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Chapter 2

Structure and Function

Insects display an unparalleled evolutionary success in terms of their diversity of species. Like all arthropods, their forms and functions are derived by a body of repetitive segments, jointed appendages, and hardened exoskeleton. This deceptively simple body plan masks a daunting complexity of tissues and organ systems that yield beautiful shapes, hallucinogenic colors, spectacular structures, and marvelous functions. While the functions performed by insects—feeding, digestion, locomotion, reproduction, respiration, and circulation—are familiar to all life, the ways these are accomplished are often curious and quite unlike vertebrates. What is perhaps more remarkable are the myriad examples of convergent evolution—unrelated lineages developing similar features. From single cells to whole organism, the wild diversity of insect form is truly unparalleled.

← Insects can have bizarre body modifications. Flies in the family Celyphidae have converged on a beetle-like appearance because of a hardened shell covering the abdomen and wings.

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Insect Body Plan

Due to the constraint of having an external skeleton, the insect body is composed of a series of repeated units or segments called metameres. Although each metamere can potentially be unique and vary from another, they have become organized into three main functional groups, or tagmata: the head, thorax, and abdomen.

The Generalized Form

Each tagma performs a different task and, for the most part, in each insect is formed from the same number of segments. The head is composed of six segments, the thorax of three (this becomes modified in some Hymenoptera), and the abdomen of eleven (although the eleventh is lost in most insects that have complete metamorphosis). Metameres often bear a pair of appendages and fuse within tagma for basic functions, such as the fused segments in the head bearing mouthparts for feeding, the fused segments in the thorax bearing legs and wings for walking and flying, and the apical segments in the abdomen bearing modified genital appendages for reproduction and egg laying. Great versatility is afforded because tagmata are comprised of several segments. Consequently, aside from participating in these basic functions, each segment may derive additional features, yielding astounding variation in both structure and function.

Hox Genes

How does an organism made up of repeated units diversify to such fantastic forms? The answer lies partially in the role homeobox (Hox) genes play in the development of the segments. These genes are master regulators, specifying the identity of a segment and its appendages. Ancestrally there are 10 Hox genes organized into a single complex in which the chromosomal order of the genes reflects their spatial arrangement along the length of the body. However, the organization of Hox genes has been disrupted in several insect groups. For example, they are organized into two clusters in the fruit fly *Drosophila melanogaster*, namely the Antennapedia and Bithorax complexes.

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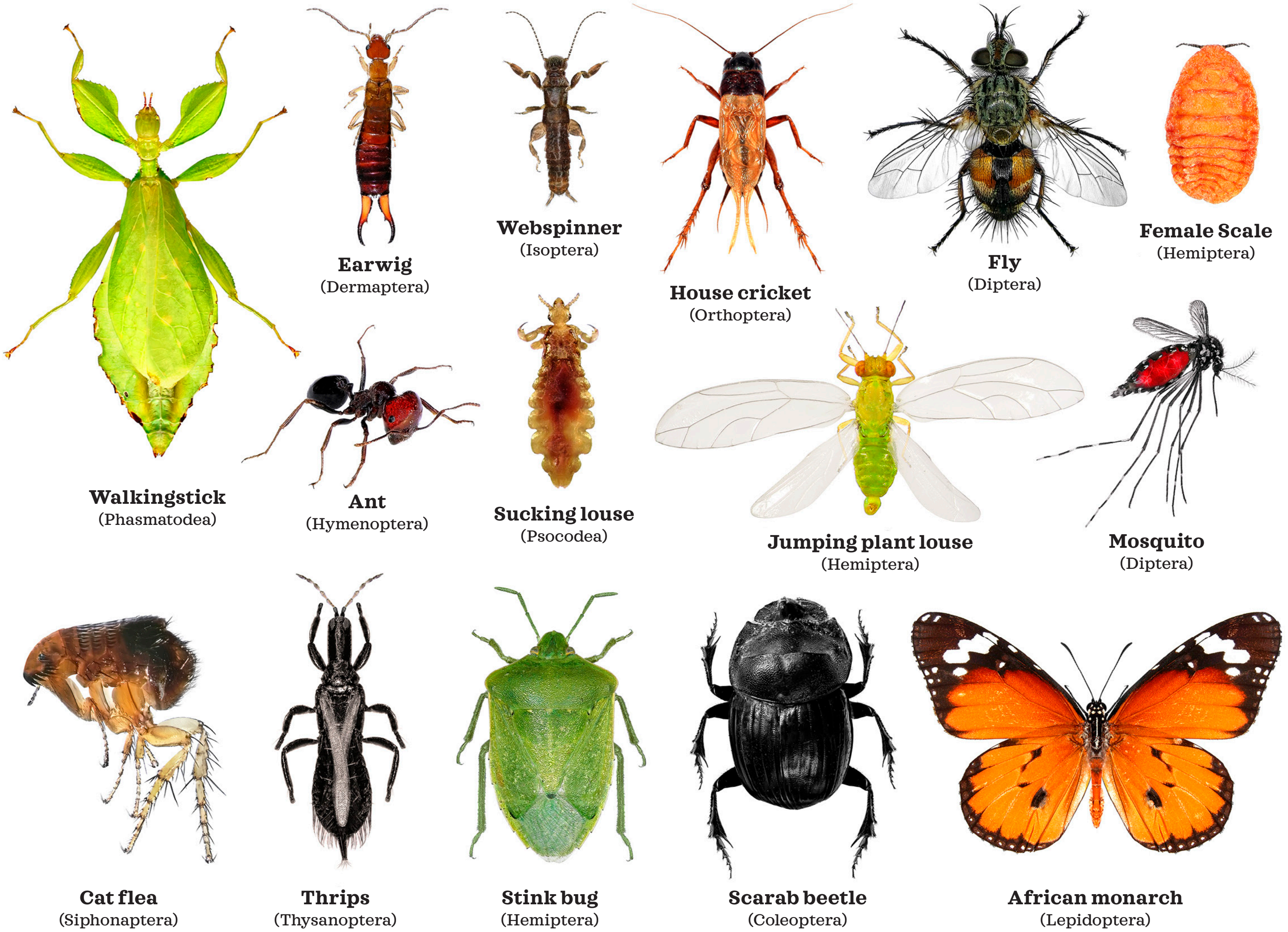

Walkingstick (Phasmatodea)

Earwig (Dermaptera)

Webspinner (Isoptera)

House cricket (Orthoptera)

Fly (Diptera)

Female Scale (Hemiptera)

Ant (Hymenoptera)

Sucking louse (Psocodea)

Jumping plant louse (Hemiptera)

Mosquito (Diptera)

Cat flea (Siphonaptera)

Thrips (Thysanoptera)

Stink bug (Hemiptera)

Scarab beetle (Coleoptera)

African monarch (Lepidoptera)

↑ The insect body plan is fairly conserved in having three body regions, yet a bewildering diversity of forms have evolved.

The remainder of the answer lies in the downstream targets that Hox genes regulate, various appendage patterning genes, and other signaling proteins that interact in complex networks. These signaling pathways are genetic cascades that pattern the complex features of the insect body. Changes that occur in any step of the pathway or network lead to the staggering arrays of colors, textures, and forms that are visible in the insect radiation.

→ Although the fruit fly, *Drosophila melanogaster*, is itself fairly derived from the basic insect body plan, research on this species has led profound insight into the genetics of insect and animal development alike.

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↑→ Both silverfish and cockroaches have fairly generalized and flattened bodies modified for scurrying quickly across the ground and fitting into tight spaces.

Modifications of Form

While insects share a basic body plan of segmented regions with appendages, the segments and their associated appendages are modified in ways that reflect evolution as well as function. Because they descend from a common ancestor, silverfish (Zygentoma) resemble one another more than they do insects in other orders, as is the case for cockroaches (Blattodea). Despite being unrelated orders, silverfish and cockroaches actually have somewhat similar body types (flattened). Primitive wood wasps and parasitoid wasps are more closely related (as they both belong to the Hymenoptera), yet their bodies are quite different. While segments and body features change substantially in such cases, it is not too challenging to identify features shared due to common ancestry among the groups.

←↑ Wood wasps have stout bodies for ovipositing into plants, whereas parasitoid wasps have slender, flexible bodies for ovipositing into mostly other insects.

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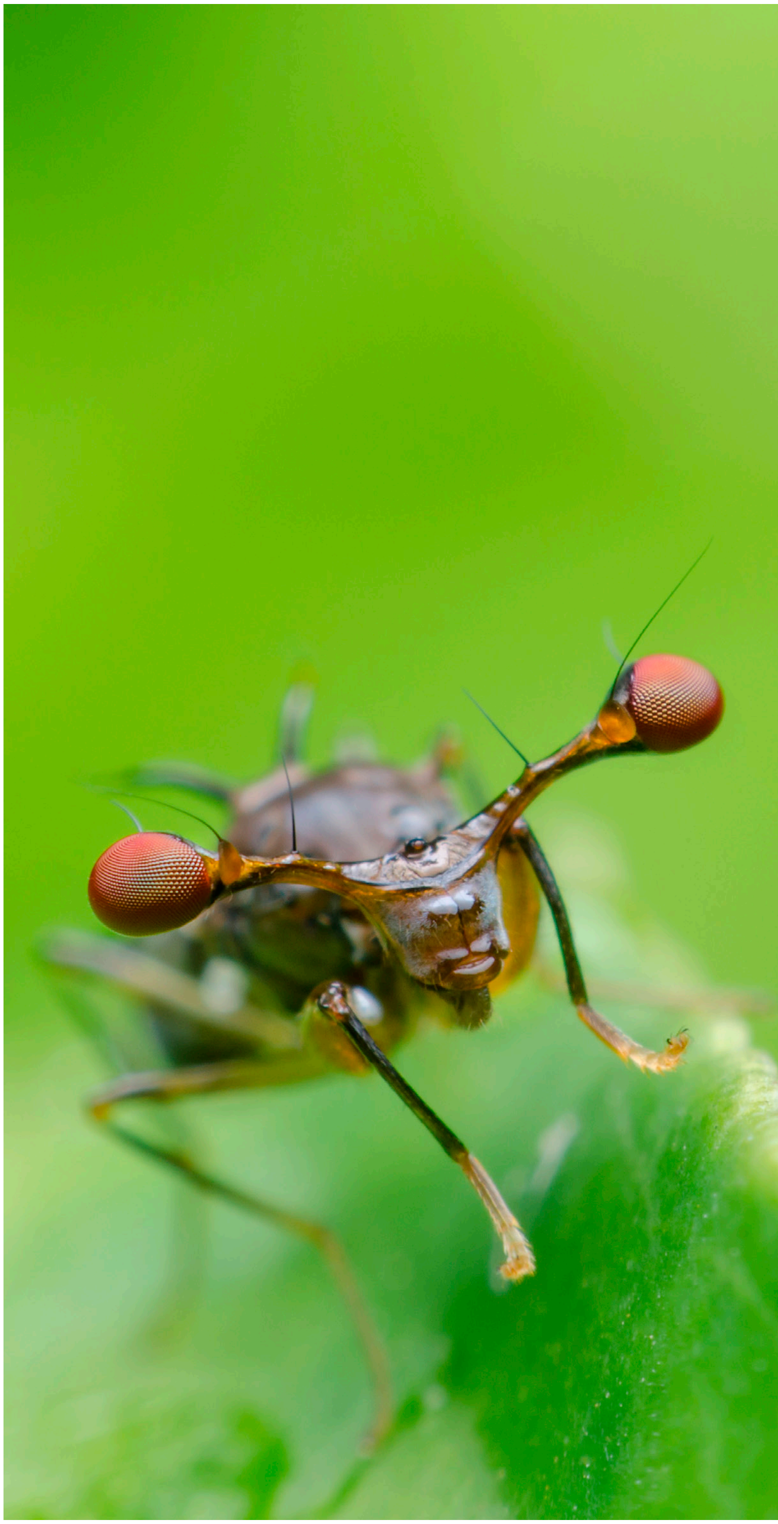
Extremes

In other cases, modifications can become so extreme that recognizing the shared body plan becomes difficult. Several evolutionary pressures may produce wildly derived forms, including sexual selection, mimicry, and modes of life history. Sexual selection can produce exaggerated phenotypes, such as modified appendages, horns, and color patterns. Mimicry produces surprising color forms and striking body-plan modifications in unrelated groups. Insect inquilines (species living with ants and termites) often have strangely adapted features for avoiding detection and feeding in ant and termite colonies, perhaps the best example involving host mimicry syndromes in rove beetles. Plant mimicry is also common, in which parts of the body come to resemble colors, textures, and shapes of stems, flowers, bark, and green or dead leaves. Lastly, the same life history can produce the same bizarre body forms but in unrelated taxa, such as enlarged pretarsal claws, reduced head appendages, loss of wings, and stiff bristles along the body, a phenotypic syndrome that develops repeatedly among insects that are ectoparasites of birds and mammals.



