INVITED REVIEW

Why grow up? A perspective on insect strategies to avoid metamorphosis

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Abstract. 1. Insects with complete metamorphosis (holometaboloy) are extremely successful, constituting over 60\% of all described animal species. Complete metamorphosis confers significant advantages because it enables organisms to optimise life-history components through temporal partitioning, and thereby to exploit multiple ecological niches. Yet holometaboloy can also impose costs, and several lineages have evolved life cycle modifications to avoid complete metamorphosis.

2. In this review, we discuss different strategies that have evolved that result in the loss of complete metamorphosis (type I and type II paedomorphosis). In addition, the ecological pressures and developmental modifications that facilitate this avoidance are considered, as well as the importance of life cycle complexity in life-history evolution.

3. Interestingly, only female holometabolous insects have entirely avoided complete metamorphosis, and it is always the ancestrally juvenile morphology that is retained. These findings point to a strong sex-biased trade-off between investment in reproduction and development. While the loss of complete metamorphosis in females has occurred independently on several occasions across holometabolous insects, only a small number of species possessing this ability have been described.

4. Thus, complete metamorphosis, which originated only once in insects, appears to have been almost fully retained. This indicates that significant modifications to the holometabolon metamorphic ground plan are highly constrained, and suggests that the transition to complete metamorphosis is evolutionarily irreversible.

Key words. Evolution, Holometabola, life cycle, life history, neoteny, paedogenesis, phenotypic plasticity, progenesis.

Introduction

Everybody knows that the butterfly emerges from the pupa, and the pupa from a quite different thing called a larva, and the larva from the butterfly’s egg. Ernst Haeckel. The Evolution of Man, 1897

Haeckel’s law of recapitulation (Haeckel, 1866) proposed that when developing from egg to adult, animals ‘recapitulate’ successive stages in evolution. While the law is appealing in its simplicity, support for it gradually waned (Garstang, 1922). Empirical and theoretical advances to clarify the many exceptions to Haeckel’s law have since contributed significantly to our understanding of the evolution of phenotype (Gould, 1977), with implications for concepts such as evolvability and phenotypic plasticity (Yang, 2001; Minelli & Fusco, 2010; Pigliucci & Müller, 2010). Specifically, the view that traits distributed over the entire animal life cycle can be targeted by natural selection has gained additional significance in light of these developments (Minelli, 2003). While the importance of considering the entire life cycle has long been recognized in evolution (Bonner, 1965; Werner, 1988), an adult-centric view has nonetheless persisted in developmental biology (Minelli, 2003, 2015). A focus on the adult stage and the neglect of others is undermined by knowledge that most animal species undergo some form of metamorphosis (Werner, 1988), and that complex life cycles composed of discrete developmental stages – and associated shifts in ecology – are the norm (Moran, 1994). Indirect development, wherein a post-metamorphic adult is but one of...
several well differentiated life cycle stages, is clearly a dominant means by which animal life histories are organised (Davidson et al., 1995; Raff, 2008).

Complete metamorphosis (holometaboly) in insects evolved once, some 344 million years ago (95% confidence interval: 372 to 317) (Misof et al., 2014). Today, more than 60% of all described animal species are holometabolous insects. Whether relating to measures of abundance, ecological function or species richness, holometabolous insects are extremely successful (Whiting, 2004). Thus, holometaboly appears to have been a key innovation in the most successful radiation of animals during evolutionary history. Holometaboly evolved from a system of direct development with multiple moults but just two life-history stages: nymph and adult. In directly developing insects, adults are morphologically similar to nymphs, except for the addition of wings and genitalia. This process of morphological change is referred to as incomplete metamorphosis or hemimetaboly. A third category, ametaboly, includes direct-developing insects that show no morphological changes except for growth between nymph and adult stages. In contrast to hemimetabolous insects, holometabolous insects have evolved two unique stages in place of the nymph stage (Truman & Riddiford, 1999) – larvae and pupae – and so have three discrete life-history stages: larva, pupa and adult. This increase in life cycle complexity is thought to be adaptive for two reasons: (i) it facilitates stage-specific resource utilisation (Bonner, 1965) and structural specialisation (Bryant, 1969), such as adaptation of different sets of mouthparts for alternative food sources (Labandeira, 1997); and (ii) it encourages population growth by reducing intraspecific competition between stages (Ebenman, 1987). Thus, the compartmentalized or ‘modular’ nature of holometabolous life cycles is thought to have enabled insects to optimize life-history components, such as growth and reproduction, through temporal partitioning (Moran, 1994). In addition, holometaboly is hypothesised to have led to increased evolvability (e.g. an increased capacity for adaptive evolution; Kirschner & Gerhart, 1998), due to an expansion of baseline phenotypic variation upon which selection can act, and a concomitant decoupling of selective pressures across different life cycle stages (Yang, 2001). Yet despite the apparent virtues of holometaboly, some insects have minimised or even lost the holometabolous lifestyle, at least from some part of the life cycle. For example, ovoviparous insects, such as the termiteophilous beetle Corotocha (Staphylinidae) or certain flies (Hippoboscidae), have minimised the role of metamorphosis by depositing larvae that are so developmentally advanced, they are almost ready to pupate [Crowson, 1981; Meier et al., 1999 (citing Seevers, 1957)]. With respect to holometabolous insects that have entirely lost complete metamorphosis, this has only occurred in females, where it has been achieved via the deletion of the pupal and post-metamorphic stage (i.e. the ancestral ‘adult’), via a developmental process known as paedomorphosis.

