

# Development & Metamorphosis



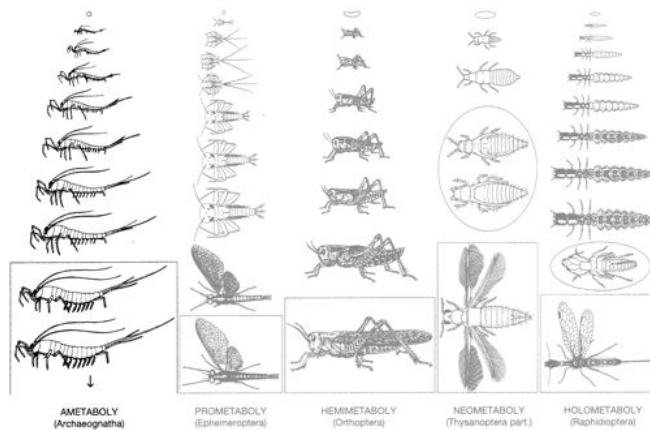
Prepared and presented by David Merritt

## Ametaboly

J0: juvenile wingless  
Q: quiescent stage

apterous ametaboly  
J0-J0-J0-J0-J0-J0-J0-A0-A0  
primarily wingless insects

Primitive developmental pattern. The only major change from instar to instar is increased size. Multiple adult moults. Found in the orders Zygentoma (silverfish) & Archaeognatha (bristle-tails)



Sehnal, Svacha and Zrzavy (1996) Evolution of insect metamorphosis. In: Metamorphosis : postembryonic reprogramming of gene expression in amphibian and insect cells / edited by Gilbert, Tata, Atkinson. pp. 3-58. (QL494.5 .M48)

**Prometaboly**

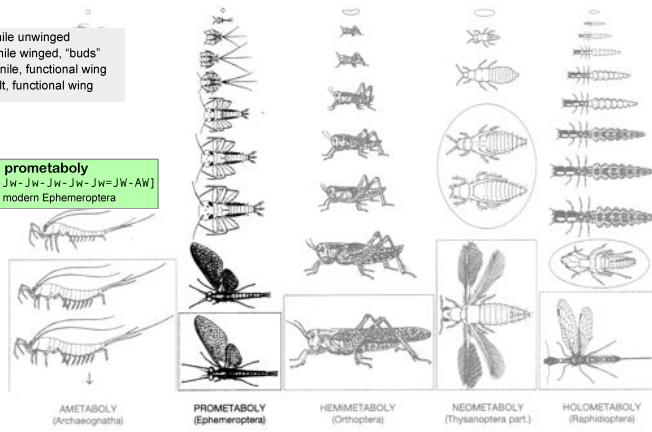
Ephemeroptera (mayflies) have two winged stages. Wings develop in the pre-adult stage or subimago.

Have 2 “postmetamorphic” stages.

In all other pterygotes only adults have wings

J0: juvenile unwinged  
 Jw: juvenile winged, “buds”  
 JW: juvenile, functional wing  
 AW: adult, functional wing