← The evolutionary modification of insect body shape and color has led to stunning forms of crypsis and plant mimicry, as demonstrated by this well-camouflaged katydid.

↑ Sexual selection in insects has led to bizarre forms, such as in stalk-eyed flies. While females may have short eye stalks, those of males in some species can reach absurd proportions, about as long as their bodies.

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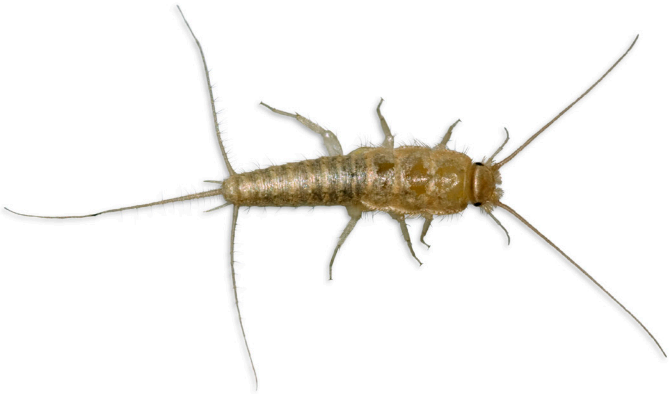
Developmental Changes in Form

The development of an insect from egg to adult proceeds in several steps, but interestingly these steps are not equivalent in all insect groups.

Ametabolous Orders

The most primitive orders, the bristletails (Archaeognatha) and silverfish (Zygentoma), are ametabolous—there is no metamorphosis. The immature stage (nymph) hatches from the egg as a miniature version of the adult. With the exception of possessing functional genitalia, the immature stages are all similar and experience minimal tissue change, only increasing in size through successive molts.



↑→ Ametabolous insects, including the most basal orders Archaeognatha and Zygentoma, undergo few developmental changes from immature stages to adult. As highlighted by the tracheal system in the immature (right) and adult (far right) silverfish shown here, there are essentially no changes in its architecture from immature to adult.

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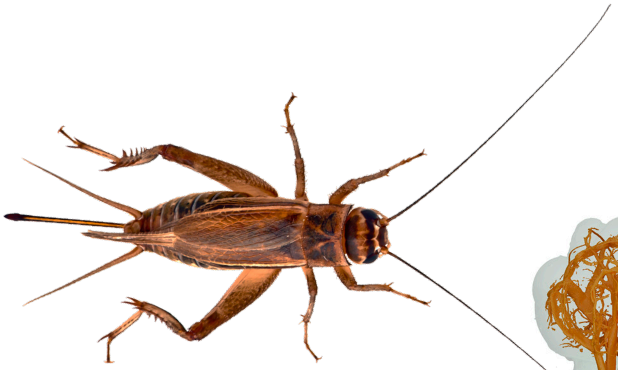
Hemimetabolous Orders

Within the Pterygota (winged insects) the hemimetabolous orders undergo incomplete metamorphosis. This includes all orders between the ametabolous groups and Hymenoptera. In these groups, immature stages bear some resemblance to the adult but lack functional genitalia and wings. Adult features grow incrementally through successive molts. Developing wings occur as immobile wing pads and parts of terminalia, such as ovipositors, begin as short projections that increase in length. Aside from the slow growth of such adult features, little tissue change occurs between stages.



↑→ Hemimetabolous insects, including many orders such as Odonata, Blattodea, and Orthoptera, undergo a range of developmental changes from immature stages to adult, although the immature (nymphal) stages typically resemble the adult. Most changes seen in these insects involve appendage growth (for example, in the wings, legs, and genitalia). As highlighted by the tracheal system in the house cricket shown here, the immature (right) is similar but shows some changes to that of the adult (far right), particularly in the thorax where the wings develop incrementally in the immature stages.

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Holometabolous Orders

Insects that undergo complete metamorphosis—the holometabolous orders—include the remaining pterygotes, from Hymenoptera to Lepidoptera. An insect hatches as a larva, an immature stage distinct from the adult and bearing no resemblance. Transformation to the adult stage proceeds after several larval instars into a unique transitional stage, the pupa. Pupae range in degrees of motility but all have in common a remarkable and often rapid progression of tissue remodeling and growth in which the larval epidermis, including many other tissues and organs, transition to, and are replaced by, adult tissues. The amount of tissue turnover depends on the insect lineage, but the precursor cells of these imaginal tissues (in small sacs called imaginal discs, for some groups) were all determined early in the embryo.

The regulation and evolution of such different developmental modes is covered in more detail in Chapter 4, but the vivid contrasts in tissue remodeling that occur in these three developmental categories need to be highlighted. Through visualization of the respiratory system in different developmental stages, we can begin to appreciate the dramatic variation of changes in form that take place in the various insect lineages.

↖ Following pupation, the adult holometabolous insect that emerges is often strikingly different from its former immature stages. Immense tissue remodeling, involving both cell growth and death, is responsible for this remarkable transformation.

← In contrast to ametabolous and most groups of hemimetabolous insects, in which the immature stages resemble the adult, the immature stages of holometabolous insects, such as this butterfly larva, bear little resemblance to their adult stage.

→ Holometabolous insects, including Diptera, Lepidoptera, Coleoptera, and Hymenoptera, undergo drastic developmental changes during metamorphosis from immature (larval) stages to adult. For example, the tracheal system of this weevil larva (top) significantly contrasts to that of the adult (bottom), while its transitional stage, the pupa (middle), shows some changes distinct from the larva. Nearly all regions of the head, body, and abdomen, show striking changes in tracheal architecture from larva to adult.

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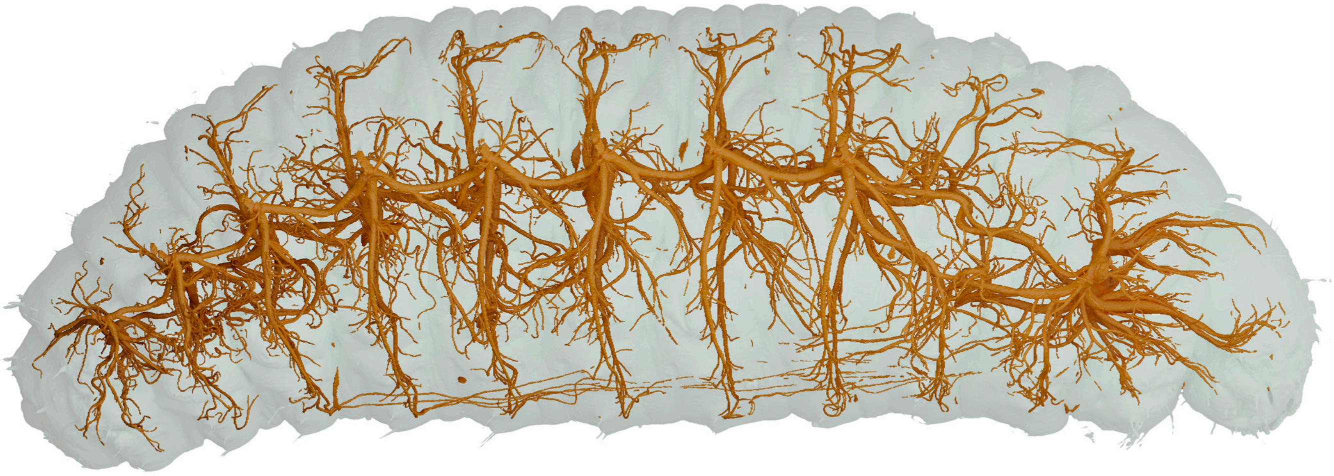