**Extreme paedomorphosis**

Within Holometabola, only females have lost the ability to completely metamorphose. Even in the most extreme cases, complete metamorphosis is retained somewhere in the species’ life cycle, through adoption of a multi-generational strategy that includes complete metamorphosis on a facultative basis and/or via permanent retention of complete metamorphosis in males. Importantly, the loss of complete metamorphosis from ancestrally holometabolous females does not feature a reversal to hemimetaboly, but instead represents a derived state of holometaboly with incomplete larval development. Specifically, the larval stage is retained and reproductive maturity is differentiated by the development of sexual traits (i.e. the development of the germ line and genitalia) without progression to a discrete pupal stage or a metamorphic terminal imago. This type of incomplete larval development where metamorphosis is avoided is an extreme form of paedomorphosis, and two general processes are recognised: a ‘progenesis’ type, and a ‘neoteny’ type (Gould, 1977; Bergstrom & Dugatkin, 2011, p. 437), here termed type I and type II paedomorphosis, respectively. The former terms have been used inconsistently or ambiguously in the past (Pierce & Smith, 1979; Reilly et al., 1997), largely due to difficulties in interpreting the developmental modifications that underpin the varying life cycle adaptations. A schematic of the developmental changes associated with type I and II strategies is provided in Fig. 1, and a detailed description of definitions, in particular relating to previously adopted terminology, is given in File S1.

We conducted a literature search of articles on holometabolous insects that display type I and II paedomorphosis. Articles were selected using the ‘Web of Science’ section of the ISI Web of Knowledge database (http://apps.webofknowledge.com), and search criteria were as follows: TS = (((Holometabol* OR Diptera OR Coleoptera OR Hymenoptera OR Strepsiptera OR Lepidoptera OR Trichoptera OR Neuroptera OR Megaloptera OR Raphidioptera OR Siphonaptera OR Mecoptera) AND (Neoteny OR Neotenous OR Neotenic OR Paedogenes* OR Paedogenetic OR Pedogenesis OR Pedogenetic OR Progenesis OR Progenetic OR Paedomorph*)) AND (Coro-...)) OR (Type I paedomorphosis OR Progenesis)). After removing duplicate or inappropriate results, we identified 200 relevant articles spanning five holometabolous insect orders (Fig. 2). The paedomorphic taxa of the following insect groups have not entirely lost complete metamorphosis and are not considered in detail in this review: Psychidae (Lepidoptera); Paussine (Carabidae, Coleoptera); Scolypine (Curculionidae,
Insects that have lost complete metamorphosis via type I paedomorphosis are known from several independent dipteran lineages (Johannsen, 1910; Wyatt, 1961, 1963, 1967; Ibrahim & Gad, 1975; Hodin & Riddiford, 2000) and the unusual beetle species *Micromalthus debilis* (reviewed in Pollock & Normark, 2002). Common to all insects possessing this strategy, development and maturation of the germ line are accelerated and occur during the larval stage, resulting in arrested development of the soma, no further bodily growth, and parthenogenetic reproduction. Here, females are characterised by the ability to facultatively “choose” to undergo complete metamorphosis, or not, as part of a mixed life cycle strategy that contains both metamorphic and paedomorphic cycles. Insects that have lost complete metamorphosis via type II paedomorphosis are thought to have evolved once in derived lineages of the endoparasitic order Strepsiptera (Kathirithamby, 1989; Pohl & Beutel, 2008; McMahon et al., 2011a, 2011b), and several times in the beetle superfamily Elateroidea (Mjöberg, 1925; Cicero, 1988; Wong, 1996; Bocak & Matsuda, 2003; Bocak et al., 2008; Jeng, 2008; Kundrata & Bocak, 2011; Kundrata et al., 2014). In insects that have lost metamorphosis via type II paedomorphosis, development of the soma is also terminated during or at the end of the larval stage (Cicero, 1988; Jeng, 2008), but development of the genitalia continues into an undifferentiated terminal stage (see later for discussion of the strepsipteran cephalothorax). Importantly, instead of an associated acceleration of germ line development as in type I paedomorphosis, the rate of maturation of the germ line continues normally, which, unlike in type I paedomorphosis, permits extended body growth. A further difference from type I species is that complete metamorphosis cannot be facultatively regained in type II females in response to external environmental cues, although as is common to both strategies, it is retained in males.

