

Grzimek's Animal Life Encyclopedia

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Insects**

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Evolution and systematics

Fossil insects and their significance

Given the tiny and delicate bodies of most insects, it is perhaps surprising that remains of these organisms can be preserved for millions of years. After all, most fossils represent only hard parts of other organisms such as bones of vertebrates or shells of mollusks. Fossil remains of soft-bodied animals such as worms or jellyfish are extremely rare and can only be preserved under very special circumstances. In contrast to the large number of living insect species, fossil insects are rare compared to other groups. One obstacle for the fossilization of insects is that most insect species do not live in water. Because they can usually only be preserved as fossils in subaquatic sediments (amber is an exception to this rule), they thus have to be accidentally displaced into the water of an ocean or a lake.

Since most insects are terrestrial animals, the fossil record for these species is poor. Freshwater groups such as water-bugs and water-beetles, as well as the larvae of mayflies, dragonflies, stoneflies, alderflies, and the vast majority of caddisflies, live in rivers or lakes, and their fossil record is much better. Comparatively few insect species live in brackish water and in the tidal area of seashores, and only a single small group of water-bugs has evolved to conquer marine habitats: it is the extant (i.e., living) sea skater, or water strider, genus *Halobates* of the family Halobatidae, which only recently in Earth's history evolved to live on the surface of the ocean.

The first and most important prerequisite for fossilization is the embedding of the insect body in a subaquatic environment with stagnant water that allows undisturbed formation of layered sediments on the ground. Terrestrial insects can be washed into lakes by floods, and flying insects can be blown onto the surface of lakes or the sea during heavy storms. Dwellers of rivers and brooks must also be washed into lakes, lagoons, or the sea to become fossilized, because there are no suitable sedimentation conditions in running water. Aquatic insects that live in lakes and ponds can be preserved in sediments on the ground of their habitat, a type of preservation known as "autochthonous preservation."

Further conditions must be fulfilled for an insect to be fossilized. First, the insect must penetrate the water surface and sink to the bottom. This is achieved most easily if the insect is displaced alive into the water and drowns, so that its inter-

nal cavities become filled with water. Insects that have been entangled in floating mats of algae can easily sink down more rapidly with it. However, if dead or even desiccated insects are blown onto the water surface, they may float for a very long time and will start to rot or be eaten by fish, enhancing disarticulation of their bodies (especially wings), which will have a chance to sink down and be preserved as isolated fossil remains. Dead terrestrial insects washed into water bodies by rivers or floods can become completely fossilized depending on the length of time and distance of specimen transport and drift. Consequently, the state of preservation and the completeness of fossil insects are good indicators for the conditions of embedding. A further important factor is the chemical makeup of the water where the insect is embedded. When the water body includes an oxygen-rich zone with abundant fish life, sinking insect bodies may be eaten by fish and never reach the ground. In contrast, hostile conditions such as hypersalinity, digested sludge with poisonous hydrogen sulfide, and low oxygen content prohibit the presence of ground-dwelling scavengers (e.g., worms, mollusks, and crustaceans) and make the preservation of insect fossils more likely. Such conditions near the bottom of the water body usually are present only in deep, calm water without any significant water exchange.

Finally, a dead insect or other carcass must be rapidly covered with new sediments, so that the body can be preserved as a fossil when these sediments are later consolidated into rock. Very often such sedimentation events occur in regular intervals. The resulting rocks are then fissionable in plates (e.g., lithographic limestone) along the former interfaces between two sedimentations. When the fossils are situated directly on the surface of these plates, they are immediately visible after the rock has been split and need only minor preparation. However, when the fossil insects are concealed within the plates, they can only be recognized by an inconspicuous bulge and/or discoloration of the plate surface, and must be prepared with great care and suitable tools (e.g., pneumatic graver and needles) in order to remove the covering rock without damaging the fossil.

Types of fossils

Impressions

The particular way the fossil insect is preserved strongly depends on the types of sediments and the chemical compo-



Fossil of a dragonfly in limestone matrix, from Sohnhofen, Germany, Jurassic era. The wingspan is approximately 8 in (20.3 cm). (Photo by Jianming Li. Reproduced by permission.)

sition of the water as well as the circumstances of the transformation of the sediments into rock. Most often the insect bodies completely decay in the course of time and only an impression of the animal remains as fossil. This is the case with fossil insects from Carboniferous coal layers, the Lower Jurassic oil shales of Middle Europe, and most limestones throughout the world. Even though these fossils are impressions, some body parts may be accentuated and traced with a secondary coloration if diluted metal oxides (e.g., iron oxide or manganese oxide) penetrate the body cavities in dendritic fashion. Dendrites can be reddish to brown (iron oxide) or black (manganese oxide). This phenomenon is exemplified in wing venation of fossil dragonflies from the Solnhofen lithographic limestones from the Upper Jurassic of Germany.