Larva

Pupa

Adult

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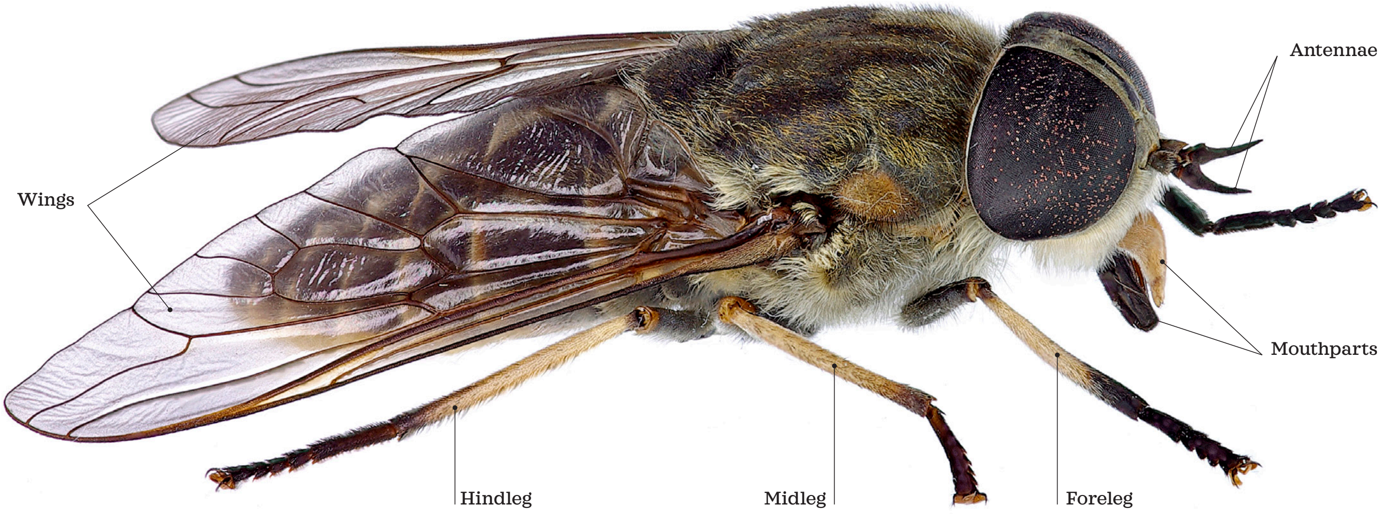
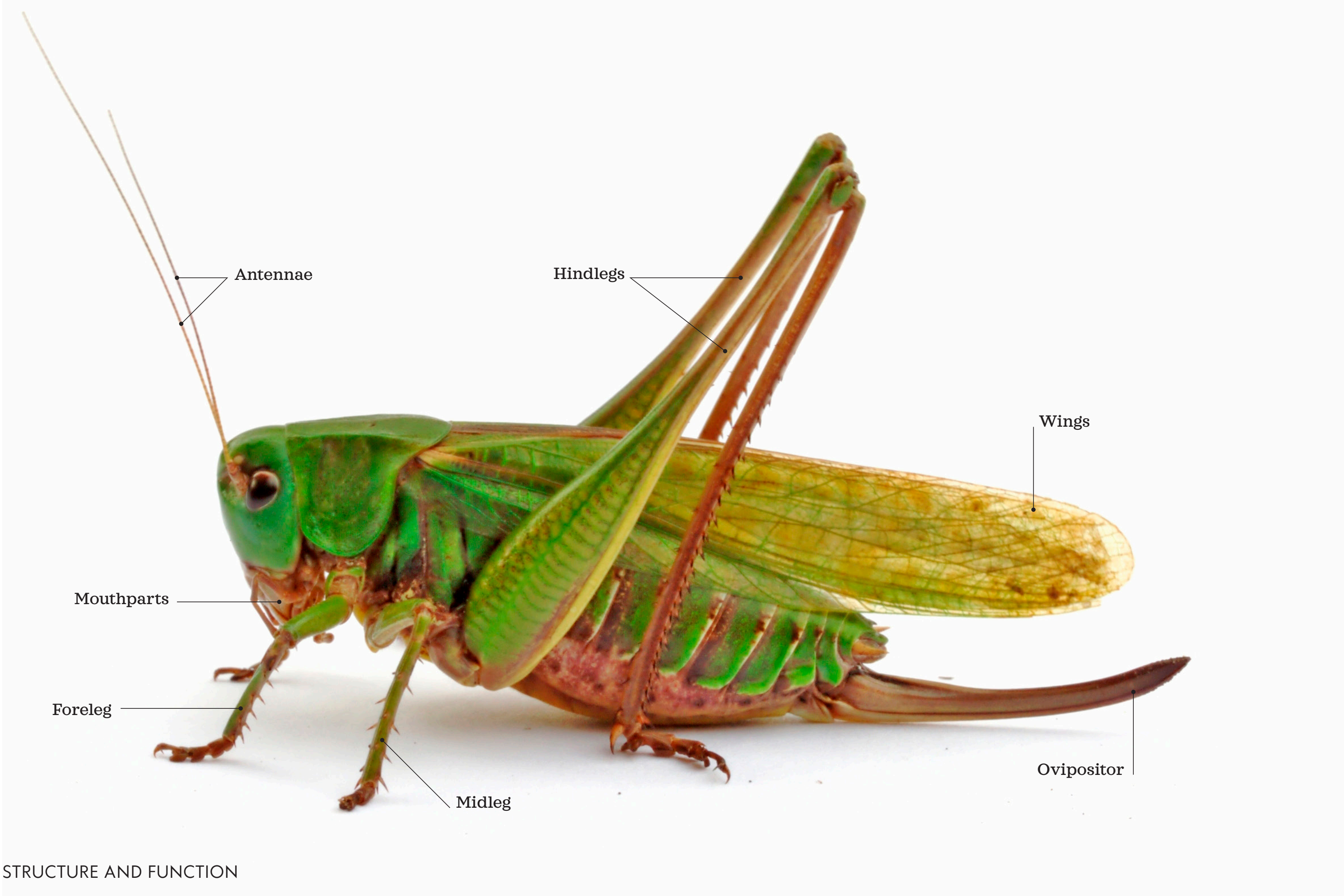


Appendages

We tend to think of appendages as those that allow for common movements, such as walking, running, swimming, and, in most cases, flying. Indeed, the appendages of insects and other arthropods perform these, and many other functions, through a broad range of forms. Ancestrally in hexapods, these appendages were largely composed of repetitive segments. Across orders and families, the appendages change in quality by modification of the existing segments and the number of segments. Insect appendage types include those on the head (antennae and mouthparts), the thorax (wings and legs), and abdomen (terminalia and sometimes leg remnants). In many cases, appendages exhibit specialized forms that are suggestive of function, examples of which follow.



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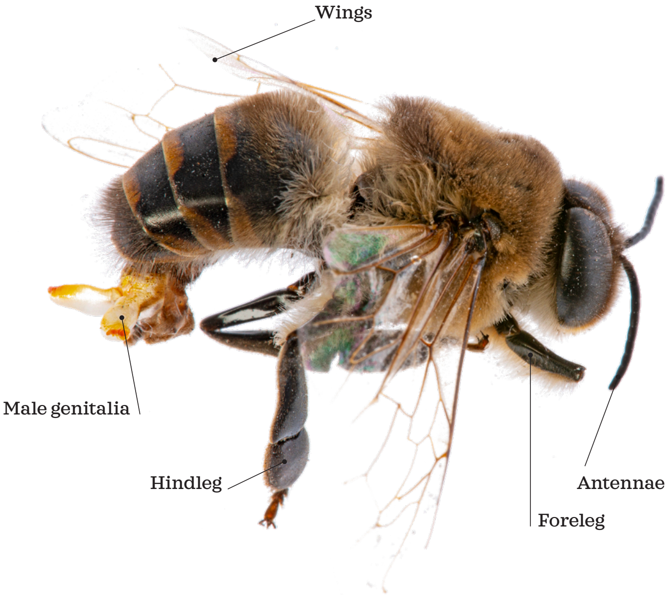
On the head: Antennae may be short and spindly as in Hemiptera and brachyceran flies; or long, bead- or threadlike, to sawlike and highly branched and strongly sexually dimorphic as in many Lepidoptera and some beetles and parasitoid wasps. Mouthparts can vary from the more common and robust chewing type to those of mopping, piercing, and delicate, elongated sucking forms as in Hemiptera, various dipteran groups, and Lepidoptera. Both antennae and mouthparts are discussed in greater detail on pages 54–57.

On the thorax: The three ventral, or lower, appendages (legs) are mainly used for walking/running, swimming, digging, or predatory/other behavioral functions and are often adapted for such purposes. The dorsal, or upper, thoracic appendages are the wings. Although their primary function is for flight, they have been reduced and modified in numerous ways, often relating to differences in life histories. See page 58 for a wider discussion of ventral and dorsal appendages.

On the abdomen: The terminal segments have appendages involved in reproduction (the terminalia), including structures used for transfer of sperm in the male and eggs in the female, termed genitalia. Forms of terminalia can vary wildly and possess an array of extensions, spines, and cuticular projections. While the majority of adult insects do not have abdominal appendages aside from the terminalia, the most basal insect orders (Archaeognatha and Zygentoma) possess ventral appendage remnants in the form of styli and eversible sacs/vesicles. Abdominal appendages are discussed in greater on page 59.

Gills

While the general appendage descriptions hold true to some degree for immature and adult stages of ametabolous and hemimetabolous insects, there are exceptions in groups of the latter, such as Odonata and Ephemeroptera. In these groups immatures have developed modified appendages in the form of gills for aquatic respiration.



↑ Appendages are wildly different among orders of insects. The antennae, mouthparts, wings, and legs, and even the genitalia exhibit bewildering differences.

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The Convergence of Horn-Like Appendages

Enlarged, horn-like mandibles are well-known features in some groups of insects, most notably in male stag beetles (Lucanidae) and the dobsonfly family (Corydalidae). These enormous mandibles are a sexually dimorphic pair of appendages that males use for combat. Interestingly a very similar pair of appendages has converged on the mandible form in a different order of insects but at the opposite end of the body, the abdominal apex. Earwigs (Dermaptera) have an enlarged pair of modified cerci, which are filamentous and multisegmented in many insects, but in earwigs they resemble various types of mandibular horns in lucanids, even bearing different-sized teeth. Extinct earwigs retained elongated, filamentous, and multisegmented cerci, but extant ones only have these stout cerci, modified into forceps and used for prey capture, defense, and mating. It would not be too surprising if similar developmental modes are responsible for the formation of these two similar yet very different forms of appendicular horns.

Stag beetle

Earwig

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Appendage-Like Extensions

There are many kinds of cuticular extensions, projections, and expansions, so it can be confusing to distinguish these from true appendages. One key difference is that appendages are segmented and/or jointed, and moveable. Just the way appendages can be extremely modified, the same is true for appendage-like features. Non-appendicular horns and large outgrowths without any articulations can form on any part of the body. These outgrowths not only take the form of giant horns, but may also appear as tusks, antlers, eye stalks, expanded winglike extensions, and thoracic and abdominal paranotal lobes. The latter are striking in many recent insect forms and could be very elaborate in extinct lineages such as the beaked, Palaeodictyopterida. These so-called winglets may be serially homologous to the two pairs of functional thoracic wings but were not jointed or movable and therefore cannot be considered true appendages. Appendage-like projections can also form from true appendages themselves, such as from wings and legs. While not segmented or jointed, it is fascinating that these appendage-like extensions likely form by co-opting or integrating parts of appendage-patterning genetic pathways. It has been demonstrated that this is true in a few of the above examples and it likely is true to some degree in the others.

↑ Although not true, jointed appendages, the spines and horns present on many beetles, such as this leaf-rolling weevil, and other insects share some developmental aspects to appendages.

→ Spines can be present on nearly every segment and body region, such as on the thoracic segments in this ant.

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↑ The heads of flies often bear robust bristles and large compound eyes, but the appendages can differ drastically. Some flies have long, filamentous antennae, while others very short and knob-like. Mouthparts can be modified for piercing various tissues and sucking, others for essentially mopping liquids, as in this fruit fly.

↑↑ Insect heads, reminiscent of those of their crustacean relatives, are like Swiss Army knife toolkits, equipped with several sets of appendages modified for diverse functions. The large scissor-like mandibles of this tiger beetle head illustrate a few features typical of active predators.

The Insect Head

The head is the anterior-most tagma of all insects. It is formed of six segments, four of these bearing appendages, and includes: the ocular, antennal, intercalary, mandibular, maxillary, and labial segments. The ocular segment bears the compound eyes and up to three simple eyes (ocelli), although neither of these are appendages. The eyes and antennae serve sensory functions and may have fantastic modifications to serve such purposes. Compound eyes are present in immature and adult stages of ametabolous and hemimetabolous insects and the adult stage of holometabolous insects (larvae bear another form of simple eye, stemmata). One exception to this is in scorpionflies, in which the larvae possess compound eyes that are more representative of larval eyes of primitive holometabolans. While ocelli generally have poor visual acuity, sensing mostly differences in light intensity, larval eyes are quite different and vary in their visual acuity.

Altogether, changes in individual head segments produce extraordinary variation in head shape and structure. Even among unrelated lineages that appear to have similar head shapes, the same shape or form can be produced in nearly unlimited ways because any of the six segments can change.