We found that the loss of complete metamorphosis has occurred repeatedly, originating independently several times in divergent lineages distributed across three holometabolous insect orders. Given the lack of knowledge concerning the pre-pupal biology of most insects (Hodin & Riddiford, 2000), which can be both highly cryptic (Kathirithamby & Johnston, 2004) and difficult to study (Mjöberg, 1925), the loss of complete metamorphosis may be more common than is currently appreciated. Knowledge of the phylogenetic relationships among putatively independent lineages also remains equivocal for many groups (although see Bocak et al., 2008; Kundrata & Bocak, 2011; McMahon et al., 2011a; Masek et al., 2015). Nonetheless, known independent losses are highly uneven in their taxonomic distribution, with a conservatively estimated minimum of four, four and one independent losses in Diptera, Coleoptera and Strepsiptera, respectively (Table 1).

**Loss of complete metamorphosis via type I paedomorphosis**

**Diptera**

Diptera contain possibly the highest number of known independent evolutionary losses of metamorphosis via type I paedomorphosis. Flies that have lost complete metamorphosis via type I paedomorphosis are most prominent among the more basally located dipteran clades (Wiegmann et al., 2011), including the gall-midges, Cecidomyiidae (Wyatt, 1961, 1963, 1967), Chironomidae (Johannsen, 1910) and Syrphidae (Ibrahim & Gad, 1975; Achterkamp et al., 2000). However, knowledge of paedomorphosis in Chironomidae and Syrphidae stems from indirect observations, and requires further experimental validation. The richest diversity and best understood examples of type I paedomorphosis in holometabolous insects come from the Cecidomyiidae. In gall midges such as *Mycophila speyeri* (Fig. 1a), larval parthenogenesis proceeds via viviparous thelytoky, i.e. mothers give birth to live all-female progeny initially developing from unfertilised eggs (Hodin & Riddiford, 2000; Normark, 2003). Ovaries develop extremely rapidly, with follicle formation and oocyte production occurring within the first 24h after hatching, and embryogenesis of progeny beginning prior to the (mother’s) moult to the second larval stage. Larval progeny hatch in the mother’s haemocoel some 6days after the mother larva herself hatches, after which they feed internally on the mother larva’s tissues before eventually emerging from the mother’s cuticle. Alternatively, females can reproduce sexually by foregrowing parthenogenesis and undergoing complete metamorphosis and mating with males, which all undergo complete metamorphosis. Sexually reproducing females undergo a normal metamorphic cycle, where ovary development is no longer accelerated, and follicle and oocyte formation occur during the pre-pupal and early pupal stages, respectively (Hodin & Riddiford, 2000). The trigger for switching between parthenogenesis in larval forms or sexual reproduction in normal adults is an ecological one. Many gall midges are mycetophagous and feed on fungus: when feeding on older fungal mycelia, complete metamorphosis is induced and sexual adults are produced, whereas when feeding on fresh fungal mycelia (<3 days), larval parthenogenesis is induced, and complete metamorphosis is avoided by undergoing type I paedomorphosis (Went, 1979). Within the Cecidomyiidae, at least four genera have
been described with type I development: *Miastor*, *Heteropeza*, *Mykoplia* and *Tekomyia* (this genus is thought to reproduce parthenogenetically during the pupal stage; Wyatt, 1961). *Miastor* and *Heteropeza* are thought to be closely related lineages, as are *Tekomyia* and *Mykoplia* (Mamaev & Krivosheina, 1993; Roskam, 2005). Although the exact phylogenetic relationships among cecidomyiid genera remain uncertain, it is reasonable to conclude that loss of complete metamorphosis by type I development has evolved at least twice in Cécidomyiidae.

