INSECTS · DEVELOPMENT

Metamorphosis

From silverfish that barely change to blister beetles that change shape four times: how insects remake their bodies, and the hormones that control it.

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> A caterpillar doesn't simply grow wings. Inside the chrysalis most of its body is broken down and rebuilt from groups of cells that have been waiting since before it hatched. Metamorphosis is one of the main reasons insects are so successful.

01 What is metamorphosis?

Metamorphosis is a profound change in form from one stage of an animal's life to the next. It is not only an insect story. It also happens in:

ARTHROPODS

Insects and crustaceans

The focus of this note is insects.

MARINE INVERTEBRATES

Molluscs, echinoderms, cnidarians

Starfish, sea urchins and sea cucumbers; corals, jellyfish and anemones.

CHORDATES

Sea squirts

Tunicates have a free-swimming larva that settles and transforms.

VERTEBRATES

Frogs and some fish

A tadpole becoming a frog is metamorphosis. Thyroid hormone plays a central role in both frog and flatfish metamorphosis.

02 How insect metamorphosis evolved

Molecular dating places the origin of insects in the Early Ordovician, about **479 million years ago**. The earliest insects developed much as silverfish do today: the young looked like small adults.

Insects with complete metamorphosis (the **Holometabola**) had split off by the **Late Carboniferous**, more than 300 million years ago. Their young look and live completely differently from the adults. This is widely thought to be a key to their success, because larvae and adults no longer compete for the same food and habitat.

~83%

COMPLETE METAMORPHOSIS

Holometabolous insects make up roughly 83% of all insect species (Labandeira 2011).

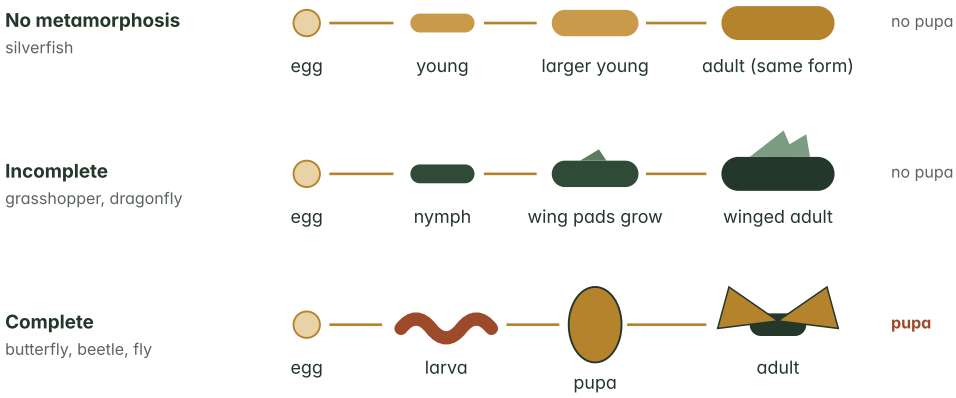
Most of the rest

INCOMPLETE METAMORPHOSIS

Grasshoppers, bugs, termites, dragonflies. Only a few primitive insects have no metamorphosis at all.

03 The types at a glance

BASIC TYPE	DETAILED TYPE	MEANING	EXAMPLES
None	Ametabolous	*a-* = without; *meta* = change; *morph* = form	Silverfish, bristletails
Incomplete	Paurometabolous (gradual)	*pauro-* = little	Cockroaches, grasshoppers, termites, mantids
	Hemimetabolous	*hemi-* = half	Dragonflies, damselflies, mayflies
Complete	Holometabolous	*holo-* = whole	Beetles, butterflies, moths, flies, mosquitoes, bees, wasps, caddisflies
	Hypermetabolous	*hyper-* = excess	Blister beetles, bee flies, mantis flies, small-headed flies, Eucharitidae wasps



Simplified life cycles. Only complete metamorphosis has a pupal stage.

04 No metamorphosis (ametabolous)

The young hatch looking like small adults, differing only in size and in having immature reproductive organs. They grow by moulting (**ecdysis**). Silverfish (*Lepisma*) and bristletails are examples. Springtails, close relatives of insects, also grow this way.