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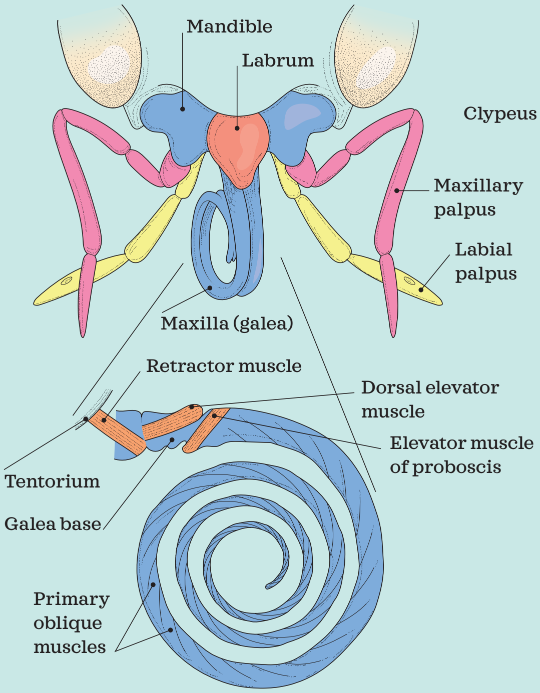
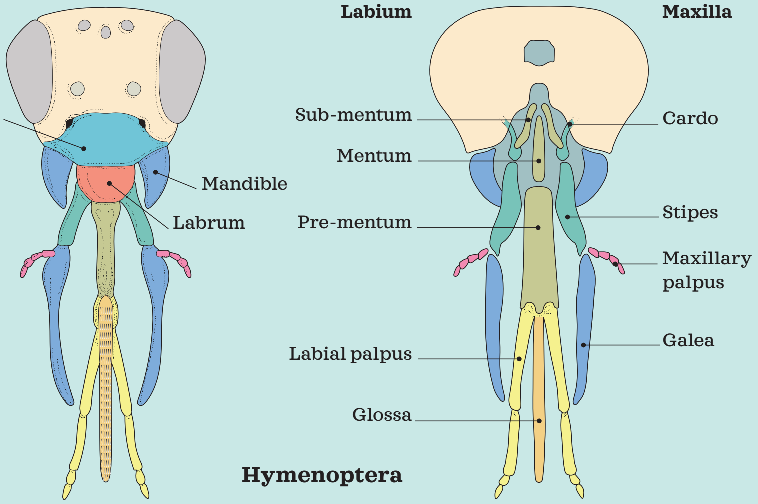
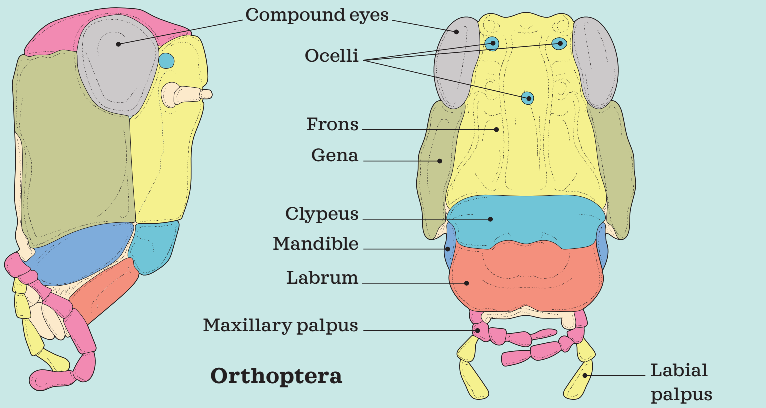
Insect Heads and Mouthparts



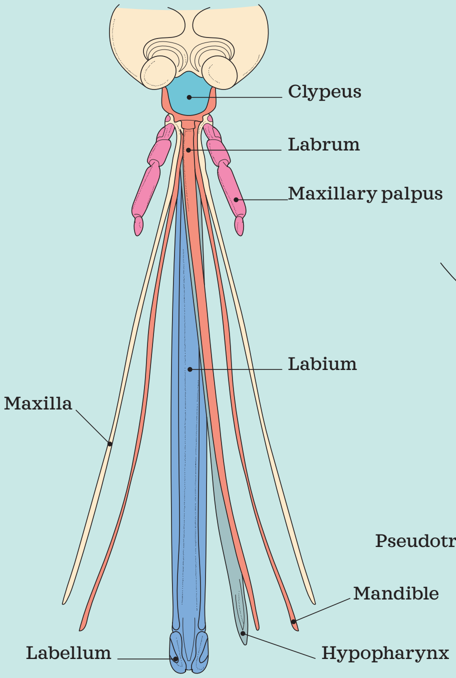
Lepidoptera



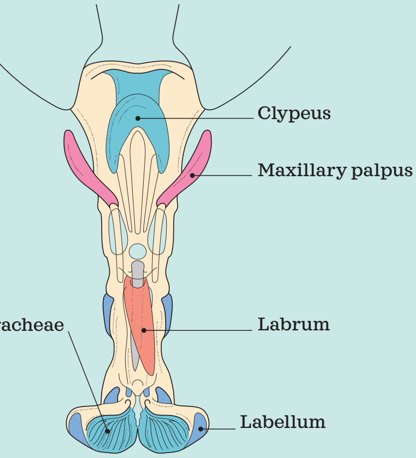
Hymenoptera



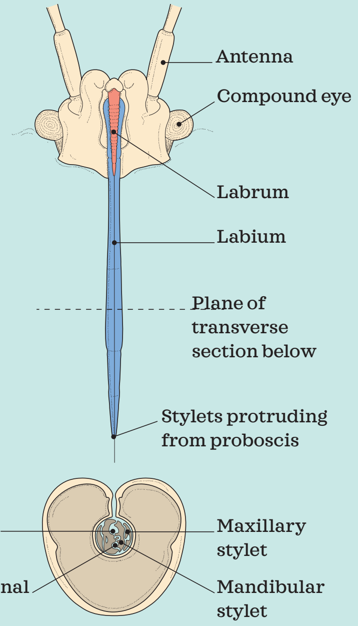
Orthoptera



Diptera (mosquito)



Diptera (fly)



Hemiptera

Variation in insect head shape and structure is vast such that it can be quite staggering to know they are produced from a homologous set of six segments and their associated appendages (when present).

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Antennae

This pair of appendages ranges from being barely noticeable to several times the length of the body. They may be simple and filamentous or highly branched and feathery, the differences sometimes being attributable to sexual dimorphism. Antennae also have various sorts of sensilla (sense organs) to detect things from surface and airborne pheromones and other molecules to ones in food, but also humidity and vibrational movement.

Mouthparts

The mandibles, maxillae, and labium may serve multiple functions, including sensory, chewing and ingestion of food, application of silk, grooming, fighting and defense, and carrying objects to organize and build domiciles, cocoons, and pupation chambers. Related to such adaptations, the mouthparts have evolved myriad forms, but as with so many hexapod features, convergence is a major theme. For example, while several groups of insects use elongated, tubelike mouthparts to ingest fluids (such as water, nectar, and blood), many of these forms have evolved independently and their unique structural variations reveal such differences in evolutionary history.

↑↑↑ Longhorn beetles have antennae that often surpass the length of the body. Such long antennae are common in nocturnal insects, those that are active primarily at night.

↑↑ The antennae of ground beetles in the subfamily Paussinae have expanded segments packed with glands, the secretions of which allow the beetles to interact with ants.

↖ Adult antlions, within the order Neuroptera, have antennae that often are held erect and can have a small bulb at their apices.

↑ In Lepidoptera, although mandibles are still present in a few of the most basal families, the vast majority possess an elongated proboscis formed by just a subsection of the maxillary appendage.

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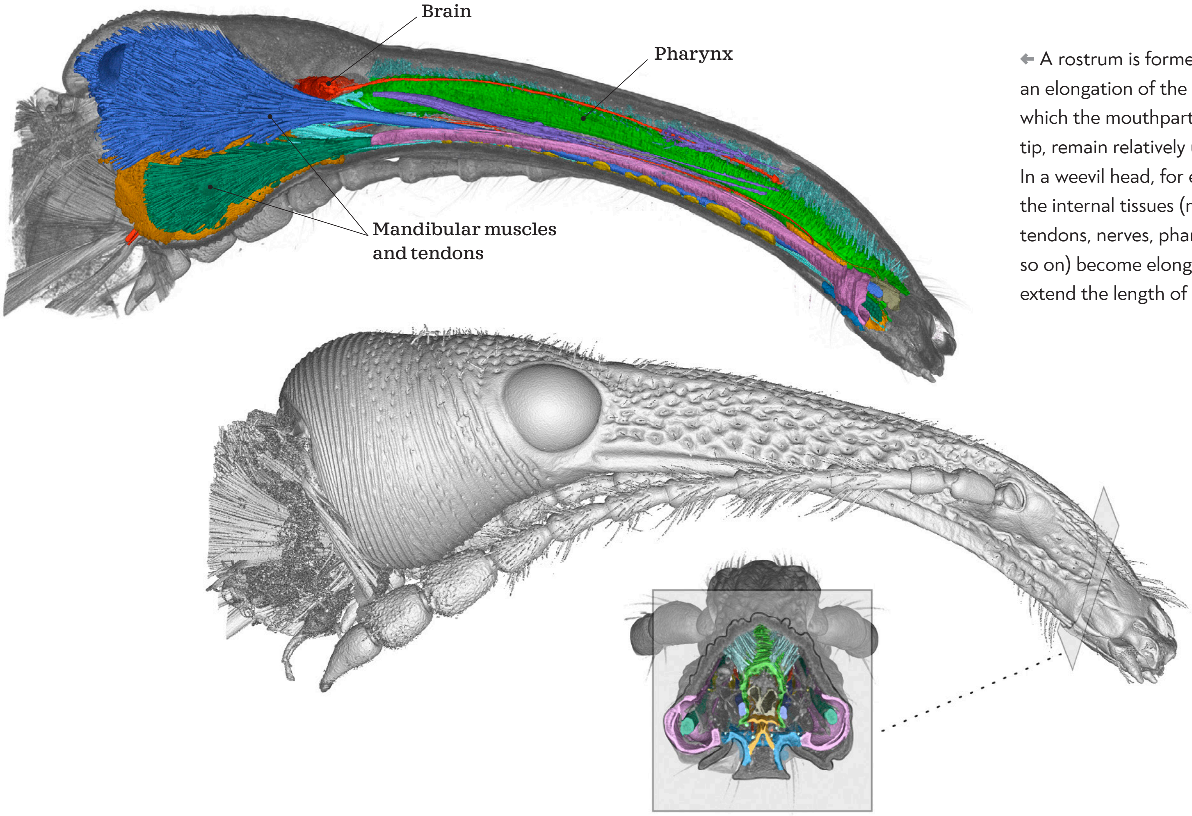
Insect Rostra: The Convergence of Snouts

Among the many fascinating anatomical features in insects that have evolved convergently is something best-known in the weevils—the snout, or rostrum—an elongation of the head where the mouthparts, typically unmodified, are situated at its apex. The rostrum in weevils (superfamily Curculionoidea) is formed by a number of head segments and can be several times longer than the body, with tiny chewing mouthparts at the tip, which can be nearly absent. They can project from the head at various angles and be adorned with all sorts of projections, setae, and scales.

Although weevils have capitalized the most on rostrum form, they are not the only insects to do so. Other beetle lineages, both extant and extinct, have members with rostra, including the families Salpingidae, Staphylinidae, Laemophloeidae, and Lycidae. These rostra are all present in the adult stage; however, one taxon possesses a rostrum in the larva—*Metaxyphloeus* (Laemophloeidae). Furthermore, other insects aside from beetles have evolved rostrate taxa, including scorpionflies (Mecoptera, see page 62) and a unique genus of sweat bees, *Chlerogella*. While all of these rostrate insect groups look superficially similar, they independently evolved such structures by modifying the head segments in different ways and for various functions, most related to feeding.