**Micromalthidae**

Constituting the only species of the family Micromalthidae, *Micromalthus debilis* (the ‘telephone-pole beetle’) surely possesses one of the most remarkable life cycle strategies adopted by any animal. Individual parthenogenetic female larvae are either thelytokous, arrenotokous or amphitokous. In the thelytokous form, multiple female offspring are produced via viviparity inside the larval mother. In the arrenotokous form, females produce a single male egg, giving rise to a larva that subsequently cannibalises the mother and grows over several instars before undergoing complete metamorphosis to become a dispersive adult (Scott, 1938). Amphitokous forms follow both of the aforementioned pathways (Pollock & Normark, 2002). In addition, as in dipterans, individual *M. debilis* females can reproduce sexually by undergoing complete metamorphosis instead of parthenogenesis (although functional sexual reproduction is yet to be confirmed between post-metamorphic *M. debilis* males and females). No other extant coleopteran species is known with a similar or even intermediate life cycle or mode of reproduction. Unlike in Cécidomyiidae, the trigger for the induction of sexual vs. parthenogenetic cycles is not clear, although habitat dryness is speculated to be an important factor (Pollock & Normark, 2002). Some analyses argue for phylogenetic placement of *M. debilis* within one of the basal-most coleopteran lineages – the Archostemata (Beutel *et al.*, 2008) – although its exact position within Archostemata remains unclear (Hörnsclemeyer, 2009).

**Loss of complete metamorphosis via type II paedomorphosis**

**Strepsiptera**

Among the derived families of the order Strepsiptera (the so-called ‘twisted-wing parasites’), in genera such as *Xenos*, male and female development is similar until the fourth larval instar (Beani *et al.*, 2005). At this point, males continue to develop normally, undergoing one more moult before pupation and eclosion. Females, on the other hand, avoid pupation and continue to grow and develop the germ line. Further gross modifications to the body cease at the fourth larval instar in females, except in relation to the formation and extrusion of the cephalothorax through the host cuticle. The cephalothorax is extruded when the female reaches sexual maturity, and is a highly modified structure that is derived from the female head and thorax, but functionally acts as...
the genitalia. Its developmental origins, particularly in relation to regulatory mechanisms ancestrally associated with pupation, remain unclear. Extrusion of the cephalothorax is timed to coincide with eclosion of winged adult males (Hrabar et al., 2014). At this point, a powerful sex pheromone is released by the permanently endoparasitic female to attract mates (Cvačka et al., 2012; Tolasch et al., 2012). After mating, strepsipteran females can produce close to 1 million planidial first-instar larvae via viviparity (Kathirithambry, 2009). Additionally, as in other parasitic or phoretic insects such as the Meloidae (Coleoptera) and Euchariidiae (Hymenoptera), Strepsiptera display ‘hypermetamorphosis’ due to the additional moult from the motile first-instar larva to a grub-like second-instar larva. Unsurprisingly, oogenesis is also quite unusual in Strepsiptera with a number of derived modifications to the normal insect pattern (Buning, 1998). Oocyte production in derived Strepsiptera probably also has an earlier onset point during development as compared with pupating females of strepsipteran species that are closer to the putatively ancestral condition. However, this remains unconfirmed (see File S1 for further explanation).

**Elateroidea**

In contrast to Strepsiptera, elateroid beetles are free-living and non-parasitic. However, in common with Strepsiptera, females from several distant elateroid lineages have permanently lost metamorphosis. In one of the more unusual examples, the so-called ‘trilobite larvae’ of the Platerodrilini (Lycidae), females are both soft-bodied and substantially larger than their male counterparts (Bocakova et al., 2007; Bocak et al., 2008) (Fig. 3). A single report describes the terminal moult and sexual behaviour of *Platerodrilus ruficollis* (syn. *Duliticola hoiseni*) females in some detail (Wong, 1996). It corroborates Mjöberg (1925) in stating that the final stage differs from the previous larval stage only in the development of the genitalia and describes the first successful mating of lycids in the laboratory (although the hatched larvae subsequently died). Despite being much larger than strepsipteran females, mated lycid females produce far fewer eggs (hundreds), but these are much larger. Outside of the Platerodrilini, a total lack of metamorphosis via type II paedomorphosis is strongly suspected in at least three other lineages within the Lycidae alone (Levkanicova & Bocak, 2009; Malohlava & Bocak, 2011; Masek et al., 2014). Other definitive cases of total loss of pupation in the Elateroidea have occurred independently (Lycidae, Phengodidae and Lampyridae). This is a very conservative estimate, and it is more likely to have originated at least eight or nine times when the strongly suspected cases in poorly characterised and/or equivocally positioned elateroid lineages are considered. These include at least four times in Lycidae, twice in Lampyridae and potentially once or more in each of Phengodidae, Rhagophthalmidae and Telegeusidae. Cicero (1988) and Jeng (2008) define the varying states of type II paedomorphosis in Elateroidea, wherein only ‘ultimate’ (Jeng’s categories 7 or 8) forms of paedomorphosis meet the criteria of our review (undifferentiated between larval and terminal stage). We therefore do not include elateroid species such as those in the Omalisidae, Omithidae, *Diaphanes* (Lampyridae), Drilini and Cebriionidae (Elateridae), where females harbour independently evolved but only intermediate paedomorphic traits. We wish to emphasise that due to the poorly understood biology and/or equivocal phylogenetic positions of some groups, the total species diversity and number of independent losses of complete metamorphosis within Elateroidea via type II paedomorphosis are likely to be much higher than presented.