05 Incomplete metamorphosis

GRADUAL (PAUROMETABOLOUS): EGG → NYMPH → ADULT

Seen in cockroaches, grasshoppers, mantids and termites. Nymphs hatch looking broadly like the adult and live in the same place, eating the same food. They lack wings and mature reproductive organs. Wings start

as small **wing pads** on the second and third thoracic segments and get bigger with each moult. There is **no pupa**.

HEMIMETABOLOUS: EGG → NAIAD → ADULT

Dragonflies, damselflies and mayflies have aquatic young called **naiads**, which breathe with gills, while the adults live on land. When a dragonfly or damselfly naiad is ready, it climbs out of the water and the winged adult emerges. Mayflies first emerge as a winged **subimago**, which moults again within hours. Again, there is **no pupa**.

MAYFLY NAIAD

Abdominal gills

Gills along the abdomen, from simple plates to feathery tufts.

DRAGONFLY NAIAD

Rectal gills

Gills sit inside the rectum. Squirting water out also gives a burst of jet propulsion.

DAMSELFLY NAIAD

Caudal lamellae

Three leaf-like gills at the tail, used for breathing and swimming.

Naiads usually live far longer than the adults, and the adult's main job is breeding. Mayflies are the extreme case. Their life cycle can last from a few weeks to several years, mostly as an underwater nymph. Adults don't feed and rarely live longer than a few hours to a few days. Some dragonfly larvae spend up to five years underwater.

06 Complete metamorphosis (holometabolous)

Egg → larva → pupa → adult. The larva looks nothing like the adult, and there is always a pupal stage. Larvae feed hard and grow quickly, moulting several times before they pupate.

LARVAL TYPES

TYPE	DESCRIPTION	EXAMPLE
Apodous ("no feet")	Legless and worm-like; the head may be distinct or much reduced	Fly maggot; mosquito "wriggler"
Campodeiform	Elongated, flattened, with well-developed legs; active, often predators	Ladybird and ground beetle larvae
Scarabaeiform	C-shaped grub with a down-facing head and short legs; sluggish; often feeds on plants	White grubs (scarab beetle larvae)
Eruciform (polypod)	Caterpillar: distinct head with strong jaws, three pairs of jointed legs and fleshy, unjointed **prolegs** on the abdomen	Butterflies and moths

THE PUPA

The pupa doesn't feed and is usually still, sometimes inside a protective **cocoon**. During this stage the larval body is dismantled and the adult is built.

PUPA TYPE	WHAT IT LOOKS LIKE	EXAMPLES
Exarate (free)	Legs and other appendages are free, not stuck to the body	Most beetles, bees and wasps
Obtect	Appendages are glued against the body; can only wriggle a little	Butterfly **chrysalis**; mosquito pupa ("tumbler")

PUPA TYPE	WHAT IT LOOKS LIKE	EXAMPLES
Coarctate	An exarate pupa enclosed in the hardened last larval skin, a barrel-shaped **puparium**	Many flies, such as house flies

07 Hypermetamorphosis: changing shape more than once

In hypermetamorphic insects, at least one larval stage (usually the first) looks very different from the rest. The first stage is often a tiny, very mobile larva called a **planidium** (“wanderer”). Its only job is to find food, either by walking or by hitching a ride on another insect. After it moults, the larva becomes a sluggish feeding grub.

Not every dramatic change counts. Young swallowtail caterpillars look like bird droppings and later turn leaf-green, but they keep the same basic body plan, so they are ordinary holometabolous insects.

THE BLISTER BEETLE: FOUR PHASES

1. **Triungulin.** A mobile first-stage larva. Depending on the species it finds grasshopper egg pods by itself, or hitches a ride on a bee to reach its nest.
2. **First grub phase.** After feeding, it moults into a grub-like (scarabaeiform) larva and grows quickly up to about the fifth or sixth stage.
3. **Coarctate phase.** The larva becomes immobile and heavily armoured. Its muscles break down and its breathing slows so much that it can survive more than a year if necessary. Most species spend the winter or dry season like this.
4. **Second grub phase, then pupa and adult.** The muscles regrow, it moults into a grub again, and then it pupates.