Nut weevil



← A rostrum is formed by an elongation of the head in which the mouthparts, at the tip, remain relatively unmodified. In a weevil head, for example, the internal tissues (muscles, tendons, nerves, pharynx, and so on) become elongated and extend the length of the rostrum.

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↑ In flies, hindwings have become reduced to small knob-like structures called halteres. Many large bristles, all mechanoreceptors, also project from the fly thorax.

The Thorax

The thorax—a powerhouse for locomotion—is a tagma composed of three segments. These subdivisions are easily discernable in primitive insects such as silverfish (Zygentoma), but become more obscure and modified in the winged insects, the Pterygota. The thorax can become so modified in form that sometimes the best way to delineate its segments is by examining the attachment of its appendages, the wings and legs.

The additional modification in the thorax of winged insects seems due to how the wings evolved and the formation of the pleuron or the side wall of the thorax. These two events likely occurred together, as at least the base of the wing (the joint or hinge region) and the pleuron appear to be formed from an ancestral proximal leg segment. This hardened pleuron, between the dorsal tergum and ventral sternum, paved the way for other thoracic modifications. For example, in beetles the pleuron of the first thoracic segment (prothorax) becomes largely fused with the sternum and tergum to form a fortified segment. In a subset of Hymenoptera (Apocrita), while the thorax appears relatively normal, its last segment is actually the first abdominal segment that is fused to the metathorax (the third thoracic segment).

Aside from changes in shape and structure, additional thoracic modifications can take the form of thoracic hearing organs (tympana), as in some moths, or sound-producing stridulatory or amplificatory structures, as in some extinct and extant grasshoppers and locusts.

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The Abdomen

Despite being a rather basic tagma with repetitive segments, the abdomen bears much of the visceral organ volume and is crucial to digestion, excretion, and reproduction. Excepting the basal two insect orders Archaeognatha and Zygentoma, all other orders generally lack appendages along the adult abdominal segments preceding the genitalia. Surprisingly, novel appendage-derived features occur in the adults of a few other insects, such as in Cixiidae planthoppers and Sepsidae flies. Abdominal appendages are also present in the immature stages of many orders, such as the abdominal gills of mayflies (Ephemeroptera), lacewings (Neuroptera), dobsonflies (Megaloptera), and some beetles (Coleoptera), as well as the abdominal appendages (prolegs) of Lepidoptera, scorpionflies (Mecoptera), and some Hymenoptera.

↖ Silverfish, along with jumping bristletails, are the most basal two insect orders and the only to bear remnants of abdominal appendages. Various types of abdominal appendages have subsequently evolved in many insect groups.

← Appendage-like feet have evolved on the abdomen of immature stages of various insects, such as in Lepidoptera, Mecoptera, and some Hymenoptera. Other abdominal extensions may also be present, such as the whiplike abdominal filaments in this puss moth larva, *Cerura vinula*.

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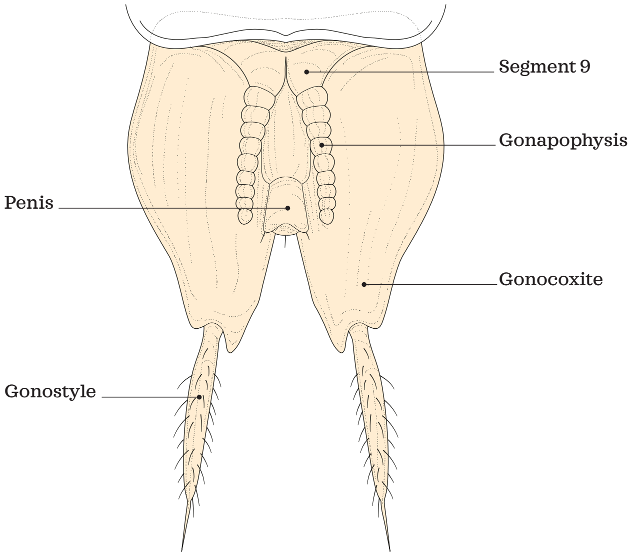
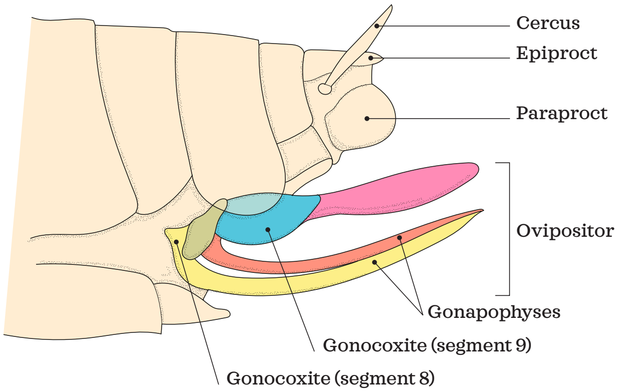
Insect Genitalia

In all insects, the abdominal segments bearing the genitals, namely eight and nine, have ventral appendages that have been modified for copulation and oviposition. These structures are fairly simple in the apterygotes and become heavily modified in pterygote orders to the extent they are unrecognizable as appendages. Generally, the female appendages are present in the form of two pairs that fit together as an egg-laying structure enclosing the central egg canal, or as a single pair in which the second pair is reduced or lost. The male appendages generally form a clasping device for maneuvering and holding onto the female for sperm transfer. Again, excepting the apterygotes, copulation is largely a mechanical process that occurs via a lock-and-key mechanism. Accordingly, structural changes in the copulatory organs of one sex of a species usually reflect analogous changes in the other. That said, the extraordinary complexity of male genitalia in most insects leads us to wonder how closely these copulatory features fit together and in what fashion. This complexity is routinely used by entomologists to separate and define closely related species of insects.



Male genitalia



Female genitalia

➜ Pterygote insect orders show an amazing diversity of genitalic forms. For example, scorpionfly males bear enlarged, bulbous genitalia (resembling a scorpion sting) that are fit with clasping devices to maneuver the female copulatory organs.

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Needles for Appendages: The Convergence of Stylets

The modification of insect appendages into stylet-like structures has not only occurred independently numerous times, it has done so on both the head and the abdomen. Stylet-like mouthparts have evolved in the adults of Thysanoptera, Hemiptera, Psocodea, Lepidoptera, Mecoptera (extinct families), Siphonaptera (extant and extinct families), and Diptera, as well as the extinct superorder Palaeodictyopterida. They are used to draw up liquid foods by piercing a variety of plant and animal tissues, including those of other insects.

Mouthparts: Stylets can be produced from any of the mouthpart appendages (labium, maxilla, mandible, or labrum) and collectively may be referred to as a proboscis or haustellum (a sucking proboscis). Some groups possess relatively rigid stylets, such as in many Hemiptera and the dipteran families Tabanidae and Culicidae, while others have more flexible stylets, such as Thysanoptera and most Lepidoptera. A variety of proboscides have evolved that incorporate these pairs of mouthpart appendages in different combinations and to varying degrees. Some bear long stylets from all sets of mouthparts as in mosquitoes (Culicidae), some with stylets from the maxillae and labium as in the extinct scorpionfly lineage Pseudopolycentropodidae, others with stylets from the maxillae and mandibles as in Hemiptera and thrips (Thysanoptera), and still others with just one pair of stylets from the maxillae as in most Lepidoptera. Although thrips have stylets from both the maxillae and mandibles, the mandibular stylets are not paired (one side having been lost).

Ovipositors: At the posterior end of female insects in several groups, stylet-like appendages also occur in the form of an egg-laying structure, the ovipositor. These stylets, termed gonapophyses, are modifications of ventral abdominal appendages from segments eight and nine. Ovipositors are present in many insect orders in some form, but stylet-like ones are less common. Ovipositors can be remarkably flexible and extremely different in length. Stylet-like ovipositors can be found in the orders Orthoptera, Hymenoptera, and Rhaphidioptera. In both Orthoptera and Hymenoptera, ovipositor stylets can reach lengths surpassing that of the body. While a stylet-like ovipositor typically is used to insert eggs into compacted soil or woody plant tissues, in the parasitic Hymenoptera it functions as a hypodermic needle to deliver eggs inside a host's body. The hosts, however, can sometimes be deep within a plant or substrate. Some insect groups have solved such oviposition dilemmas without stylets by evolving elongated, telescoping genital segments. Ovipositor length roughly corresponds to the distance the eggs must travel from the insect to the host, penetrating the tissue or substrate in between.

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The Integument

Considering the near endless variation of shapes, colors, and sizes of insects, it is extraordinary to realize that the source of all of this diversity emanates from a simple, single-cell-layer-thick epithelium. This layer of epithelial cells is responsible for secretion (and digestion during molting) of the cuticle and its marvelous modifications. It not only forms the entire external surface of the insect from egg to adult, including the eyes and cuticular adornments such as horns, setae, and scales, but invaginates inward to form strengthening structures, tendons for muscle attachment, the entire respiratory system, as well as to line the fore- and hindguts.

The integument, consisting of both the living epidermis and non-living cuticle, serves multiple functions. It supports the body and provides attachment sites for skeletal muscles—that is, an exoskeleton. It also protects the body from physical harm, parasites, and reduces dehydration. Although the epidermis generally proliferates through developmental stages, from egg to adult, it also undergoes much reorganization and cell death. Particularly in the holometabolous orders, much of the larval epidermis is degraded and replaced by adult-specified epidermis from imaginal tissue or imaginal discs.

↑→ Cuticular types may not change drastically between immature and adult stages of hemimetabolous insects, such as these treehoppers, but can be quite different among stages of holometabolous insects.

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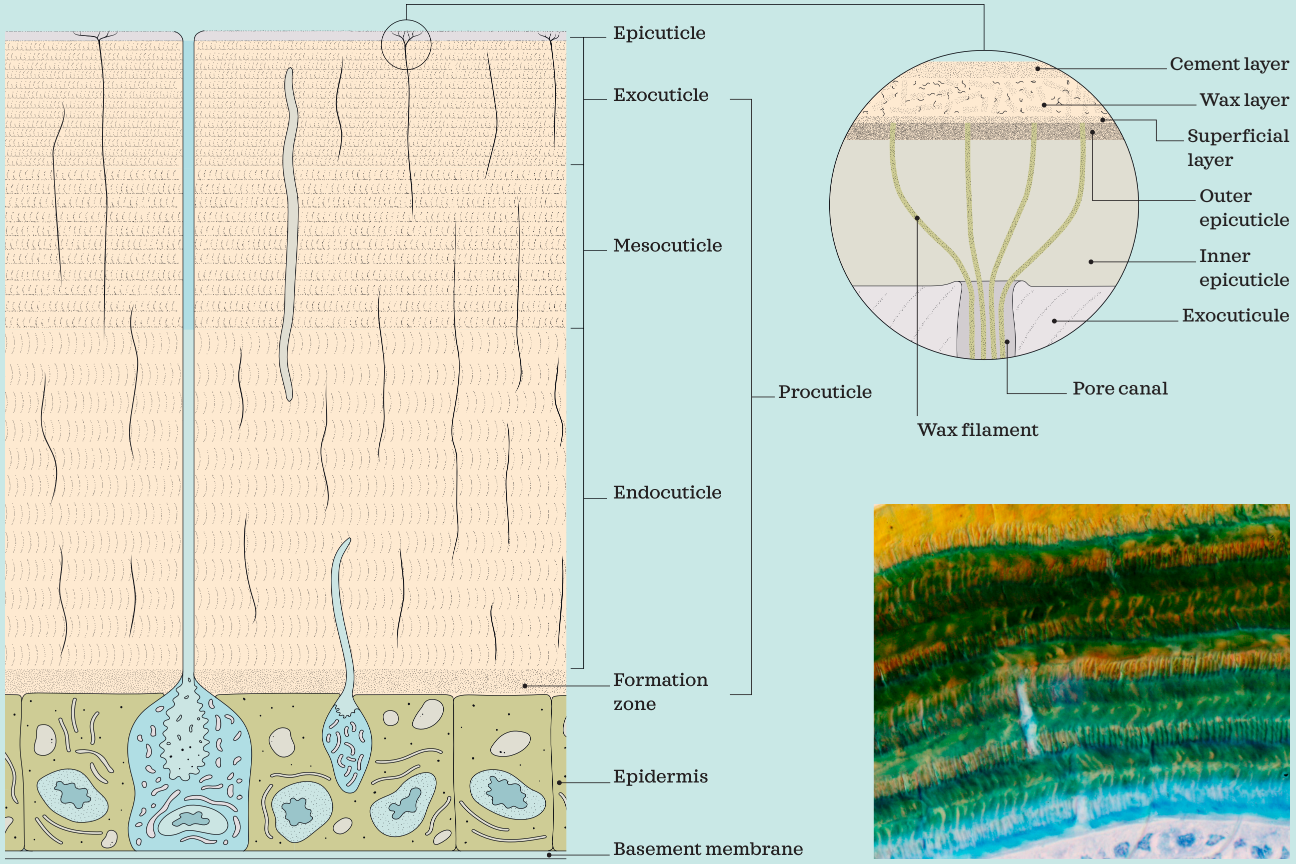
Cuticle Structure



