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How the simple shape and soft body of the larvae might explain the success of endopterygote insects

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ABSTRACT

The body forms of the larvae of most endopterygote insects are remarkably similar. I argue that their typical worm-like shape cuts costs; in particular, this allows the larvae to benefit from cheaper moulting and from less costly provision of fuel and oxygen to their respiring tissues. Furthermore, the shape confers a reduction of larval mortality in moulting. Together, these factors allow endopterygote larvae to grow fast and as this speedy growth reduces the dangers of predation, attack by parasitoids and disease before the larvae can reach adulthood, they increase offspring survival. I argue that this goes a long way to explain the very pronounced success of endopterygote insects.

KEY WORDS: Body form, Cost, Endopterygote, Survival

Introduction

The major groups of insects are the exopterygotes (Heterometabola) and the endopterygotes (Holometabola) (see Glossary). The endopterygotes can be seen as the most successful lineage of living organisms – it is claimed that they account for between 70% and 80% of all species of arthropods and, indeed, between 45% and 60% of all living organisms (Kristensen, 1999). The group is thought to be monophyletic (Peters et al., 2014). Some think that there could be as many as 4 million endopterygote insect species and that they dwarf in number all other terrestrial clades (Meier and Lim, 2009). These could be extreme claims, but the success of endopterygote insects is undeniable. Especially successful in terms of the number of species are endopterygote insects of the four orders Coleoptera (beetles), Diptera (flies), Hymenoptera (wasps, bees, ants, etc.) and Lepidoptera (butterflies and moths).

Although the group is monophyletic, the morphology of the adult endopterygotes has evolved to be very varied. Much less so the larvae, which are broadly similar to one another and appear not to have much adapted the simple morphology of the ancestral pronymph (Truman and Riddiford, 1999). This argues that this is a superior design. As an approximation, typical endopterygote larvae are more or less cylindrical in shape with little tanned cuticle (see Glossary) in their exoskeletons and, importantly, no, or only short, appendages (Fig. 1). The body cuticle is mostly soft endocuticle. In sharp contrast, exopterygote nymphs (see Glossary) typically have a greatly extended morphology, with much longer appendages (Fig. 1), and the body cuticle typically has a high content of tanned exocuticle.

In this Commentary, I advance the hypothesis that these features of their larvae give endopterygote insects significant advantages, in particular much reduced costs, especially in feeding, moulting and respiration, which in turn allow them to grow faster and reduce predation. These factors contribute significantly to high offspring survival, an important characteristic of successful organisms (see, for example, Queller, 1994).

Feeding, growth and predation

High offspring survival to adulthood, so important to success, involves two interdependent elements – a high rate of growth but also protection from the danger of predation while growing.

Endopterygote larvae are highly adapted for feeding, which enables them to achieve high rates of growth. This in itself means that they are at less danger of predation as they are vulnerable for less time. However, there is a downside – as specialised feeders, their mobility is often poor, which must increase the danger of predation.

That endopterygote larvae can grow fast is shown, for example, by *Drosophila* larvae, which, remarkably, take only 96 h to grow from hatching to pupation (Santos et al., 1997). Similarly, honeybee larvae grow to their adult size, an increase of 800 times, also in only 96 h (Bishop, 1961; Huang and Otis, 1991), no doubt helped by the fact that they can be examined by specialised nurse bees more than 1900 times and fed up to 140 times in that time (and queens can be fed 1600 times!).

The possession by endopterygotes of a worm-like larval form has the important consequence that it allows them to exploit forms of food that are denied to the long-legged, more heavily sclerotized exopterygotes. The key advantage is that they can burrow into such foods as the internal parts of plants, other insects, cadavers, wood, dung, etc. Dipteran maggots and hymenopteran larvae typify this form of feeding.

Clearly, the locomotory costs incurred while feeding like this are much reduced. It is also likely that feeding inside food material will provide the additional advantage of protection against predation. Indeed, if predation risk is sufficiently reduced, then feeding need not be so fast. For example, wood-boring insects can take many months to reach adult size. It is the combination of fast and/or safe larval feeding that contributes to offspring survival.

Perhaps the most successful of endopterygote larvae with a burrowing lifestyle are the parasitoid Hymenoptera (see Glossary). Their successful invasion of other insects, often larval lepidopterans, means that their worm-like simple shape with very little exocuticle allows them to grow fast and hidden from the external world, and, once they are established, their survival rates are high. The first-stage larvae often have impressive fighting mouthparts of tanned cuticle, but successive larvae do not and so can grow and moult more rapidly (Paladino et al., 2010).