The finer the sediments, the greater the number of details that may be preserved in the fossil insects, so that even delicate bristles or facets of complex eyes are still visible. Sediments exposed to strong pressure and compaction during the transformation into rock often result in completely flattened impressions. However, if layers harden relatively fast, impressions can retain a three-dimensional profile of parts of the former insect body, for example the corrugation and pleating of the wings.

Under particular chemical circumstances, the organic matter of the insect body can be impregnated or replaced by mineral substances and therefore preserved in the original shape with all of its three-dimensional properties (e.g., the pleating of the wing membrane). This occurs in all fossil insects from the Lower Cretaceous Crato limestones from northeastern Brazil, where insect bodies were preserved as iron-oxide-hydroxide (limonite). These fossil insects are tinted reddish brown and are often very distinct from the bright yellowish limestone. This special mode of fossilization has even permitted the preservation of soft parts such as muscles or internal organs. In some cases, the color pattern of the wings of cockroaches, bugs, beetles, and lacewings is still visible. This rare phenomenon provides information on the appearance of extinct animals that is usually not available in fossils.

Incrustation

A second mode of preservation involves decay processes in which the insect body induces a chemical reaction that leads to the precipitation of minerals around the dead insect. This process can produce bulbs of rock (geodes or concretions) in which the fossil insect is preserved three-dimensionally. Fossil insects from Mazon Creek, a famous locality from the Carboniferous era of North America, are preserved this way. Incrustation with sinter, the chalk generated by hot wells, can preserve dead insects as three-dimensional impressions that have fallen into this mineral water. There, hollow molds can be filled with composition rubber to obtain perfect copies of the original insect bodies.

Embedding

The third and rarest method of fossilization involves the embedding of insects within crystals, for example dragonfly larvae in gypsum crystals from the Miocene of Italy. These crystals developed in a desiccating coastal water body in the Tertiary age, when the Mediterranean Sea was separated from the Atlantic Ocean by a barrier at the Strait of Gibraltar. However, this hypersalinity of the water was not the habitat of the enclosed dragonfly larvae, because they are close relatives of extant dragonflies that never live in such environments. The enclosed dragonfly larvae are not the animals themselves, but only dried skins from the final molting of the larvae into adult dragonflies. Such skins (exuviae) are very robust and are transported during storms to habitats such as that mentioned above.

Insect inclusions in amber represent the most important exception from the rule that insects can only be fossilized in subaquatic environments. These animals are preserved in fossil resins with their natural shape with all details in a quality that is unmatched by any other kind of fossilization. The oldest known fossil insect inclusions in amber were discovered in Lebanon and are of Lower Cretaceous age (about 120 million years old [mya]). The insects of the famous Baltic amber and the Dominican amber from the Caribbean are much younger (45–15 mya) and have been dated to the early to mid-Tertiary. Insects enclosed in the latter two fossil resins are already much more modern than those of the Lower Cretaceous amber, which were contemporaries of dinosaurs and pterosaurs. The novel and subsequent movie *Jurassic Park*, in which scientists revive dinosaurs by using the DNA of dinosaur blood imbibed by mosquitoes fossilized in amber is highly unlikely, since no suitable DNA has ever been discovered in insects fossilized in amber.

Even preservation of more imperishable exoskeleton (chitin) comprises relatively recent insect fossils, and then only under very favorable circumstances. More frequently, chitin is preserved in subfossil insects from relatively recent layers, for example from the Pleistocene asphalt lakes of Rancho La Brea near Los Angeles, which are only 8,000–40,000 years old. The oldest known fossil insects with preservation of chitin are of Tertiary age. However, the preservation of metallic colors in some small damselflies from the Lower Cretaceous Crato limestones of Brazil could indicate that the original exoskeleton was preserved in these cases, but confirmation of this would require chemical analysis.

A trained eye is necessary to discover and recognize many insect fossils. They are often not situated on easily cleavable places but instead are concreted in stone matrix. Once fossil insects are found, their features such as wing venation may become more visible when submerged in alcohol.

Paleoentomology can be cumbersome and hard work, but discoveries of fossil insects can provide us with knowledge of the history of life on Earth. Study of insect fossils increases our knowledge about past biodiversity, past climate and habitats, extinction events, changes in the geographical distribution of groups, sequence of anatomical changes in the course of evolution, minimum age of origin of extant groups or the lifespan of extinct groups, and types of organisms and adaptations that do not exist anymore. For example, extant snakeflies (Rhaphidioptera) are restricted to the Northern Hemisphere and only live in temperate (cooler) areas, but fossil snakeflies from the Lower Cretaceous Crato limestones of Brazil correspond to a warm and arid area with savannah-like vegetation. The extinction of all tropical snakeflies at the end of the Cretaceous could be related to climatic consequences of the meteorite impact that also led to the extinction of dinosaurs. Only those snakeflies that were adapted to cooler climates survived.