Blister beetles contain **cantharidin**, a blistering chemical that is highly toxic to mammals if swallowed or absorbed through the skin. Horses have been poisoned by beetles baled into hay.

08 What happens inside the pupa?

Very early in development, an insect sets aside two kinds of cell:

FOR THE LARVA

Larval cells

They do the work during the larval stage. In fruit flies, larval skin cells are large, polyploid cells that don’t divide.

FOR THE ADULT

Imaginal cells

Small clusters of undifferentiated cells inside the larva. **Imaginal discs** grow during larval life; **histoblasts** stay dormant until metamorphosis.

In the pupa, larval tissues are broken down (**histolysis**). The imaginal cells divide and differentiate to build the adult’s wings, legs, mouthparts, muscles and organs (**histogenesis**). Not everything is rebuilt from scratch. When researchers CT-scanned living painted lady butterfly chrysalises (Lowe et al. 2013), most of the adult breathing system was already in place on the **first day** of the pupa. The midgut had reached its adult size and position by about day 7.

09 The hormones in charge

BRAIN

PTTH

Prothoracicotropic hormone (“brain hormone”) switches on the prothoracic glands.

PROTHORACIC GLANDS

Ecdysone

A **steroid** hormone that triggers each moult. Its active form is 20-hydroxyecdysone.

CORPORA ALLATA

Juvenile hormone

A **sesquiterpenoid**, not a steroid. While it is present, a moult produces another larva.

WHAT KIND OF MOULT? IT DEPENDS ON JUVENILE HORMONE



Schematic. Ecdysone triggers every moult. Juvenile hormone decides whether the result is another larva or a step towards the adult.

10 Waiting it out: diapause and quiescence

DIAPAUSE

A planned pause

A hormonally regulated shutdown of development and metabolism. It begins in anticipation of bad conditions and can’t simply be switched off the moment conditions improve. It occurs at a fixed life stage for each species.

QUIESCENCE

A quick reaction

A dormancy triggered directly by bad conditions and reversed quickly once they improve. It is less profound than diapause.

- **Obligate diapause** happens every generation regardless of conditions. It is most often found in **univoltine** insects (one generation a year).
- **Facultative diapause** starts only when conditions turn bad. It is most common in insects with two or more generations a year (**multivoltine**).

RECORD HOLDER

Stored larvae of the yucca moth *Prodoxus y-inversus* produced adult moths after **30 years in diapause** (Powell 2001), the longest insect dormancy on record.

WITH A CATERPILLAR OR CHRYSALIS — HOW TO SAY IT

“Inside that chrysalis the caterpillar isn’t just growing wings. Much of its body is being taken apart and rebuilt. Groups of cells it has carried since it was an embryo, called imaginal discs, build the butterfly. The switch is a hormone. While juvenile hormone is present the caterpillar keeps moulting into a bigger caterpillar. When the hormone drops away, the next moult makes a pupa, and then an adult. About four out of five insect species grow up this way.”

11 Key terms

Ecdysis	Moulting: shedding the old exoskeleton.
Instar	The stage between two moults.
Nymph / naiad	Young of insects with incomplete metamorphosis; a naiad is an aquatic nymph.
Imago	The adult insect.
Imaginal discs	Clusters of cells in the larva that build adult structures.
Puparium	The hardened last larval skin that encloses a fly pupa.
Planidium / triungulin	A mobile first-stage larva in hypermetamorphosis; a triungulin is the blister-beetle version.
Univoltine / multivoltine	One generation a year / several generations a year.

In summary

- Three basic routes: **none** (silverfish), **incomplete** (no pupa) and **complete** (with a pupa).
- About **83%** of insect species have complete metamorphosis.
- In the pupa, larval tissues are broken down and **imaginal discs** build the adult.
- **Ecdysone** (a steroid) triggers moults. **Juvenile hormone** (a sesquiterpenoid) decides larva or adult.
- Hypermetamorphic insects such as blister beetles change shape more than once.

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