The Cuticle

The cuticle is secreted by the epidermis as a fluid of complex composition that differs in its structure and components both spatially and temporally. It then goes through a process of polymerization with the addition essentially of chemical accelerants to form the exoskeleton. It is generally composed of three distinct layers: the innermost procuticle, the epicuticle, and the envelope. This last is the outermost, thinnest cuticular layer, composed of cuticulin. Slightly thicker is the epicuticle, composed of polyphenols. The procuticle is the thickest layer, except in tracheoles, the smallest diameter tracheae that lead to tissues, where it is absent. The procuticle is the only layer containing the polysaccharide chitin, and being the thickest, also bears distinct layers: the exo-, meso-, and endocuticle.

Above the cuticle are wax and cement layers of varying thickness. Depending on the developmental stage and body location, these cuticular layers, in particular the procuticle, can vary tremendously in thickness and composition. Segment regions (those bearing sclerites) generally have a thick cuticle, while a thinner cuticle (arthrodial membrane) exists between segments and sclerites to allow for movement. The procuticle is largely comprised of chitin and proteins, the latter of which more than 200 have been identified that are specific to the cuticle. Chitin is present in parallel fibers that are arranged in lamina within a matrix of proteins, inorganic elements, and water molecules (similar to reinforced concrete). The orientation of the fibers within each lamina changes, producing a helical pattern from the stacked layers of chitin and protein.

The exocuticle is heavily cross-linked and insoluble, while the meso- and endocuticles are reduced in such properties. Due to the degree of cross-linking, protein composition, and ratio of chitin to proteins, insect cuticle displays a fantastic range of hardness, flexibility, elasticity, and durability.

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Secretion and Molting

The process by which a single cell layer produces a compositionally and topologically complex suit of armor is fascinating. It is a well-orchestrated sequence of secretion events by the epidermis that is spatially and temporally regulated by individual cells. Depending on the developmental stage and region of the body, not all of the cuticular layers may be present. For example, the larval and pupal cuticles of holometabolous insects typically are much softer and elastic compared to that of the adult stage.

Different suites of proteins may be secreted to form unique cuticles in egg, larva, pupa, and adult stages. And, as if the process of forming a suit of armor was not already amazing, insects must remove it and synthesize a new one several times during their lifetime to accommodate the development of organs and tissues and a general increase in body size. The process involving digestion of the old cuticle and preparation for secretion of a new one is that of molting.

When the insect emerges from the old cuticle, its newly formed epi- and exocuticles are still soft and appear lighter colored. Various chemical agents (quinones) are then secreted into these newly formed layers to facilitate sclerotization. Following sclerotization, although the insect has completed the molting process, the remaining meso- and endocuticles continue to be secreted for variable periods of time depending on the type of insect and may not complete until shortly before the next molting cycle. As a reminder, in addition to the cuticle on the exterior of the body, the cuticle of the foregut, hindgut, and tracheal system must be shed as well. How is this accomplished? As the old cuticle is detached from the epidermis and the insect slowly wriggles out, it too pulls out the old internal cuticle linings. Although the smallest tracheal branches are not shed, the remaining tracheal branches are pulled out of the body, a truly amazing feat to undergo not just once but several times in the insect's life.

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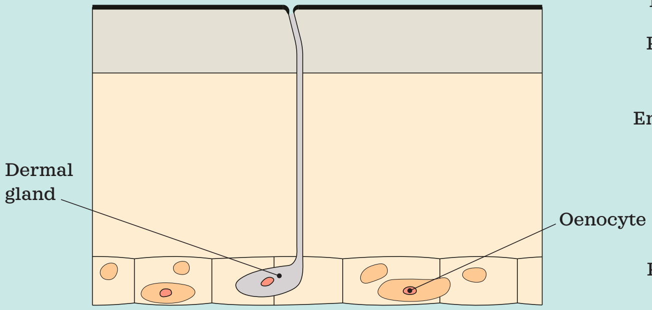
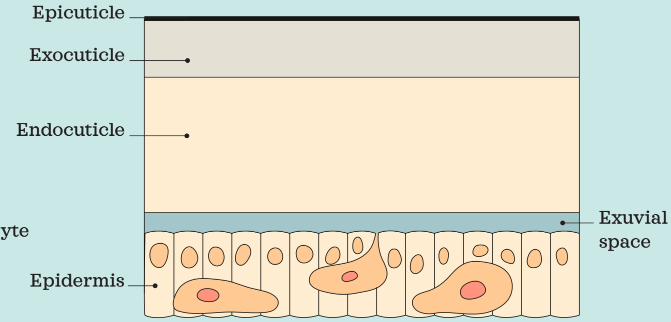
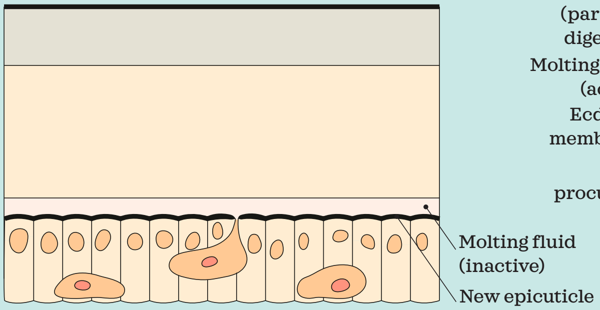
Cuticle Control of Molting



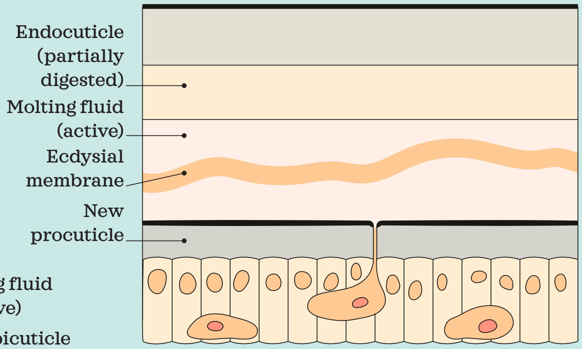
1. Mature cuticle The mature cuticle is composed of an epicuticle and a fully differentiated procuticle.



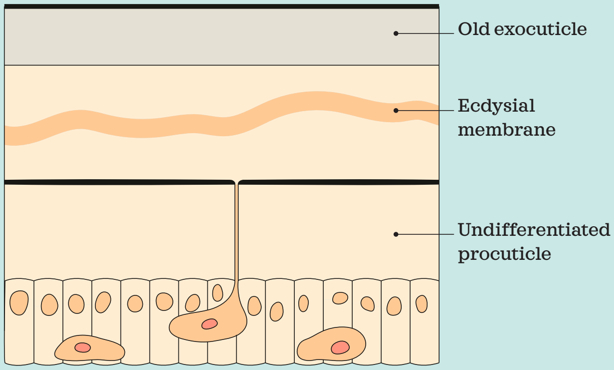
2. Apolysis As the epidermal cells divide and proliferate, they change shape, causing the cuticle to detach and a space (the exuvial space) to open between it and the epidermis.



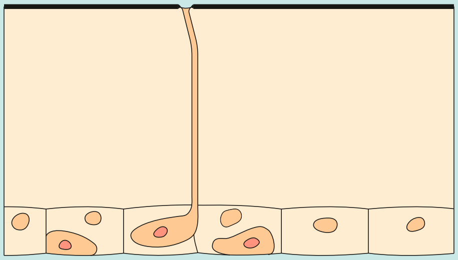
3. New cuticle produced The epidermal cells secrete a new envelope and epicuticle, which quickly become cross-linked or sclerotized for protection from later digestion. A fluid containing enzymes (at first, inactive), such as chitinase and protease, is secreted into the exuvial space.



4. Endocuticle digested The so-called molting fluid then digests the old endocuticle (and mesocuticle if present), leaving the old exocuticle and epicuticle intact due to their sclerotization. At the same time begins secretion of the bulky procuticle, beginning with the outer exocuticle and followed by the meso- and endocuticles.



5. Molting fluid resorbed The procuticle continues to be secreted, thickening, and the molting fluid and digested products are resorbed. Before shedding the remnants of the old cuticle, waxes are secreted to the surface of the outer epicuticle via ducts extending from the epidermal cells, called pore canals.



6 New cuticle after ecdysis (undifferentiated) The old cuticle then breaks along weakened points on the body as the insect goes through a period of peristaltic muscular contraction and the swallowing of air to increase body volume and escape the cuticle. To reach a mature, differentiated cuticle, the procuticle later undergoes sclerotization, although the basal-most layers may continue to be secreted for variable durations in the intermolt period.