Key differences between the loss of complete metamorphosis via type I and II paedomorphosis are that reproduction remains primarily sexual in type II groups (although see Silvestri, 1943; Kathirithambry et al., 2003 for possible exceptions to this rule in Strepsiptera) and there is a single life cycle strategy in type II groups. Unlike type I species, the sexes in type II species are permanently dimorphic for complete metamorphosis (i.e. males undergo complete metamorphosis, while females do not). Conversely, loss of complete metamorphosis via type I paedomorphosis is characterised by a mixed life cycle strategy composed of short parthenogenetic cycles and longer dispersive sexual cycles. Type I species are also characterised (but not necessarily defined) by atypical genetic systems. *M. debilis* is haplodiploid (Scott, 1938), whereas cecidomyiids, as in some sciarid dipterans and scale insects, have an unusual form of paternal chromosome elimination (Stuart & Hatchett, 1991), whereby males have no influence on the sex of the progeny (Stuart & Hatchett, 1988).

**Developmental regulatory mechanisms**

The developmental mechanisms that underlie different forms of metamorphosis are just beginning to be elucidated and much work remains in this area. The hormones 20-hydroxyecdysone (20E) and juvenile hormone (JH) are responsible for regulating metamorphosis in insects. In holometabolous insects, a small increase in the expression of 20E in the absence of JH during the final larval instar induces pupal commitment, leading to epidermal expression of the transcription factor *brood* (*br*) (Zhou & Riddiford, 2001). *Brood* regulates various metamorphosis-specific target genes and is essential for successful larval to pupal transition in insects with complete metamorphosis (Suzuki et al., 2008). In hemimetabolous insects, *br* expression occurs at each nymphal moult, except between the last nymphal stage and the adult (Erezylma et al., 2006). Recent work on the strepsipteran *Xenos vesparum* has demonstrated that *br* is expressed in typical holometabolus fashion in male *X. vesparum*, which undergo pupation and metamorphosis...
Fig. 3. Loss of complete metamorphosis in holometabolous insects and consequences for life cycle complexity. Key developmental stages of representative paedomorphic holometabolous insect taxa are shown with accompanying schematic depiction of the effect on the life cycle of elimination of complete metamorphosis in females. (a) Loss of metamorphosis in representative species with type I paedomorphosis: *Mycophila speyeri* (Cecidomyiidae) and *Micromalthus debilis* (Micromalthidae). For *M. debilis*, an arhenotokous and a thelytokous female in the terminal moult stage are shown, constituting a recently born haploid male son (highlighted in blue, left image) and unborn viviparous daughter larvae still inside the mother (highlighted in red, right image), respectively. (b) Loss of metamorphosis in representative species with type II paedomorphosis: *Xenos vesparum* (Strepsiptera) and *Platerodrilus ruficollis* (Lycidae). For *X. vesparum*, the terminal moult images are of a female resident inside the wasp host abdomen, with the blue arrow indicating the extruded cephalothorax (left image), and the entire female dissected from the host (right image). For *P. ruficollis*, the image of the winged *Platerodrilus* male is not *P. ruficollis*, but it is representative of this species' gross morphology (Wong, 1996). Life cycles: complete metamorphosis to an ancestral adult stage is retained in each life cycle strategy; *M. debilis* and *M. speyeri* may intermittently exist as both metamorphic adult males and females, depending on ecological conditions. Type I paedomorphosis enabled a dramatic shortening of the life cycle (life cycle innovation, in red). In *X. vesparum* and *P. ruficollis*, males undergo pupation to an ancestrally adult stage, whereas females are permanently larviform and do not undergo complete metamorphosis. Type II paedomorphosis facilitated a dramatic increase in size, and additionally, in the case of *Strepsiptera*, a completely endoparasitic lifestyle (life cycle innovation, in red) (see main text for discussion). Images have been adapted for use in this figure with permission from the publisher and authors, to whom all rights are reserved (*M. speyeri*, Hodin & Riddiford, 2000; *M. debilis*, Scott, 1938; *P. ruficollis*, Wong, 1996), or are under creative commons licences CC BY 4.0 (*X. vesparum*, Erezyilmaz et al., 2014; *Platerodrilus* sp. winged male, Masek & Bocak, 2014) and CC BY-SA 3.0 (metamorphic adult image of *M. debilis*; credit David R. Maddison).
to emerge as winged adults (Erezyilmaz et al., 2014). In contrast, no evidence of elevated br expression was observed for female X. vesparum, which do not enter the pupal stage and remain larviform at maturity, suggesting that a lack of br up-regulation may underlie loss of complete metamorphosis via type II paedomorphosis (Erezyilmaz et al., 2014). However, the mechanism that prevents br up-regulation is unknown, and further studies to identify this and to confirm the pattern in other strepsipteran taxa and in elateroid beetles are required.