In the social hymenopterans, the larvae are fed by adults, usually directly related to them. The worm-like shape of the larvae allows them to be close packed, as in the hexagonal array of larval cells in honey bees. This reduces costs for both adults and larvae; the larvae have no need to move and the adults' movements while feeding the larvae are reduced. It might be no coincidence that the young of the most successful eusocial endopterygotes are well protected by

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Glossary

Cerci
Thin cuticular appendages, usually a single pair, that are carried on the last abdominal body segment.

Cuticle
The external skeleton of an insect. It is composed of microfilaments of the polysaccharide chitin embedded in a matrix of protein.

Exocuticle
Cuticle that is tanned by chemical cross-linking of the protein content, which leads to dehydration and a great increase in hardness and stiffness. It cannot later be reclaimed by digestion.

Endocuticle
Cuticle that is not tanned. It is relatively soft and can be digested and reabsorbed when the insect moults.

Endopterygote
The superorder of class Insecta that includes all those insects that have larvae very different from the adult forms and have an intermediate form, the pupa, to allow the larvae to metamorphose into the adult form.

Haemocytes
The blood cells of an insect responsible for encapsulatimg objects such as eggs or larvae of parasitoids that may appear in the haemolymph.

Hymenoptera
An endopterygote order of insects that includes bees, wasps, ants, etc.

Instar
Any one of the several stages of postembryonic development which an insect undergoes between moults, before it reaches sexual maturity.

Nymph
The young forms of exopterygote insects that resemble the adult forms.

Parasitoid
An organism that lives in close association with its host and at the host's expense, and which sooner or later kills it.

cooperating adults while they feed. The survival of these larvae is much higher than if they did not benefit from parental care. Arguably, this cooperative parental care might underlie the origin of eusociality (Queller, 1994).

So, the energy costs involved in finding food in many larval endopterygotes are much reduced. If, in addition, the food source is a nutrient-rich one, ingestion of sufficient material to support growth will be cheap, so one can see why growth rates can be so high.

An exception to this is that larval lepidopterans, which are herbivores, do not achieve the very rapid rates of growth that many other larval endopterygotes show. Their diet is less rewarding than that enjoyed by many other insects as there are clear limitations imposed by plant defence measures, such as production of toxins and tannins. And because they are relatively slow to grow, they are more open to attack by predators and parasitoids. Not surprisingly, therefore, they are highly adapted for rapid ingestion and processing of their food. They have very large guts that occupy much of the space within them, which allows them to process large amounts of food at a time (Reynolds et al., 1986).

Lepidopteran larvae have evolved a striking countermeasure against the effects of tannins in their diets. They are able to produce extremely high pH values in their midguts – up to 12 in some cases, the highest known for any biological system (Dow, 1992). This acts to force the dissociation of tannin–protein complexes, which in turn allows faster digestion of protein. To aid defence against parasitoids, lepidopteran larvae are, remarkably, able to supply oxygen to the haemocytes (see Glossary) in the haemolymph through the possession of lungs in the 8th abdominal segment (Locke, 1997). This allows the larvae to supply oxygen to the haemocytes, which in turn enables them to be more active in encapsulating eggs and larvae of parasitoids introduced into the haemolymph.