**prometaboly**  
 J0-J0-Jw-Jw-Jw-Jw-Jw=JW-AW]  
 most modern Ephemeroptera

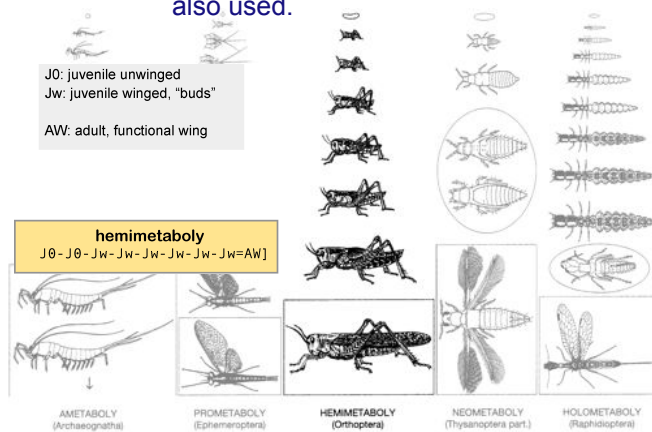


**Hemimetaboly**

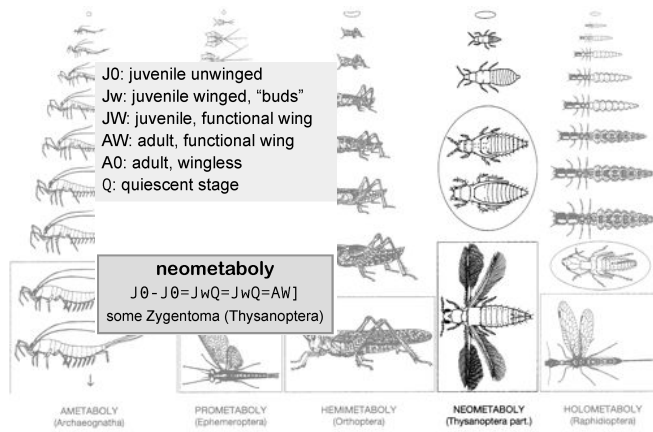
Immatures resemble the adults. Metamorphosis is not as marked as in holometabola. Functional wings and adult genitalia appear in the final stage. Wing pads are visible in earlier stages. No quiescent pupal instar. Usually immatures called nymphs, “larvae” is also used.

J0: juvenile unwinged  
 Jw: juvenile winged, “buds”  
 AW: adult, functional wing

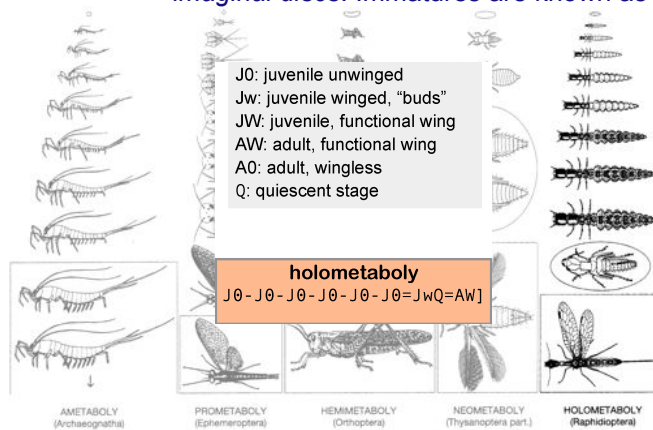
**hemimetaboly**  
 J0-J0-Jw-Jw-Jw-Jw-Jw=AW]

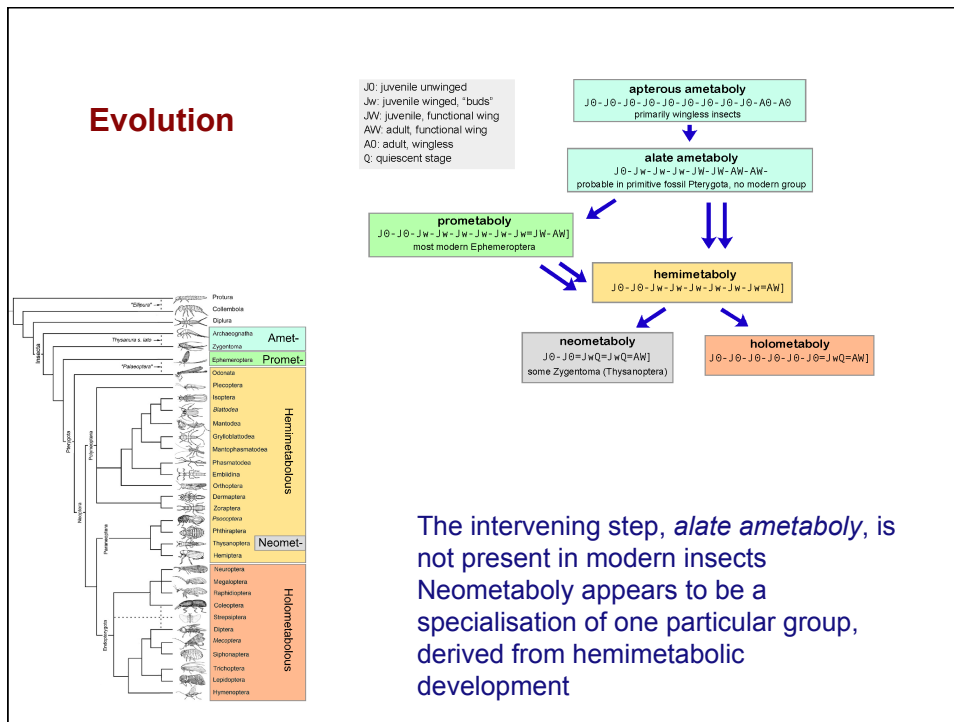


**Neometaboly** 2 resting stages (circled). Thysanoptera (common name: thrips)



**Holometaboly** External wing rudiments not seen until the pupal instar. The pupa is the intervening, relatively quiescent, instar between larva and imago. Pupa is sometimes capable of movement. Wing rudiments may develop as internal in-pocketings, termed *imaginal discs*. Immatures are known as *larvae*.