There are multiple means by which pupation can be avoided. In type I paedomorphosis, gall midges have evolved an alternative strategy involving early up-regulation of ecdysone receptor (EcR) and ultraspireacle (USP) in the ovaries. These nuclear receptors form a dimer that mediates tissue-specific responses to 20E, and their expression regulates the timing and progression of ovarian differentiation (Yao et al., 1992, 1993). In Drosophila melanogaster, EcR and USP are up-regulated only in the final larval stage (Hodin & Riddiford, 1998). This is also the case in gall midges with the capacity for paedomorphosis, when available fungal hyphae are old (low-quality food) and flies undergo metamorphosis (Hodin & Riddiford, 2000). However, when fresh fungal hyphae are present (high-quality food), up-regulation of EcR and USP occurs early in the first larval instar, leading to paedomorphic development (Hodin & Riddiford, 2000). Interestingly, the pattern of precocious up-regulation of EcR and USP is highly similar in both species of paedomorphic gall midge so far examined (Heteropeza pygmaea and Mycophila sypvetri), despite the proposed convergent evolution of type I paedomorphosis in these species (Hodin & Riddiford, 2000). Further investigation to identify the connection between larval nutrition and ovary-specific induction of EcR and USP is required, because, as with type II paedomorphosis, the ultimate causal mechanism behind the avoidance of metamorphosis is unknown (Hodin & Riddiford, 2000). Thus, while tantalising glimpses of the mechanisms underlying paedomorphosis have been gained in recent years, current understanding is limited, presenting a rich field for future exploration.

**Ecological factors favouring the loss of complete metamorphosis**

The retention of a larval lifestyle is expected to carry some life-history costs, particularly in terms of the ability to disperse and efficiently locate potential mates. However, there may also be benefits gained by avoiding a pupal and terminal moult that may outweigh the cost of being deprived of a diverse suite of holometabolous adult traits. It is worth noting that paedomorphic reproduction is likely to be especially favoured in females because of the relative enhancement of fecundity (and therefore fitness) that accompanies the avoidance of a costly metamorphic stage. For example, pupation requires extensive remodelling of morphology (Truman & Riddiford, 1999) and so is a time-consuming and energetically expensive process. Meanwhile, as an entirely sessile stage, the pupa is vulnerable to attack from a multitude of predators and parasitoids (Godfray, 1994). Additionally, it is likely that some risk must accompany the maintenance of beneficial over detrimental (i.e. pathogenic) symbiotic interactions while the gut lining is renewed during pupation (Johnston & Rolff, 2015). Given both potential costs and benefits of pupation, we consider how life-history traits interacted with ecological factors to facilitate the loss of complete metamorphosis, and how sex-biased trade-offs may have favoured investment in reproduction over development.

In type I paedomorphic species, the ephemeral nature of high-quality resource patches on which they feed may favour a shortened life cycle (Fig. 3a). In M. debilis (Micromalthidae), as an alternative to all female diploid broods (approx. 10 daughters), the mother larva can also produce a single haploid son that consumes the mother before pupating into a fully metamorphosed adult. Males are costly because a single son consumes the mother. As with the normal metamorphic female pathway in both M. debilis and cecidomyiid flies, cannibalism by M. debilis males leads to a dispersive adult stage (which could be viewed as a form of sex change by a paedomorphic female). As in other type I paedomorphic species, the metamorphic pathway can be viewed as a response to deterioration in quality of the resource patch, or as an inbreeding avoidance strategy (Pollock & Normark, 2002).