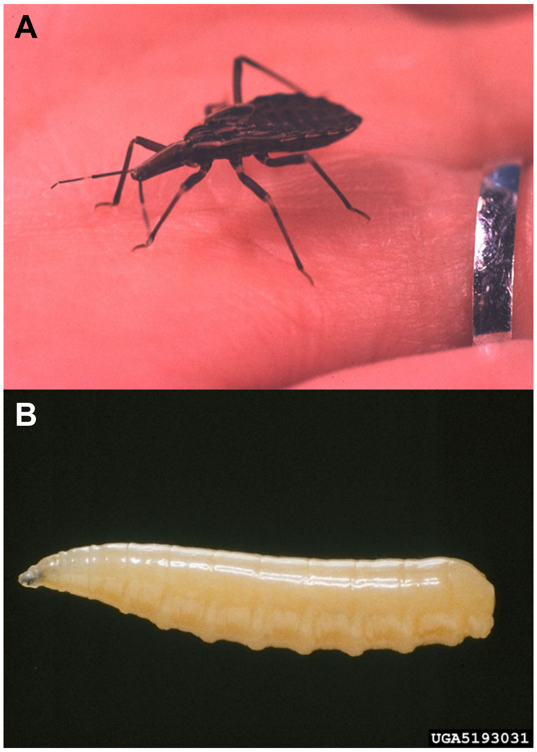

Fig. 1. Diversity of form in exopterygotes versus endopterygotes. (A) A typical exopterygote nymph [5th stage instar (see Glossary) of the kissing bug *Rhodnius prolixus*]. (B) A typical endopterygote larva (the Mediterranean fruit fly, *Ceratitis capitate*; Florida Division of Plant Industry, Florida Department of Agriculture and Consumer Services, Bugwood.org). Note the worm-like shape and lack of appendages.

These adaptations allow lepidopteran larvae to grow relatively rapidly, even on a difficult diet. Sawfly larvae (Symphyta) are rather similar to lepidopteran caterpillars and it is likely that similar considerations apply to them, but they have been less well studied.

Energy savings in endopterygote larval growth

What is it about endopterygotes that allows them to grow so fast? Here, I argue that the costs of growth are reduced in endopterygote larvae from energy savings in moulting, respiration and blood circulation.

Moulting

The cuticle of endopterygote larvae is not heavily sclerotised. Most of it consists of endocuticle (see Glossary), which, although much less strong, confers significant advantages. First, the body size can increase by a large amount without the need to moult. This is because, unlike tanned exocuticle (see Glossary), the endocuticle can be 'plasticised' and stretch to accommodate the larger body size. Caterpillars – lepidopteran larvae – can, for example, grow in mass by a factor of as much as 10 between moults (Grunert et al., 2015). Not many parts of the cuticle have to be tanned; among these are the mouthparts (and the head capsule cuticle to provide purchase for the muscles that operate the mouthparts) and the lining of the tracheal system, which needs to be strengthened by tanning to keep the tracheae from collapsing. The replacement of the inextensible lining of the tracheal system is necessary to allow faster respiration as the larvae grow – indeed, this could be a major reason why insects moult. A few other organs require tanned cuticle, in particular sense organs such as eyes and sensory bristles. And caterpillars often have protective bristles and claws on their short legs that need to be tanned. But overall it is true to say that endopterygote larvae have much less tanned cuticle than do exopterygote nymphs.

The important consequence of this is that, in endopterygote insects, very much less material is lost when the larvae moult because they can digest and reabsorb the endocuticular parts of the skeleton and only lose the relatively small amounts of tanned cuticle that cannot be digested. As a result, moulting must be significantly less expensive than in other insects with more extensive tanned cuticles.

Finally, it is worth noting that endopterygote larvae have a significantly lower surface area to volume ratio than exopterygotes, because of their body shape and lack of long appendages. So, less cuticle has to be produced for the same body mass. This will also be reflected in a lower cost of growth and moulting. Furthermore, it is likely that moulting a less-extensive and morphologically less-complicated surface cuticle will also be easier, quicker and less likely to fail than in an exopterygote nymph.

Respiration and haemolymph circulation

Insect tissues are aerobic and need oxygen and fuel to respire. This causes problems for exopterygote nymphs because their elongated body appendages such as legs, cerci (see Glossary), antennae and wings require circulatory mechanisms to supply respiratory substrates to the cells in them.

By contrast, most endopterygote larvae have much reduced numbers of appendages – they mostly have no antennae or cerci and no or only short legs (Gullan and Cranston, 2014).

How oxygen is supplied to insect appendages has received much attention. However, although oxygen supply to a long appendage can be costly (Kaiser et al., 2007), the supply of nutrients to insect tissues must be significantly more expensive. This is because diffusion in water is about 10,000 times slower than in air. And water is much more viscous than air. So, if ventilation of long tracheae is essential (Weis-Fogh, 1964), the circulation of haemolymph in legs, antennae and other appendages is absolutely crucial.

Circulation of haemolymph to the tips of long thin insect appendages such as antennae or cerci must be relatively expensive. Poiseuille's law shows the rate of flow along a tube is proportional to the fourth power of the radius and inversely proportional to the length. Given that haemolymph is not only dense but also likely to be viscous, the rates of flow to the tip of the appendages will necessarily be slow to cut the expense of circulation.

