc formation. For species in black, the proliferation of the wing primordium is delayed until the final larval instar. For species in red the wing-disc primordium is set aside from the general larval epidermis before the last larval stage and forms an invaginated imaginal disc that can grow more or less independently of the larval moult cycles. The red lines show where such imaginal discs would arise if the ancestral condition was to delay primordium formation until the last larval stage. They would have had to arise at least three times in the Coleoptera and at least once in the Diptera, Hymenoptera and Lepidoptera. SP, genus and species not determined. u.s., unidentified species. Reference numbers for wing-disc development are shown in parentheses. The phylogeny of the holometabolous orders is from ref. 64; that for the beetles is from ref. 65.

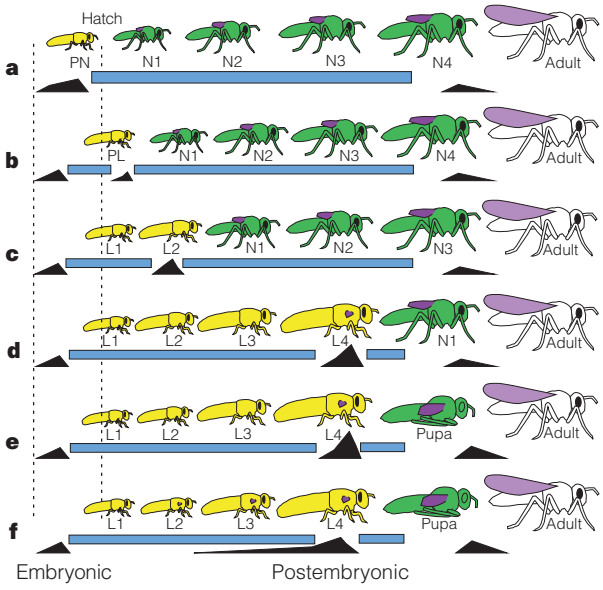

Figure 5 Possible steps in the transition from a hemimetabolous to a holometabolous life history and their relationship to timing of JH production (blue bar) and to growth directed towards the imaginal form (black triangles). The pronymphal (PN), protolarval (PL) and larval (L) instars are in yellow, and the nymphal (N) and pupal stages are in green; wing buds, wing imaginal discs, and wings are in purple. See text for explanation.

The main benefits ascribed to metamorphosis are the ability of larvae and adults to utilize different habitats and food resources, and the evolution of rapid life cycles. The selective pressures that initially gave rise to complete metamorphosis probably had to do with the former benefit of separating the resources used for the growth of the immature form from those needed for reproduction of the adult. After complete metamorphosis was established, the ability of imaginal discs to form and grow early in larval life then provided a mechanism that would allow the compression of life cycles[10].

Evolution and wing primordia

The pattern of wing growth also has implications for the relationship of the pronymph to the larva. It is generally considered that the wing primordia grow as evaginated wing buds in hemimetabolous nymphs and as invaginated wing discs in holometabolous larvae. In hemimetabolous insects, the wing buds typically appear in the first or second nymphal instar and increase in size with subsequent nymphal moults. The appearance of wing buds in early nymphal instars is also evident in fossil hemimetabolous and ametabolous insects[2], so it seems to be a ubiquitous feature of both extinct and modern hemimetabolous insects. If the larva was derived from the nymph, then we have to conclude that this ability to form and grow wing primordia in preterminal nymphal stages was lost in the ancestor of the Holometabola but was then reacquired after metamorphosis evolved[10]. However, if the pronymph became the larva, then larvae would be expected to lack wing primordia, as all described pronymphs lack these structures. The wing primordia would form at the end of larval growth when the nymphal (pupal) stage was finally achieved. When they formed in the last larval instar, they might still have formed as evaginating structures, as is evident in some present-day larvae that have the ancestral pattern of wing formation[49]. Invagination probably became the preferred mode of formation for these primordia because there is more space in the body cavity for the growth of a large structure like a wing disc. Invagination would be essential for wing primordium growth to be shifted into the early larval instars.

Evolution of metamorphosis

Our hypothesis for the evolution of metamorphosis is based on the premise that basal insects actually have three distinct life forms: pronymph, nymph and adult. We propose that these are directly comparable to the larval, pupal and adult stages of the Holometabola. In most hemimetabolous orders, with the possible exception of mayflies, the pronymph is a non-feeding stage (Fig. 5a). The ability of this stage to feed would seem to be an essential preadaptation for it to evolve into the larva. One hint as to how this might have occurred is provided by the embryos of modern-day Lepidoptera. During dorsal closure, only part of the yolk mass is enclosed by the developing embryo. Later, the developing caterpillar feeds on this extraembryonic yolk while still within the egg. If the embryos of the ancestor to the Holometabola also failed to enclose their yolk completely during dorsal closure, there would have been a selective advantage to modify the pronymph so that it could feed while still in the egg and thereby utilize this store of extraembryonic yolk. We will call such an animal a 'protolarva'.