To accommodate both sedentary and dispersive strategies, a number of other holometabolous species in similar habitats have evolved modified life cycles and a tendency towards both parthenogenesis and paedomorphosis (although never to the extent that complete metamorphosis is entirely avoided). These habitats offer reduced predation and desiccation risk, and an (often temporary) abundance of high-quality resources (Hamilton, 1978). In the Sciariidae (Diptera), Plastosciara perniciosa is able to produce sexual micropterous larviform males and females as a facultative response to temporarily favourable environmental conditions (Steffan, 1973). The entirely parthenogenetic beetle Pitinella errabunda (Ptiliidae) exists as a below-bark morph that is blind, flightless and unpigmented and a dispersive morph that is tanned, winged and possesses compound eyes.

Multi-generational plasticity in phenotypic traits is commonplace in these insects. Furthermore, the positive correlation between paedomorphosis and life cycle plasticity points to an advantage of maintaining a fully metamorphosed flight-capable adult stage somewhere in the life cycle. This could occur via disruptive or alternating selection for sexual reproduction or for a flexible response to a heterogeneous environment. Greater knowledge of species with intermediate paedomorphic phenotypes is required to clarify the steps involved in the loss of complete metamorphosis via type I paedomorphosis, e.g. the cecidomyiids Henria psalliotae and Tekomyia populi (Wyatt, 1961) that reproduce as modified pupae or the chironomid Paratanytarsus grimmii that reproduces as a pharate (i.e. individuals that remain within the last larval skin after pupation) metamorphic adult (Chironomidae) (Langton et al., 1988). In addition, to provide deeper insight into the biology of these organisms, accurate phylogenetic placement is necessary to gain an understanding of how loss of complete metamorphosis via type I paedomorphosis originated.

The extreme sexual dimorphism exhibited by species that have lost metamorphosis via type II paedomorphism indicates a strong trade-off between efficient movement via flight...
(including dispersal ability) and fecundity, with enlarged body size and higher investment in reproduction occurring at the expense of movement (Fig. 3b) (Hodin, 2009). We argue that the basis of the trade-off is similar to many other insect groups in which females have evolved vestigial adult traits such as reduced wings. Evidence from multiple independent lineages suggests that female insects with vestigial wings have a shortened onset of egg reproduction, higher investment in gonads, and higher fecundity (Guerra, 2011). In Strepsiptera (McMahon et al., 2011a) and phylogenetically well-resolved elateroid beetles (e.g. Lycidae; Bocak et al., 2008; Masek et al., 2015), the trade-off appears to be total (no reversals are apparent across phylogeny; although see Jeng, 2008 for a wider discussion of Elateroidea).

A major step in the loss of complete metamorphosis in Strepsiptera involved a transition to complete female endoparasitism. In free-living metamorphic females of Mengenillidae, male insemination is traumatic and females can be facultatively pharate (Pohl & Beutel, 2008). Being pharate, and eventually entirely endoparasitic, could in theory serve a protective role against male damage, although this has not been tested. A second possibility is that complete endoparasitism was driven by maximal resource extraction by the parasite from the host, or, in other words, selection for enhanced fecundity. Increased body size during the transition to endoparasitism has been documented in other arthropods, such as coperpods, where it is accompanied by a steady increase in parasite body size (Poulin, 1995). Indirect support in Strepsiptera comes from evidence of female-driven host associations following the transition from a small (ant) to large (dictyopteran) host in the Myrmecolacidae (Hayward et al., 2011). A final possibility is that pressure from parasitoids on pupae or free-living soft-bodied females (of which several species are known; Silvestri, 1943) drove the transition to endoparasitism. Ultimately, whether sexual conflict, increased fecundity, parasites or a combination of these factors drove endoparasitism (and therefore type II paedomorphosis in Strepsiptera) cannot be fully addressed given current knowledge. Experimental manipulation of copulation and/or parasitoid pressure on exant, facultatively pharate, strepsipteran females, such as in the genus Mengenilla, could help to resolve this question empirically.