A way to cut these costs is to increase the haemolymph concentration of fuels and nutrients so that sufficient reaches even metabolically demanding tissues, even with relatively slow, and therefore cheaper, circulation of the haemolymph. Blood nutrients such as sugars and lipids can be 50 times higher in concentration in insects than in vertebrates (Wyatt, 1961), and this helps achieve much more rapid diffusion. However, this is nowhere near sufficient to supply nutrients to the ends of appendages merely by diffusion. Insect haemolymph is also notable for the high levels of amino acids present (Wyatt, 1961). The presence of these unusually high concentrations of metabolites strongly suggests that they have evolved from the need to cut the costs of circulating them to the body tissues, especially those in relatively elongated appendages. Thus, a slow flow of nutrient-rich haemolymph is a more economical way of provisioning insect tissues.

Evidence for unidirectional circulation of haemolymph in elongated exopterygote insect limbs is of very long standing (Behn, 1835; Brocher, 1909, 1931). Essentially, haemolymph is pumped down one side of a limb and up the other, with the two flows separated by a membrane (Kaufman and Davey, 1971). By contrast, the circulation of haemolymph to the tips of the short appendages of endopterygote larvae is likely to carry much lower costs.

Presumably, the muscular movements required to circulate haemolymph in insect limbs and other appendages also ventilate the tracheae there, although this seems to have been little studied (Wasserthal, 1996).

Finally, it is worth noting that the locomotion of soft-bodied endopterygotes will inevitably cause movement of the haemolymph and speed up the supply of nutrients to respiring tissues. And, of course, peristaltic movements of the gut will also aid haemolymph circulation, particularly in lepidopteran larvae with large, active guts.

The pupal stage of endopterygotes

The adaptation of endopterygote larvae as very efficient feeding machines carries the disadvantage that they need to be nearly totally restructured by metamorphosis during the pupal stage into the very diverse endopterygote adult stages (Gullan and Cranston, 2014), unlike their exopterygote counterparts, which have no pupal stage.

This strategy will have costs that reduce the advantage of having larvae so different from the adult form.

However, pupae, although they do not feed, can, in many cases, at least be sited so as to reduce predation losses, which increases offspring survival. In addition, they usually make no movements during the pupal stage, which is likely to make them much less evident to potential predators or parasitoids. As this is usually not a vulnerable time, metamorphosis can be relatively slow – for example, *Drosophila*, which take only 96 h between egg hatching and the start of pupation, require a further 96 h to develop to the adult.

Presumably, the extra expense of a pupal stage is more than compensated for by the reduced costs in a larva designed to be an efficient feeding machine.

Physiological adaptations of aquatic endopterygote larvae to avoid predation

I have argued that endopterygote larvae can grow fast because they are designed to reduce costs. But, of course, offspring survival to adulthood is also increased if larval mortality can be reduced.

Endopterygote larvae living in water thrive provided they can survive predation. For example, the physiological adaptation of larvae of such insects as alkaline flies (Maddrell, 1998) and larval mosquitoes (Clark et al., 2004) to allow them to tolerate very high levels of mineral salts and high osmotic concentration in natural waters means they are free from predation by fish as fish cannot survive in these waters. In other freshwater and saline-water environments, where fish can survive, insects do not exist at all, except in environments where they can hide. In open bodies of freshwater or seawater, no insects can escape predation. Hence, for example, there are no insects in open seawater or in open water in lakes (Maddrell, 1998).

Larvae of carabid and staphylinid beetles

As I have outlined above, most endopterygote larvae are worm-like in form. However, some beetle larvae – those of the species-rich Carabidae and Staphylinidae, for example – have legs, antennae and anal cerci. These adaptations allow them to live as predators that hunt down prey. Compared with exopterygote nymphs of the same size, however, their abdomina are elongated and more or less cylindrical, with much cuticle that appears untanned, and their legs and other appendages are relatively short. The advantages outlined above will be reduced but arguably are still significant. It seems that they have evolved to give up some of the advantages of a worm-like body so as to enable them to be successful active predators.

Concluding remarks

The body forms of the larvae of most endopterygote insects are remarkably similar. I argue that their typical worm-like shape cuts costs, particularly allowing the larvae to benefit from cheaper moulting and from less costly provision of fuel and oxygen to their respiring tissues. Furthermore, the shape confers a reduction of larval mortality in moulting. Together, these factors allow endopterygote larvae to grow fast and, as this speedy growth reduces the dangers of predation, attack by parasitoids and disease before the larvae can reach adulthood, together they increase offspring survival. I argue that this goes a long way to explain the very pronounced success of endopterygote insects.

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Competing interests

The author declares no competing or financial interests.

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