Subtropical and tropical areas not only differ in climate from temperate or cooler regions, but also in the composition of their flora and fauna. This is observable in insect fauna: praying mantids, termites, cicadas, walkingsticks, and many other insect groups are adapted and restricted to warm climate zones. Earth's appearance and its climate have changed dramatically over time. The position and shape of continents have changed, oceans have emerged and vanished, cold or warm streams have changed their course, and the polar caps have disappeared and reappeared and expanded dramatically during ice ages. Freezing, barren regions like the Antarctic formerly had a warm climate with a rich vegetation and fauna. Areas of North America and Middle Europe also supported tropical or arid climates as well as cold periods with extensive glaciation.

Fossils often provide clues to reconstructing climatic changes during Earth's history. When extant relatives of a fossil organism are strictly confined to tropical or desert areas, it is tempting to assume that this was also the case with their fossil relatives. This assumption will be correct in most cases, but in other instances extant groups such as snakeflies have adapted to a cooler climate within their evolutionary history. Thus, their fossils may be poor indicators for a certain type of climate. It is therefore important to compare the complete fossil record of a certain locality with the modern relatives and their habitats. Many freshwater deposits yield a variety of fossil plants, vertebrates, and arthropods. If several of these species belong to faunal and floral assemblages that are clearly indicators for a certain climate, it is possible to reconstruct the past climate with confidence (as long as other species present are generalists or had unknown preferences). In Messel near Darmstadt in Germany, for example, lacustrine sediments of the Eocene have yielded several fossil insects such as walking sticks that suggest a previously warm climate. This is in accord with evidence from vertebrate fossils such as prosimians and crocodiles.



Fossil of a water strider in mudstone matrix from Sohnhofen, Germany, Jurassic era. The span between the legs is about 4 in (10 cm). (Photo by Jianming Li. Reproduced by permission.)

Baltic amber has also yielded numerous insects (e.g., web-spinners, walkingsticks, praying mantids, termites, and palm bugs) that indicate a warm and humid climate. Palm bugs indirectly demonstrate the presence of palm trees in the amber forest. The presence of the preserved insects is in accord with the fauna from the Messel fossils that lived in about the same period. Thus, the climate in Middle Europe was much warmer in the early Tertiary (45 mya) than today.

Fossil insects not only contribute to the reconstruction of past climates, they also provide evidence of the prevailing vegetation types and landscape. For example, the insect fauna of the Crato limestones from the Lower Cretaceous of Brazil includes not only certain species (e.g., cicadas, ant lions, nemopterids, termites) that suggest a warm climate, but also numerous insect groups (cockroaches, locusts, bugs, robber flies) that presently live in very different habitats and climatic conditions. However, their relative frequency in the fossil record from this site is in perfect agreement with insect communities in modern savanna areas and is further supported by fossils of other arthropods (e.g., sun spiders) and plants (order Gnetales). Nevertheless, this Cretaceous savanna must have been dissected by rivers and brooks, because of the presence of numerous fossils of aquatic insect larvae of mayflies (Euthyplociidae) and dragonflies (Gomphidae) that belong to modern families that are strictly riverine. Geological evidence (e.g., dolomite and salt pseudomorphs) and other evidence (e.g., fossils of marine fishes) clearly show that the Crato limestones originated as sediments in a brackish lagoon, in which the terrestrial and aquatic insects were transported by flowing water or wind. Taken together, this evidence allows for a nearly complete reconstruction of the habitat, landscape, climate, flora, and fauna of this locality in South America 120 mya.

The ancestry of insects

Insects belong to the large group of arthropods that also includes arachnids, crustaceans, and myriapods. For many decades, insects were generally considered close relatives of

myriapods, and the ancestor of insects was consequently believed to have been a myriapod-like terrestrial arthropod. However, this hypothetical assumption was not supported by any fossil evidence. It was first challenged by the finding that respiratory organs (tracheae) of various myriapod groups and insects were superficially similar but quite different in their construction, so that they more likely evolved by convergent evolution from a common aquatic ancestor that did not possess tracheae at all. The close relationship between insects and myriapods was strongly challenged by new results from molecular, ontogenetic, and morphological studies that revealed congruent evidence towards a closer relationship between insects and higher crustaceans (Malacostraca), which would also suggest a marine ancestor of insects, but of much different appearance than previously believed. The hypothetical reconstruction of the most recent common ancestor of all insects thus strongly depends on the correct determination of the position of insects in the tree of life and whether their closest relatives were terrestrial or aquatic organisms.