In platerodrilid lycid beetles (Elateroidea), long developmental times and inactivity are characteristic of females (Bocak et al., 2008). There is also evidence that some lycid beetles have a nutrient-poor diet (Mjöberg, 1925; Ng & Yong, 1991; Wong, 1996) in addition to sedentary anti-predatory adaptations, such as production of repellent substances (Moore & Brown, 1981). Together with what are thought to be very limited ancestral ranges for Platerodrilus beetles (Masek et al., 2015), such factors could exacerbate a dispersal-reproduction-based trade off, due to reduced incentives to disperse (Zera & Harshman, 2001). Interestingly, defensive coloration (Linsley et al., 1961) and luminescence (De Cock & Matthysen, 2001) represent ancestral aposematic traits of other paedomorphic elateroid lineages such as Lampyridae and Phengodidae (Bocak et al., 2008). Clearly, understanding the nature and direction of any causal relationship between paedomorphosis and the aforementioned traits is difficult. However, independent contrasts of diet, habitat range, defensive and paedomorphic traits across elateroid phylogeny could represent a potential means of testing the importance of these factors during the repeated loss of complete metamorphosis in Elateroidea. The high degree of variation in the point at which metamorphosis is arrested across diverse elateroid lineages also provides a useful comparative framework for understanding the evolutionary and developmental origins of type II paedomorphosis (Cicero, 1988, 2008; Jeng, 2008).

**Loss of complete metamorphosis is rare**

One outstanding question is why more holometabolous insect species have not lost complete metamorphosis. As discussed earlier, a number of potential benefits may arise from avoiding metamorphosis, and it is surprising on first sight that so few species possess these strategies (Table 1). While loss of complete metamorphosis in females has evolved repeatedly, it is highly uneven in its taxonomic distribution. This indicates that specific pre-adaptations may be required for paedomorphosis that not all insects possess or can easily evolve. For example, Hodin and Riddiford (2000) postulated that the loss of complete metamorphosis by type I paedomorphosis is concentrated in more basally located dipteran lineages (except for *M. debilis*) due to the predominance of early germ line development in basally occurring dipteran lineages, where this process can begin as early as embryogenesis. This is in contrast to the typical insect pattern, including the higher flies, where ovarian somatic cell types differentiate before the germ line (Hodin & Riddiford, 2000). Another necessary component may be a non-diploid/parasitoid system and an associated capacity for asexual reproduction: this is required for parthenogenetic reproduction as paedomorphic larvae. In the loss of complete metamorphosis via type II paedomorphosis, a specific combination of initial conditions may also have been necessary. For example, combinations of defensive, dietary or even restricted habitat ranges may underlie a bias towards reproduction over dispersal in female elateroid beetles, but these possibilities remain untested. In Strepsiptera, the presence of motile planidial first larvae is probably essential in enabling complete female endoparasitism, because a larviform female would both lack oviposition apparatus and the ability to control egg-laying whilst constrained inside the host. The rare occurrence of planidia, alongside a parasitoid-driven strategy centring on host immobilisation and rapid depletion of resources, could explain why parasitic Hymenoptera have never lost complete metamorphosis.

In terms of species richness, type II paedomorphosis appears to be a more successful strategy. Extremely paedomorphic lineages of Strepsiptera and Elateroidea harbour many hundreds of species compared with just a handful of described cecidomyiid species and the single beetle *M. debilis*. It is possible that the high phenotypic plasticity demonstrated by type I species may act as a brake on adaptive evolution and diversification, because highly plastic populations are likely to persist easily and undergo less genetic change (Price et al., 2003; Pfennig et al., 2010). It is also worth inserting a final caveat: the true number of type II, but in particular type I, paedomorphs may be considerably higher than is currently appreciated because many paedomorphic insects are often extremely cryptic.
Conclusions

Loss of complete metamorphosis in females has evolved independently on many occasions (conservatively at least nine times), but its occurrence within Holometabola is highly uneven. Furthermore, each transition involved the evolution of a highly derived reproduction-competent larva, rather than a reversion to hemimetabolous development. Modifications to the holometabolous larva–pupa–adult ground plan therefore appear strongly constrained, and we argue that they are likely to depend upon unusual developmental or life-history pre-adaptations. While a larval lifestyle appears highly adaptive, in holometabolous insects it occurs as just one component of a more complex life cycle. Taken together, our review supports the notion that complete metamorphosis is evolutionarily irreversible, in both a strict (direct reversion to Hemimetaboly) and a general sense (Bull & Charnov, 1985), because the transition to a derived form of direct development via type I and II paedomorphosis is never maintained across a species’ entire life cycle. While some insight into the origin and subsequent repeated loss of complete metamorphosis (via extreme paedomorphosis) has been gained in recent years, there remain major gaps in understanding of both the proximal and ultimate causes of these transitions, particularly with respect to the apparent irreversibility of complete metamorphosis, once evolved. Our hope is that this review will go some way to stimulating research in a field that offers exciting opportunities for future exploration.

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Supporting Information

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File S1. Taxing terminology.

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