The females of the Holometabola ancestor may have deposited their eggs in protected places, such as in the soil or under bark, thereby rendering them less vulnerable to predation. This behaviour would have selected for adaptations in the protolarva that allowed it to burrow efficiently out from these hiding places. As a feeding protolarva could also utilize food items that it encountered in this novel habitat (Fig. 5b), it could exploit resources that might not be available to either the nymph or the adult. If these resources were abundant, there would be a selective benefit to maintain this form into the next instar (Fig. 5c). We now consider this to be a true larval stage. Initially, postembryonic growth would be split between the larval and nymphal stages. As the nymph potentially competes with the adult for food, selection for undergoing all growth in the larval form would completely separate the resources used for growth from those used for reproduction (Fig. 5d). This would reduce the nymphal stage to a single instar that no longer needed to feed but served as the transition between larva and adult; it became the pupa (Fig. 5e). It is interesting that at least one other hemimetabolous group, the thrips (Thysanoptera), may have independently attempted this transition. They typically have two 'larval' instars followed by two non-feeding 'nymphal' instars before becoming adults.

From an endocrine perspective, we think that the shift from a pronymph to a protolarva involved a heterochronic shift in embryonic JH secretion. The earlier appearance of JH would have suppressed some aspects of embryonic growth, and its presence during the formation of the pronymph would have caused the precocious maturation of the embryonic tissues. The latter action would be necessary to transform the pronymph from a transitional developmental stage into a protolarva with functional organ and tissue systems (Fig. 5b). The continuing presence of JH then maintained the form of the protolarva/larva (Fig. 5b, c). For the protolarva/larva to progress subsequently to the nymph stage, JH would have to disappear to allow the morphogenetic growth needed for the new nymphal structures, but then JH would return to support their maturation. Once the nymphal form was achieved, it would also be stable as long as JH was present. As the time spent as a protolarva/larva was extended, the JH-free period was progressively delayed until it was finally pushed to the end of the growth period (Fig. 5d). In this view, the anomalous reappearance of JH during the larval–pupal transition is directly related to the ancestral need for JH during the pronymph–nymph transition.

As the larva and nymph diverged, the amount of proliferation and tissue reorganization that had to occur after the JH decline became progressively greater. Also, as discussed above, the ability of selected tissues to become JH-independent allowed the development of imaginal discs and the marked reduction in the duration of life cycles (Fig. 5f).

Implications

The ancestral goal of embryonic development was to produce an individual that, with minor exceptions like wings and genitalia, was basically a miniature copy of the adult. During the evolution of metamorphosis, a heterochronic shift in the time of appearance of JH during embryogenesis may have interrupted this ancestral growth trajectory. How would such an interruption have affected the genetic cascades that are used for patterning the body axis and the limbs[50,51]? In the case of an appendage such as the leg, one possibility is that the early JH secretion interrupted the progressive patterning of the limb bud and then stabilized it at an intermediate state. This intermediate set of patterning information would then be the basis for establishing the unique morphology of the larval leg. With the disappearance of JH in the final larval instar, this intermediate condition could no longer be maintained and the resumption of patterning interactions would provoke the growth of imaginal primordia, eventually resulting in the patterning of a typical adult limb.

Exogenous JH has striking effects on the embryogenesis of ametabolous insects[52] but only minimal effects on their postembryonic development[53]. In progressively more advanced groups, the effects of JH on embryogenesis become less marked while its postembryonic effects become more so. This trend suggests that the ancestral developmental role of JH was to control aspects of embryogenesis. The emergence of JH as a major postembryonic hormone accompanied the shift of some phases of embryonic growth (first of the genitalia and wings) into postembryonic life. The prospect of JH's originally being involved in embryonic development is intriguing because of the structural similarity of the JHs with the retinoids that regulate aspects of embryogenesis in vertebrates[54]. In both groups of animal, these types of compound

may be ancient regulators of embryonic growth and development, but in the insects they have achieved a postembryonic, hormonal function as greater portions of embryonic development were deferred until the end of larval growth. □

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