The discovery of genuine fossils from the stem group of insects would allow a much more profound reconstruction and also would represent an independent test for the hypothetical reconstructions and their underlying phylogenetic hypotheses. The oldest fossils that can be identified as true hexapods were discovered in the Middle Devonian Rhynie chert of Scotland (400 mya). This chert originated when a swamp of primitive plants was flooded with hot volcanic water in which many minerals were dissolved. These fossil hexapods are morphologically more or less identical with some extant species of springtails and can therefore easily be placed in the extant order Collembola. Since two most closely related groups of organisms, so-called sister groups, originated by the splitting of one common stem species, they must be of the same age. Together with the small wingless orders Protura and maybe Diplura, springtails belong to the subclass Entognatha. Consequently, the second subclass of hexapods, Insecta, which includes all modern insects with ectognathous (exposed) mouthparts, must also be of Devonian age at least. The most primitive and probably oldest members of ectognathous insects are the two wingless orders Microcoryphia (bristletails) and Thysanura (silverfish), often still known as thysanurans. No Devonian fossils of these insects have yet been discovered, except for some fragments of compound eyes and mouthparts that have been found by dissolving Devonian cherts from North America with acid.

Except for those few Devonian fossils mentioned above, the oldest fossil insects occur in layers from the lower Upper Carboniferous (320 mya). These rocks show a surprising diversity of various insect groups: not only wingless insects such as bristletails and silverfish, but also the oldest known insects with wings, such as ancestors of mayflies and dragonflies, as well as primitive relatives of cockroaches and orthopterans. Within 80 million years between the Middle Devonian and the Upper Carboniferous, the evolution of insects resulted in a great diversity of different insect groups and also allowed for the conquest of the airspace by generating a remarkable new structure: two pairs of large membranous wings with complex articulation and musculature.

Before the Devonian period, there must have been a long period of slow evolution for the ancestral line of insects, because well-preserved fossils of other arthropod groups such as chelicerates and crustaceans are known from Cambrian sediments, which are about 200 million years older than the oldest insect fossils. If insects (or insects together with myriapods) are most closely related to crustaceans, their early marine ancestors must have existed in the Cambrian as well. However, no fossils of these early ancestors have been discovered yet. These ancestors simply may have been overlooked or even misidentified because they do not look like insects but rather have a more crustacean-like general appearance. Therefore, it is important to evaluate which combination of characters would characterize an ancestor, based on the current knowledge of the relationship of insects and the morphology of the most primitive extant representatives of insects and their suggested sister group.

One of the most conspicuous characters in many modern insects, such as dragonflies, bugs, beetles, bees, and butterflies, is the presence of wings. However, the most primitive and basal hexapod orders such as springtails, diplurans, bristletails, and silverfish, as well as their fossil relatives, all lack wings. Since the closest relatives of insects, myriapods and/or crustaceans, also lack wings, it is obvious that the absence of wings in those primitive orders is not due to reduction but rather due to their branching from the insect phylogenetic tree before the evolution of wings. Consequently, ancestors of all insects must also have been wingless.

Besides numerous other anatomical details that are often not preserved or visible in fossils, all insects are characterized by a division of the body into three distinct parts: head, thorax with three segments—each with a pair of legs—and abdomen with a maximum of 11 segments that contains internal organs and genital organs but includes no walking legs. The division into three body parts is a clear distinction of insects from other arthropod groups: myriapods also have a head, but their trunk is not divided into thorax and abdomen, and all of their segments bear one or two pairs of legs of about the same size. Due to the presumed close relationship of insects to myriapods and crustaceans, it is likely that ancestors of insects still had legs (maybe already of reduced size) on the abdominal segments. Like myriapods, all insects only have one pair of antennae, while extant crustaceans have two pairs and extant arachnids have none. Unlike other arthropods, insects have a single pair of appendages on the terminal body segment.

These considerations allow for the prediction that the ancestor of all insects most probably had the following combination of characters besides the usual character set of all arthropods (compound eyes, exoskeleton, articulated legs, thorax, etc.): a distinctly delimited head with only one pair of antennae; a three-segmented wingless thorax with three pairs of large walking legs; and a longer abdomen with at least 11 segments, a pair of terminal appendages, and perhaps a pair of smaller leglets on most abdominal segments. Furthermore, it is likely that this ancestor was an aquatic marine animal.

A fossil organism (*Devonohexapodus bocksbergensis*) with exactly this combination of characters was discovered in the Lower Devonian slates of Bundenbach (Hunsrück) in Ger-

many in 2003. Its head bears only one pair of long antennae, the thorax has three pairs of long walking legs, and the abdomen has about 30 segments, each with a pair of small leglets, while the terminal segment bears a pair of curious appendages that are unlike walking legs and directed backwards. It seems to be closely related to (or more probably even identical with) another fossil organism, *Wingertshellicus backesi*, that was previously described as an enigmatic arthropod but has a very similar general appearance and combination of characters. The presence of legs on the abdominal segments is compatible with both possible sister groups of insects, because crustaceans and myriapods both possess legs or leg derivatives on the trunk segments. In myriapods these legs are more or less identical in their anatomy and size on all segments, while in crustaceans there is a difference between the anterior walking legs and posterior trunk appendages that are shorter and often of different shape. Therefore, the aforementioned Devonian fossils suggest a closer relationship of insects with crustaceans. In extant insects the abdominal leglets are either reduced or transformed into other structures (e.g., genital styli, jumping fork of springtails). However, in bristletails and some primitive silverfish, there are still so-called styli present on the abdominal segments that are quite similar to the short abdominal leglets of *Devonohexapodus*.