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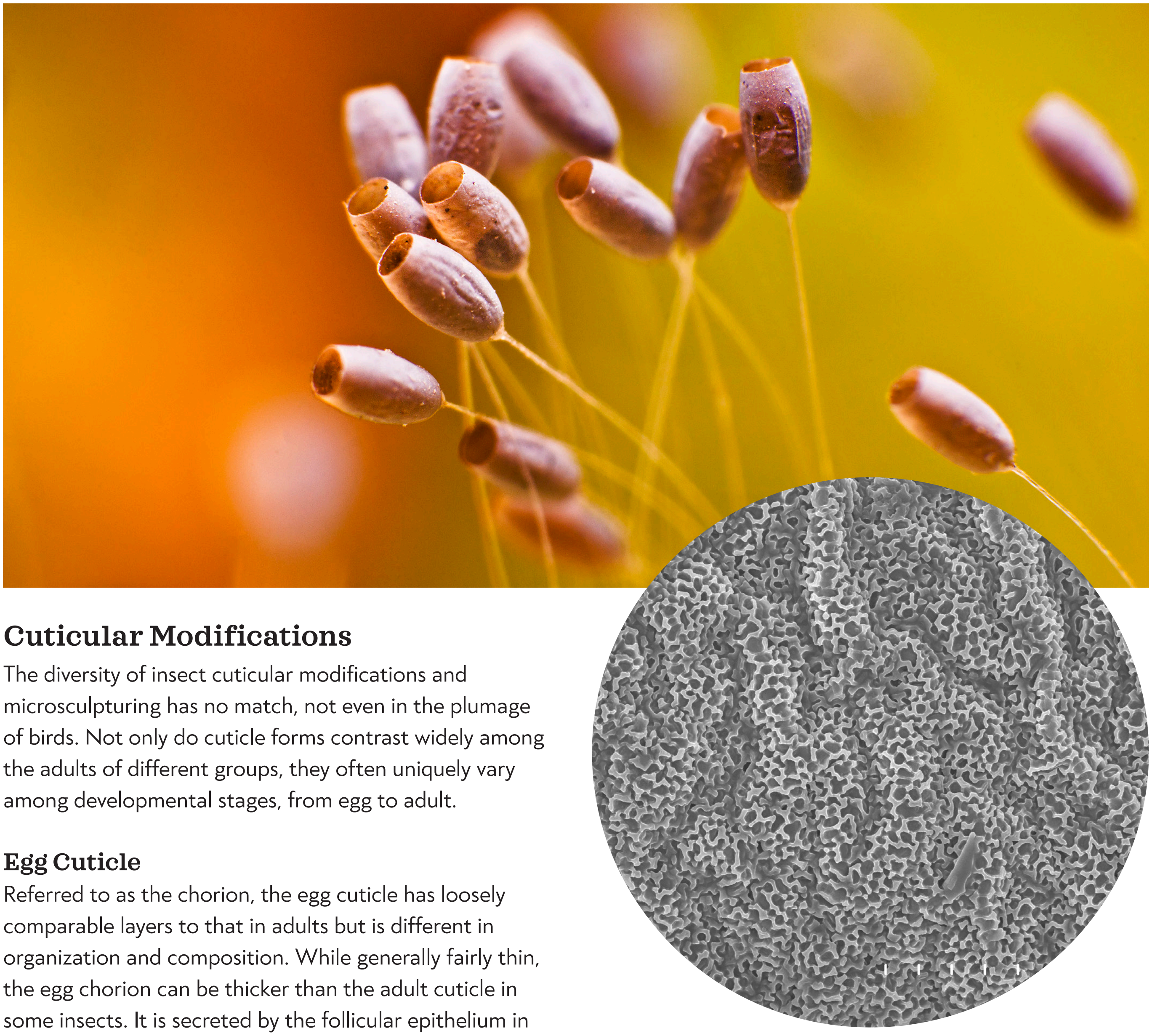

↑ Lacewing eggs are positioned at the tips of silk stalks and have a rough microsculpturing to their outer cuticle (scale 40 μm).

Cuticular Modifications

The diversity of insect cuticular modifications and microsculpturing has no match, not even in the plumage of birds. Not only do cuticle forms contrast widely among the adults of different groups, they often uniquely vary among developmental stages, from egg to adult.

Egg Cuticle

Referred to as the chorion, the egg cuticle has loosely comparable layers to that in adults but is different in organization and composition. While generally fairly thin, the egg chorion can be thicker than the adult cuticle in some insects. It is secreted by the follicular epithelium in the ovaries, also a single cell layer, except with the apical surface directed inward to the developing egg cell, or oocyte. As such, the cuticle is secreted inward instead of outward (as it occurs in all other developmental stages), much like that of the tracheae, except the follicular epithelium degenerates following secretion. The first layer to be secreted around the oocyte is the vitelline envelope, followed sometimes by a wax layer and then the chorion layers, which are akin to a procuticle. Within the layers of the chorion, the endochorion and exochorion are typically structured with labyrinth meshworks, canals, and chambers that function with systems of aeropyles, or pores, that function as a respiratory system for the egg, allowing for more efficient ventilation. Sometimes these aeropyles extend through elaborate arrangements of respiratory horns that function as snorkels for eggs laid in moist environments or partially immersed in wet substrates. Eggs that are laid in aquatic habitats typically have extra cuticular meshworks (termed a plastron) in the exochorion that facilitate gas diffusion between the air-liquid interface. After the chorion forms, the follicular epithelium degenerates. Once fertilization occurs and following oviposition, yet another cuticle is secreted between the developing embryo and the chorion from the extra-embryonic epithelium (the serosa).

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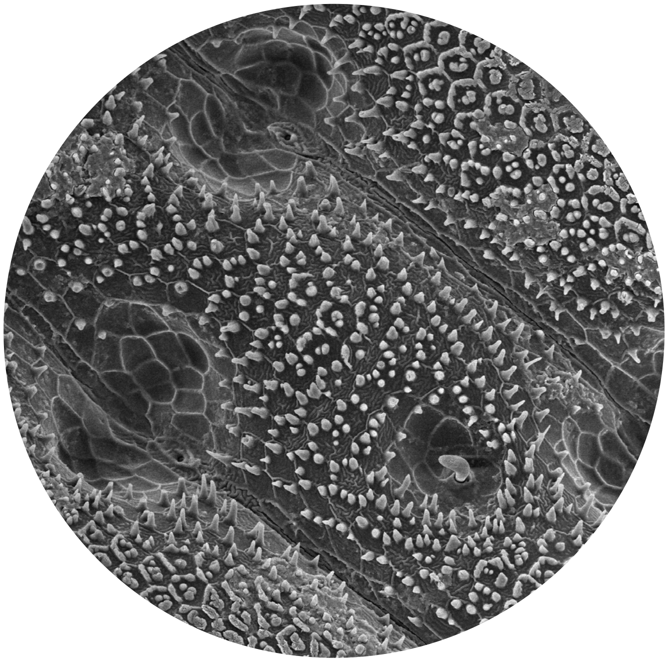
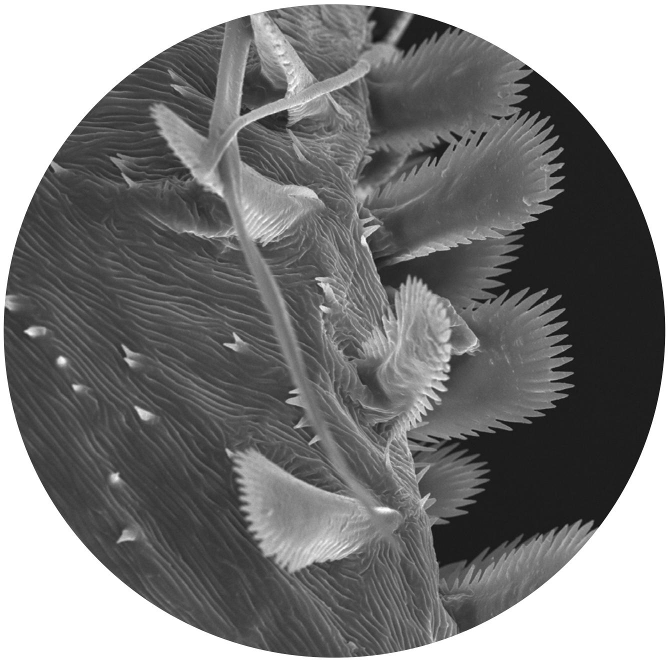
Immature and Adult Cuticles

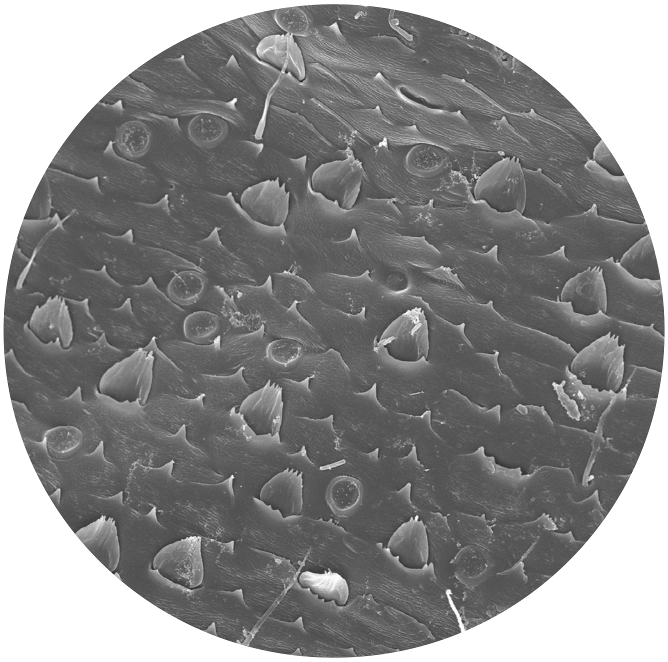
Immature cuticles can highly resemble adult cuticles in ametabolous and hemimetabolous insects. They differ much more in holometabolans and a larva often has a very different cuticle to that of the adult. In these groups, larvae typically have soft and elastic cuticles, except for perhaps the heads, legs, and sometimes body sclerites. These more pliable cuticles have thin exocuticles and are mostly composed of a less sclerotized endocuticle with larger amounts of elastic proteins such as resilin. Adult cuticles range in thickness and composition depending on the body region and insect lineage. Some insects have very thin cuticles, composed of few layers and lamellae, which afford the insect much agility. Others have thick, robust cuticles that are rigid and render the insect a small tank. Regardless of cuticle thickness, the exo- and epicuticles can be fashioned with incredible assortments of spines, processes (such as hair-like microtrichia), textures, and microsculpturing. This structural diversity applies to cuticles of any developmental stage, egg to adult.



↑ Adult cuticles display an incredible range in form and material properties, from thin to thick, elastic to rigid, and smooth to sculptured. Adult weevil cuticle often is quite rigid and although it looks smooth to the unaided eye, it can be bizarrely microsculptured as shown in this scanning electron micrograph (scale 100 μm).



↑ Immature insects often have quite different cuticles from their adult stage, particularly in holometabolous insects in which the immature stages drastically contrast with the adult. Although mosquito adults are terrestrial and fly, the immature larvae are aquatic and legless. Their ability to swim is facilitated by various setae and cuticular features along the body, as shown here (scale 30 μm).



→ Similar to mosquitoes, the immature stages of mayflies are aquatic and the adult is terrestrial with wings. Immature mayflies, however, have legs and some are adept swimmers, their agility arising from a combination of cuticular structure and sensilla, as shown here (scale 40 μm).