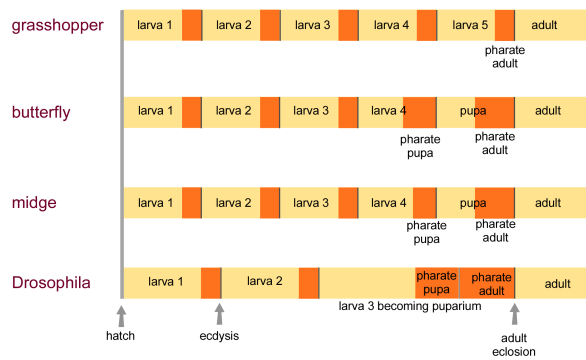
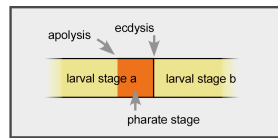




## Evolution of Metamorphosis

1. Reduction of wing rudiments in juveniles rendered juveniles less vulnerable and capable of invading new environments.
2. Predetermined final instar. Adult moults repeatedly expose insects to dangers of moulting (Disadvantages of moulting include: time loss during the apolysis-ecdysis-postecdysis phases, vulnerability to predation, risk of unsuccessful ecdysis.)
3. Fixing flight and reproductive activity into the final instar. Moulting with fully-formed wings is especially difficult.
4. Allowed the adult form to evolve further specialisations without the restrictions imposed by the requirement to moult.
5. This series of evolutionary events could apply to both hemi- and holometabola

Between apolysis and ecdysis the immature is at a "pharate" stage. Some Diptera have gone a step further and pupate inside the last larval cuticle that forms the puparium. At the pharate adult stage the immature is covered with 3 cuticles, one from the 3rd instar larva, one from the pupa and one that will be the future adult cuticle



**Extreme metamorphosis: maggot to puparium to fly**

Larvae are completely without legs: where do the adult legs arise?

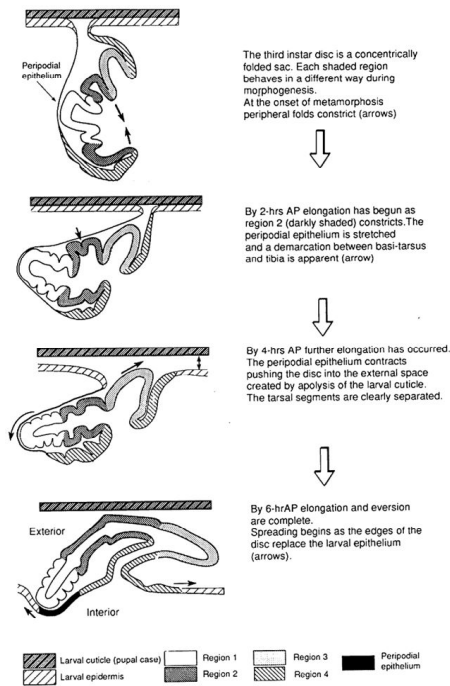
**Imaginal discs**

**Elongation and shaping of appendages**

Change in cell shape from cuboidal to squamous. Cells remain attached by zonula adherens at apical surface

**Eversion**

Contraction of the peripodial membrane by change in cell shape from squamous to cuboidal. Spreading and fusion of disc tissues



Fristrom and Fristrom, The metamorphic development of the adult epidermis. In: M. Bate and A. Martinez-Arias, Editors, The Development of Drosophila melanogaster vol. 2, Cold Spring Harbor Press, Cold Spring Harbor, NY (1993), pp. 843-897.)

### Common misconceptions about metamorphosis in holometabola

Many writers state that the larvae and adults are essentially two types of organism and thus able to utilise different habitats. Wigglesworth uses terms such as "a renewal of embryonic development", "essentially two organisms", "temporal polymorphism".

Reasons:

- Advanced flies such as *Drosophila* are most studied and they show the most extreme form of complete metamorphosis
- A high degree of histolysis and histogenesis occurs in the pupa: the pupal "soup" concept.
- The origin of a significant proportion of adult tissue from **imaginal discs**.
- Misconception that *all* larval structures are histolysed (histo=tissue: lysis=breakdown) and replaced by structures derived from imaginal discs.

In another example, Nijhout (in *Insect Hormones*) states:

"...the appendages of adult Holometabola are phylogenetically homologous to those of the Hemimetabola. But since adult appendages arise anew from imaginal disks, they are not developmentally homologous to either the larval appendages or those of the hemimetabola."

### Growth and Moulting

Many insects grow according to Dyar's rule: the ratio between a given dimension in one instar and the same dimension in the next is constant throughout all instars.

For example, head capsule width of caterpillars increases by a ratio of 1.4:1 at each moult

Growth is exponential therefore the last instar experiences most growth, measured as increase in weight or size.