As is often the case in evolutionary biology, there exists conflicting evidence that poses some as yet unsolved problems for scientists. The Upper Carboniferous fossil locality Mazon Creek in North America has yielded several fossil wingless insects, similar to extant thysanurans, that possessed true legs with segments and paired claws on eight abdominal segments just like the three pairs of walking legs on the thorax. The fossils are also smaller in size than *Devonohexapodus* and seem to have been terrestrial organisms, thus rather pointing to a myriapod relationship and origin of insects. Since they are much younger than the oldest true insects, they may already have been living fossils in their time, just like *Devonohexapodus*, which was contemporaneous with the first true terrestrial insects.

Devonohexapodus was found in a purely marine deposit, but it could have been a terrestrial animal that was washed into the sea by rivers or floods. However, if that were the case, one would expect to find other terrestrial animals and plants as well. The Hunsrück slates yielded a large diversity of marine organisms but no terrestrial plants or animals at all. Consequently, *Devonohexapodus* was probably a marine animal; the crustacean-like appearance and structure also suggest an aquatic lifestyle. *Devonohexapodus* thus seems to be the first record of a marine ancestor of insects, or considering its age, an offshoot from the ancestral line of insects that survived into the Devonian, when more advanced and terrestrial insects had already evolved from their common ancestors. This fossil, as well as evidence from phylogenetic and comparative morphological research, supports the hypothesis that insects evolved directly from marine arthropods (either related to crustaceans or myriapods) and not from a common terrestrial ancestor of myriapods and insects. Ancestors of arachnids (e.g., trilobites) and the most primitive extant relatives of arachnids (horseshoe crabs) also are marine animals, just like most crustaceans (all crustaceans in freshwater and terrestrial

environments are thought to be derived from marine relatives). The anatomical differences within the respiratory (tracheal) system in various myriapod groups suggest that these myriapods did not have a common terrestrial ancestor but that different groups of myriapods conquered land several times independently. Their ancestors may have been amphibious, which facilitated their final transition to a completely terrestrial lifestyle. Some crustaceans, such as woodlice (Isopoda), managed this transition via amphibious ancestors; the most primitive woodlouse still has an amphibious lifestyle on seashores. Since certain organs like tracheae for breathing air have clearly evolved independently in some terrestrial arachnids (and even velvet worms), apparent similarities between terrestrial myriapods and insects could simply be due to convergent evolution. Different unrelated arthropod groups obviously developed similar structures when they left the ocean and became terrestrial animals, so that all structures related to a terrestrial lifestyle may be poor indicators for a close relationship despite overall similarity.

The conquest of the land

About 400 mya during the Upper Silurian and Lower Devonian, one of the most significant events happened in the evolution of life on Earth: an increased oxygen level in the atmosphere coupled with the correlated generation of an ozone layer offered protection against harmful ultraviolet radiation, and the first primitive green plants colonized the continents. The first terrestrial arthropods appeared soon after, followed by tetrapod vertebrates. Before that time, a highly diverse ecology existed in the world's oceans, especially along continental shelves and coastal regions with shallow water, but the continents themselves were stony deserts that resembled the surface of Mars. The ancestors of insects still inhabited the oceans at this time, as evidenced by discovery of their fossils.

The first pioneers of terrestrial habitats were various algae and primitive vascular plants such as rhyniophytes (*Rhynia*) and psilophytes (*Psilophyton*), which were naked stalks lacking any leaves or roots. These primitive herbaceous plants were confined to the edges of shallow coastal waters and swamps and were not yet "true" terrestrial plants. The oldest fossil insects as well as ancient amphibians strongly adapted to aquatic habitats have been found together with fossils of these early plants. As explained above, various terrestrial groups of arthropods (e.g., velvet worms, arachnids, centipedes, millipedes, insects, and some crustaceans) conquered the dry land several times independently and are not derived from a common terrestrial ancestor, even though they show similar adaptations for a terrestrial mode of life. The emergence of plants on land was a necessary prerequisite for the first arthropods to make the transition to terrestrial life. Early land plants provided nutrition for the first terrestrial arthropods. In the Rhynie cherts of the Lower Devonian from Scotland, fossils have been discovered that provide direct evidence for the feeding on plants by myriapods and unknown arthropods with sucking mouthparts.