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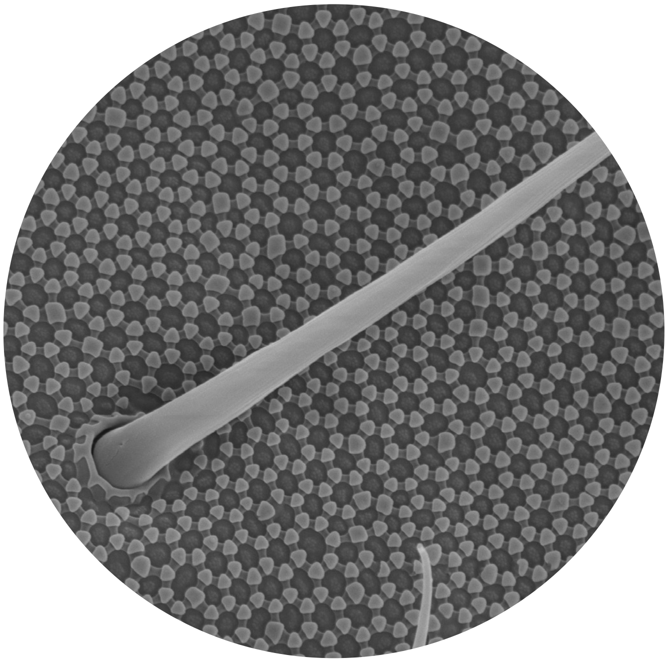
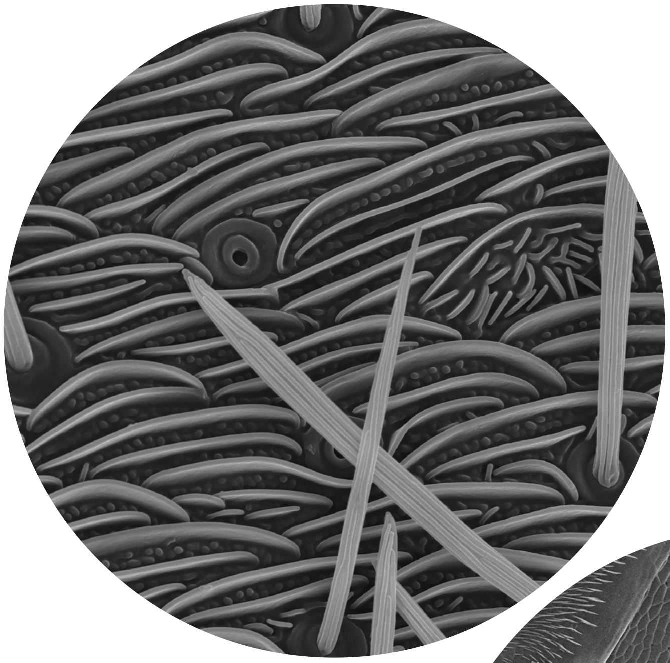
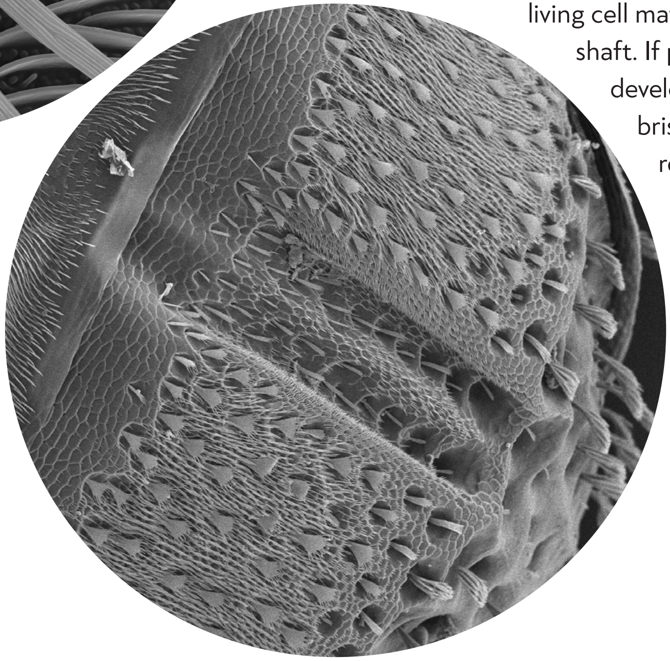
Bristles and Scales

In addition to the vast range of surface extensions and textural modifications, the cuticular landscape is complemented by another swath of exoskeletal structures, a subset of sensory structures, or sensilla, termed macrochaetae (bristles and scales) and including hair sensilla. These are long cuticularized processes formed by specialized epithelial cells. They serve a basic function of mechanoreception, but fulfill an extensive list of roles, such as insulation and temperature regulation, chemical dispersal, sound absorption (important for bat or nocturnal predator avoidance), waterproofing, and various aspects related to flight (see Chapter 4). They can be colorful and therefore function in warning coloration, camouflage/mimicry patterns, and species recognition. Scales that detach easily from the body, as in Lepidoptera, can also help as escape mechanisms, such as from spider webs. Scales are actually modified (flattened) bristles with distinct ventral and dorsal surfaces.

Macrochaetae are produced by a single epithelial cell, anchored in a socket such that the shaft can pass through the cuticle, and associated with several other cells for stabilization and sensory purposes of the structure. In development, the bristle or scale cell extends its body via the elaboration of cytoskeletal elements (actin bundles and microtubules) to produce a framework for its final shape. As in other epithelial cells, the cell then secretes layers of cuticle that sclerotize, after which the cell recedes/degrades—a trait only shared with egg follicular epithelium—leaving the hardened external structure. Aside from scales and various types of bristles, other types of sensilla, including hair sensilla, retain living cell matter in the sclerotized shaft. If present in multiple developmental stages, the bristles and scales must reform at each molting period along with the secretion of the rest of the insect cuticle.







↑↗→ An astounding array of cuticular macrochaetae, setae, bristles, and scales adorn the exoskeleton of insects. These structures are formed by single epithelial cells (scale from top to bottom: 5, 10, and 200 µm).

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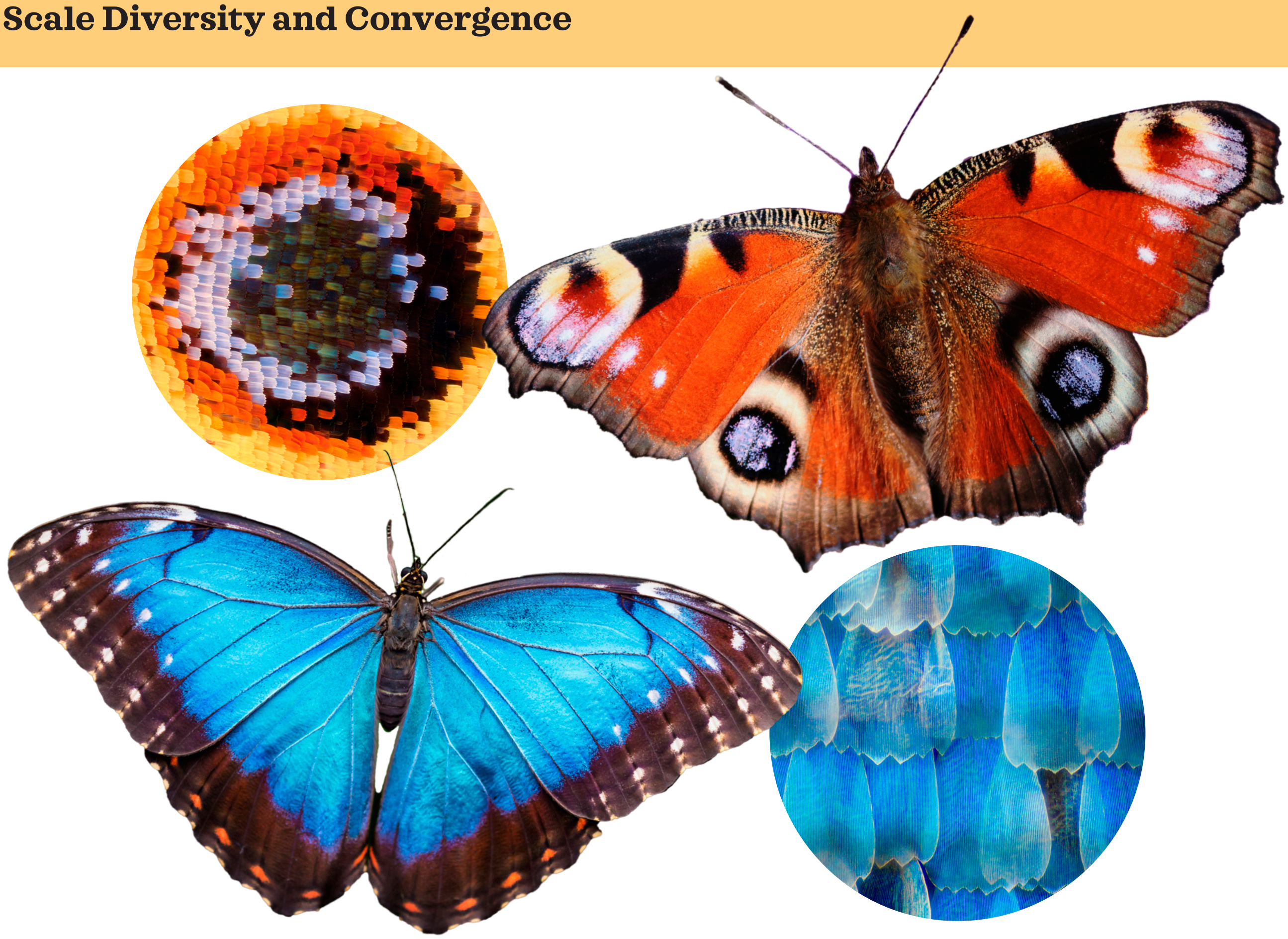
Scale Diversity and Convergence



Scales are modified macrosetae that are flattened and have distinct surface polarity. The ventral surfaces have smooth cuticle and the dorsal surfaces have textured cuticle. Scale morphology varies tremendously in insects. Scales may not only be diverse within families or orders of insects, but a species may bear several distinct types of scales on a single individual. Their shapes vary from round, rectangular, and shingle-like to somewhat amorphous, porous, frilly, and anemone-like. Scales can be relatively hollow, have internal cuticular structures, or secrete viscous liquids such as waxes or chemical volatiles. Just as in other macrochaetae, scales form a single epithelial cell via extension of the cell body. After a framework of the scale shape has been formed by cytoskeletal elements, the cuticle is secreted, it becomes sclerotized, and the scale cell recedes or degrades. Formation of surface features and textures (such as longitudinal ribs/ridges, windows, and projections) are a result of the interaction of these cytoskeletal elements and various binding proteins with the cell membrane before cuticular secretion. Internal structures, such as three-dimensional photonic crystals, are formed by the convolution of the smooth endoplasmic reticulum, also in association with various binding proteins, with the plasma membrane. After secretion of the cuticle into this convoluted framework, the cell degrades and the lattice structure remains.

Despite the already many examples of evolutionary convergence in insects, it may still be surprising that scale structures have convergently evolved in multiple lineages. Not only do scales in these different groups converge on general external appearance, they develop similar internal structures that disperse light in similar fashion, such as through photonic crystals. Scales have evolved independently in at least the orders Collembola, Archaeognatha, Zygentoma, Orthoptera, Hemiptera, Psocoptera, Hymenoptera, Coleoptera, and Diptera, but are best known in the Lepidoptera. They also appear independently within most orders.

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↑ Insect coloration can be formed by various chemical compounds/ pigments or cuticular structural features; sometimes both are involved. Many fulgorids have vivid color patterns attributed to different pigments deposited in the cuticle.

Coloration Beyond Belief

Insect coloration is generally produced in two ways—through pigmentation or physical interference (structural coloration). Either way, perceived colors are a result of the absorption, reflection, and transmission of the wavelengths in white light. If all wavelengths are reflected equally, the appearance is white, and if all are absorbed, the appearance is black. While very white and black coloration occurs in some insect groups, most appear with various amounts of other colors. Coloration can be relatively uniform along the body or appear in a wild assortment of patterns. In some cases, the structure of cuticular layers is organized is such a way as to reflect certain wavelengths while others are transmitted. In other cases, pigments are present, which may also reflect certain layers and absorb others. In other cases still, both structural and pigmentary colors may be present.

(continued...)

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