Allometric growth (some parts of the body grow at different rates to others) and isometric growth

#### Cellular basis

Mitotic increase in cell numbers is the most common form of growth.

Endoreplication: cell increases in volume and the chromosomes replicate, but the cells do not divide (common in larval Diptera).

It is most common in cells that are metabolically very active, for example secretory cells such as the salivary glands.

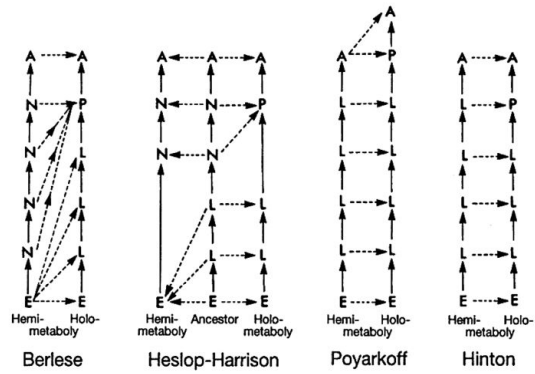
Gives rise to the polytene chromosomes, perhaps best known in the salivary glands. Because these cells have lost the ability to divide, they die at metamorphosis.

## Evolution

The main theories of the relationships between hemi- and holometaboly and on the origin of the holometabolon pupa (From Sehna et al., 1996).

E, egg  
L, larva  
N, nymph  
P, pupa  
A, adult.

A nymph is an immature instar with external wing rudiments in the theories of Berlese and Heslop-Harrison



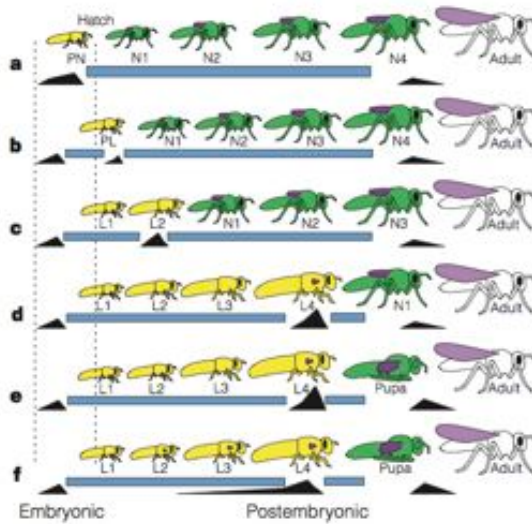
Solid arrows, ontogeny

Dashed arrows, changes leading to evolution of holometaboly from hemimetaboly (or to evolution of hemi- and holometaboly from the presumed ancestral situation in Heslop-Harrison's theory).

Sehna, Svacha and Zrzavy (1996) Evolution of insect metamorphosis. In: Metamorphosis: postembryonic reprogramming of gene expression in amphibian and insect cells / edited by Gilbert, Tata, Atkinson. pp. 3-58. (QL494.5 .M48)

## Evolution

Truman and Riddiford (1999) proposed that a stage retaining many embryonic features, called the pronymph, undertook more moults and became a true feeding stage, the larva. The nymphal stages were reduced in number and the last became the pupa. Matches the Berlese and Heslop-Harrison models. Supported by evidence from activity of Juvenile Hormone (black)

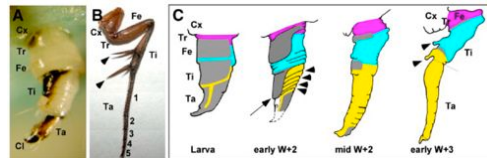


Wing-buds: purple, either as buds or imaginal discs

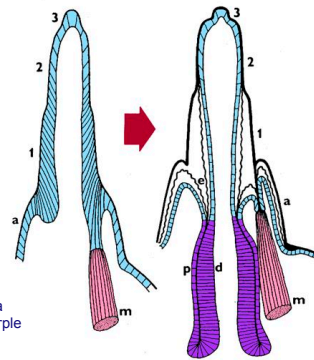
Truman JW and Riddiford LM (1999) The origins of insect metamorphosis. Nature 401:447-452.  
Erezylmaz DF (2006) Imperfect eggs and oviform nymphs: a history of ideas about the origins of insect metamorphosis. Integr Comp Biol 46:795-807.

Not so extreme metamorphosis: caterpillar to chrysalis to butterfly

Larvae (caterpillars) have short stubby legs and antennae. Where do the adult versions come from?



Larval epidermis: grey, imaginal tissue coloured



Caterpillar antenna  
Imaginal tissue purple

More extreme metamorphosis: maggot to puparium to fly

Larvae are completely without legs: where do the adult legs arise?