The earliest terrestrial insects were wingless and tiny ground-dwellers such as springtails, diplurans, bristletails, and

silverfish. Just like their modern relatives, they probably fed on detritus—organic substances on the ground composed of decaying plant material mingled with fungal meshworks and bacterial colonies. Other early terrestrial arthropods such as centipedes and arachnids were predators that fed on those small insects or on each other. As soon as the environmental conditions became suitable due to changes in the atmosphere and the evolution of land plants, the multiple conquest of the land by previously aquatic arthropods was facilitated by the evolution of certain features of the arthropod structural design. This design, which had evolved 600 mya during the Cambrian era in the ancestor of all aquatic arthropods, included the exoskeleton that later provided protection against dehydration by evaporation of body fluids, and the mechanical support for a body that was no longer supported by the water. Another important pre-adaptation was the presence of walking legs that also allowed for an active and swift locomotion on dry land.

Ancestors of most terrestrial arthropod groups during the time of the transition from aquatic to terrestrial life may have been very small amphibious creatures. They could have breathed under water and in air through simple diffusion of oxygen through their skin, which is not a very effective way of respiration. With increased demands for the efficiency of the respiratory system in completely terrestrial animals, various groups independently developed complex systems of ramified tubular invaginations (tracheae) to increase the oxygen supply for internal organs and muscles.

The origin of wings and flight

The colonization of totally new habitats represented an important step in the history of evolution. This is the case not only for the colonization of the dry land by plants and animals in the Devonian period, but also for the later conquest of the air by the four groups of animals that developed the ability for active flight: insects, pterosaurs, bats, and birds. Of these groups, insects were the first to acquire organs of flight.

Although researchers are not sure at which point in Earth's history insects developed wings and the ability to fly, a number of fossil winged insects (dragonflies, mayflies, cockroaches, and several extinct groups) are known from the lowermost Upper Carboniferous period (c. 320 mya). The oldest-known winged insect, *Delitzschala bitterfeldensis*, was described from a drilling core from Delitzsch in the vicinity of Bitterfeld in eastern Germany. This fossil is dated from the uppermost Lower Carboniferous and is about 325 million years old. It belongs to the extinct group Paleodictyoptera, which also included other primitive winged insects. The evolution of insect wings with complex wing venation and sophisticated articulation therefore must have taken place by the Lower Carboniferous if not in the Upper Devonian.

Unfortunately, there are only a few fossil insects known from the Devonian, and they all represent primarily wingless insects (e.g., springtails and bristletails). The fossil *Eopterum devonicum* from the Middle Devonian of Russia was long believed to be the most ancient winged insect, but the apparent wings have been shown to represent not an organ for flight but rather only the isolated tail fan of a crustacean.

Scientists have relied on hypothetical reconstructions of this important step in evolution, based on indirect evidence and plausible speculations. This has resulted in numerous different, and often conflicting, hypotheses about the evolution of insect wings and flight. Two alternative theories of wing development dominate the discussion among scientists: the exite theory and the paranotal theory.

The exite theory

Proponents of the exite theory believe that wings evolved as derivatives of lateral appendages (exites) of the bases of the walking legs that are present in one extant group of wingless insects, the bristletails. This theory is largely dependent on disputed fossil evidence and on the fact that the wings of all insects are supplied with oxygen by a branch of the leg trachea. Furthermore, there are functional arguments, because these exites are flexible structures and therefore better pre-adapted to be transformed into mobile appendages such as wings. The first protowings could not yet have served as flight organs but must have had a different function that later changed in the course of evolution. These mobile appendages may have served primarily as gill plates in aquatic larvae just as in extant mayflies. Wing venation systems later evolved as structures supporting the transport of oxygen. Such gill plates are present as paired dorsolateral appendages on the abdomen of fossil and extant mayfly larvae and bear a striking similarity to developing wing buds on the thorax of these insects. Some fossil insect larvae from the Carboniferous and Permian in North America have abdominal gills that are indistinguishable from thoracic wing buds. Wing buds are known to have been mobile in those Paleozoic insect larvae, while they are fused with the thorax in all extant larvae and only become mobile after the final molt to adult.

The presence of a third pair of smaller but mobile winglets on the first thoracic segment has been discovered in early fossil winged insects (paleodictyopterans, dragonflies, and protorthopterans) from the Carboniferous. (All extant winged insects possess only two pairs of wings on the two posterior thoracic segments.) This third pair of winglets is characteristic of all winged insects and has been reduced in modern insects. Their presence could also support the hypothesis that wings were derived from paired mobile appendages that were originally present on more segments than today, and that the thoracic wings represent the equivalents of the abdominal gills of mayfly larvae.

One strong argument against the exite theory exists: if wings and abdominal gills of mayfly larvae are corresponding structures of the same origin, as is strongly suggested by the fossil evidence, then the thoracic exites and abdominal styles that would have been their predecessors must be of the same origin and cannot be derivatives of walking legs because they occur together with legs on the thorax. However, there is morphological and paleontological evidence that the abdominal and thoracic styles of bristletails are different: thoracic exites and bristletails lack muscles, contrary to their abdominal styles; fossil wingless insects still have short segmented legs with paired claws on the abdomen, which strongly indicates that the abdominal styles are reduced legs and therefore of completely different origin from thoracic exites. Since only bristle-

tails possess thoracic exites, these structures do not seem to belong to the common structure of insects. Conversely, they may represent a derived feature of bristletails alone, because they occur nowhere else among insects and myriapods. The alleged presence of thoracic exites in other fossil insect groups is contentious, because it cannot be confirmed by independent studies. Consequently, it is unlikely that the thoracic exites of bristletails represent vestiges of the biramous (forked) leg of crustaceans and trilobites, as was previously believed by many scientists. Altogether, the exite theory is poorly supported and in conflict with much of the other evidence.

The paranotal theory

The paranotal theory is endorsed in most popular books about insects and textbooks of entomology. This theory states that wings originated from lateral stiff and flat expansions (paranota) of the sclerite plate (notum) on the upper side of the thoracic segments. This view is strongly supported by the ontogenetic development of wing buds in modern insect larvae, which are immobile and fused with the thorax up to the final molt. Another argument is the presence of paranotal lobes in silverfish, which are the closest relatives of winged insects among the primarily wingless insect groups. In silverfish these paranotal lobes are supplied with oxygen by a branch of the leg trachea just as for wings of winged insects. A further argument could be that the wing articulation of primitive winged insects (e.g., mayflies and dragonflies) is less sophisticated and does not allow these animals to flex and/or fold their wings flat over the abdomen. In contrast, all remaining winged insects (Neoptera) possess this ability. Most proponents of the paranotal theory believe that the lateral expansions originated as airfoils that improved the ability for long jumps followed by gliding, and that the mobility of these airfoils was a later achievement in evolution. However, the exite hypothesis—that the protowings did not evolve as organs of flight but as larval gill plates—would also be compatible with a paranotal origin of these structures. Therefore, the paranotal theory would not conflict with the interpretation of wings and abdominal gills of mayfly larvae as corresponding structures of the same origin.

No one knows why only insects, alone of all invertebrates, developed the powers of flight. It may be that other invertebrate groups did not have the chance to evolve structures such as wings. Acquisition of flight offered exploitation of an unfilled niche. The ability to fly allowed for the colonization of a new habitat (i.e., air) and movement to new habitats when local environmental conditions became less favorable; acquisition of food; ability to escape predation; and more readily enhanced gene flow between previously remote populations. There could have been a coevolution between spiders and insects, in which the predatorial threat of spiders could have exerted pressure reinforcing the development and refinement of active flight in insects, while the latter forced spiders to evolve more and more sophisticated strategies to catch them (e.g., web building).

The age and end of the giants

About 300 mya, during the Carboniferous period, many parts of the world consisted of vast swamp forests with giant

horsetails and primitive lycopod trees (e.g., *Sigillaria* and *Lepidodendron* that reached heights of up to 131 ft [40 m]). Since all of these plants had long stems with no leaves or only small crowns on top, these Carboniferous swamp forests allowed for understory insolation. Fossil remains of these forests show that the swamps were inhabited by primitive amphibians and various arthropods, such as arachnids, myriapods, and many insects such as the extinct paleodictyopterans as well as ancestors of mayflies, dragonflies, cockroaches, and orthopterans. Many of the winged insects attained giant size. Even though the average wingspan of Carboniferous species of paleodictyopterans, mayflies, and dragonflies was only 3.9–7.9 in (10–20 cm), the biggest paleodictyopterans and mayflies (e.g., *Bojophlebia prokopi*) reached maximum wingspans of 15.7–19.7 in (40–50 cm). The biggest Carboniferous dragonflies of the extinct family Meganeuridae reached a maximum wingspan of 25.6 in (65 cm). By the onset of the Permian period, a few giant species of the North American dragonfly genus *Meganeuropsis* had a wingspan of more than 29.5 in (75 cm) and thus represented the biggest insect ever known.

The largest extant insects include the longhorn beetle, *Titanus gigantea*, from the Amazon rainforest with a body length of up to 6.5 in (16.5 cm); the African goliath beetle, *Goliatus goliatus*, which is the heaviest extant insect with a weight of up to 2.5 oz (70 g) and a wingspan of up to 9.8 in (25 cm); the South American owlet moth, *Thysania agrippina*, with a wingspan of more than 11.8 in (30 cm); or the stick insect *Phobaeticus kirbyi* from Southeast Asia, which is the longest extant insect with a maximum length of 13.0 in (33 cm). The biggest dragonflies living today have a wingspan of only 6.7–7.9 in (17–20 cm) and thus are significantly smaller than their giant fossil relatives of the Carboniferous and Permian.

The loss of gigantism in insects has been attributed to changes in the composition of the atmosphere (e.g., increased oxygen levels) or climate, but none of these hypotheses are really convincing. Another more plausible hypothesis is that lack of aerial vertebrate predators allowed these insects to evolve to maximum sizes during the Carboniferous and Permian periods. These insects could therefore reach the maximum size that was physically allowed by their general body plan. Respiration with tracheae, by diffusion and weakly effective active ventilation, and constructional constraints of the exoskeleton and the muscle apparatus were the major factors that posed an upper limit of growth, so that insects could not evolve to have a wingspan of more than 3.3 ft (1 m). There may have been a competitive evolutionary race for the increase in body size between plant-feeding paleodictyopterans with sucking mouthparts and their predators, dragonflies. No comparatively large ground-dwelling insects are known from fossils, perhaps because predators such as large amphibians, early reptiles, and large arachnids prohibited such a dramatic size increase.

Early pterosaurs such as *Eudimorphodon* from the Upper Triassic of Italy are the oldest known flying vertebrates that have a typical insect-feeding dentition. Because these early pterosaurs had the same perfectly developed wing apparatus as successive pterosaurs, the group probably evolved significantly earlier in Earth's history, possibly in the early Trias-

sic. It is tempting to assume that the extinction and permanent disappearance of giant flying insects right after the Permian is directly correlated with the predatorial threat by the first pterosaurs in the early Triassic. The high air drag of the large wings and the limited power of the flight muscles compared to the size of the wings did not allow these insects a fast and swift flight, as some modern insects are capable of. These clumsy giants could not escape the new aerial predators that were faster, swifter, stronger, and more intelligent and were thus doomed to extinction. Even before the extinction of pterosaurs, birds started their successful history to become the pterosaurs' successors as rulers of the air, and in the Tertiary the evolution of bats made even the night a dangerous time for flying insects, so that after the Triassic there was no chance for insects to evolve giant flying forms ever again.

The coevolution of insects and flowers

The relationship between flowering plants and pollinating insects was first described only 200 years ago by the German teacher and theologian Christian Konrad Sprengel. Sprengel presented his discoveries in his 1793 book *Das Entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen* (The unraveled secret of nature about the construction and pollination of flowers). A long history of evolution was necessary to create and advance such wonderful symbioses between the myriad types of flowers and their pollinators. The most primitive plants such as mosses, clubmosses, horsetails, and ferns still possess flagellate male germ cells that need rainwater for them to reach the female gametes for pollination. The famous maidenhair tree *Ginkgo biloba*, which is considered a living fossil, has retained this type of water-bound pollination. Within the gymnosperms, which include conifers, pollination by wind evolved. In the Gnetales, the closest relatives of flowering plants, pollination is achieved by the wind as well but is also accomplished with the help of various insects such as beetles and flies. Angiosperms, the genuine flowering plants, are predominantly pollinated by insects. However some tropical flowering plants are specialized for pollination by birds (e.g., humming birds), bats, or other mammals (e.g., monkeys, marsupials), but this must be a relatively recent and secondary phenomenon because these vertebrate pollinators appeared much later in evolution than flowering plants. Only angiosperms

have developed sophisticated adaptations of their inflorescences, such as particular attractive color patterns and scents, nectar glands, and highly complex types of blossoms that are often only accessible for a single species of insect that is specialized and dependent on them.

The first pollinators may have been beetles that fed on pollen and secondarily acted as pollinators when they visited succeeding conspecific flowers while having some pollen attached to their body. Pollination by beetles is still common among primitive flowering plants such as water lilies (and cycads, one of the few nonflowering plants that are still pollinated by insects). Pollination in these plants is probably costly to the plant because the pollen contains numerous nutrients and substances that are energetically expensive to produce. This may be one reason why plants later evolved better strategies to attract and satisfy their pollinators, for example by offering bees and butterflies relatively cheap sources of food such as watery sugar solutions produced by special nectar glands.

The oldest fossil flowering plants are known from deposits from the Lower Cretaceous (130 mya). Alleged fossil angiosperms from the Lower Jurassic of China are also of Lower Cretaceous age. Most modern insect orders and many suborders are also known from the Lower Cretaceous fossil record. For example, the Crato limestones from the Lower Cretaceous of northeastern Brazil have not only yielded various early flowering plants but also early putative pollinators such as bees, certain flies, and moths, but no diurnal butterflies. Butterflies appeared much later in Earth's history in the Moler-Fur formation from Denmark and in Baltic amber, both of Lower Tertiary age (40–50 mya).

The enormous diversity of flowering plants and insects is a result of coevolution between these two groups. The specialization among various groups of pollinators on certain flowers has allowed multiple species in the same habitat. Most modern insect subgroups (e.g., bees, moths, flies, beetles) were present after the coevolution of plants and their pollinators. The diverse insect fauna of various Tertiary amber localities (e.g., Baltic and Dominican amber) is therefore not greatly different from the modern one, except for changes in the distribution of some groups due to climatic changes in the Tertiary.

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